SENSITIVITY OF NESTING GREAT EGRETS (*ARDEA ALBA*) AND WHITE IBISES (*EUDOCIMUS ALBUS*) TO REDUCED PREY AVAILABILITY

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ABSTRACT.—Life-history theory suggests that long-lived bird species will adjust their nesting effort according to current conditions to balance the costs and benefits of current reproduction with their long-term needs for survival and future reproduction. However, responses to the same habitat conditions may differ between species, even within the same ecosystem, to produce different nesting and population patterns. We examined differences in the nesting ecology of two sympatric wading species, Great Egret (*Ardea alba*) and White Ibis (*Eudocimus albus*), between years with high (2006) and below-average (2007) prey availability in the Florida Everglades. Clutch size of White Ibises decreased by ~19% from 2006 to 2007, whereas Great Egret clutch size remained constant. Model selection identified rain, water depth, Julian date, year, and prey biomass as parameters that most influenced daily survival rates (DSR) of White Ibis nests, whereas nest stage, region, Julian date, water depth, and the quadratic form of water recession rate most influenced Great Egret nest DSR. Daily survival for both Great Egret and Whites Ibis nests was higher in 2006 (DSR = 0.992 and 0.999, respectively) than in 2007 (DSR = 0.981 and 0.979). Our results support the hypothesis that prey availability and hydrological factors play crucial roles in regulating populations of wading birds in the Florida Everglades. Results also demonstrated that White Ibis reproduction was more sensitive to changes in hydrological conditions and prey availability than Great Egret reproduction. *Received 21 August 2009, accepted 23 January 2010.*

Key words: *Ardea alba*, clutch size, *Eudocimus albus*, Florida Everglades, Great Egret, nesting ecology, nest survival, White Ibis.

Sensibilidad de Individuos de *Ardea alba* y *Eudocimus albus* que se Encuentran Anidando a Reducciones en la Disponibilidad de Presas

RESUMEN.—La teoría sobre historias de vida sugiere que las especies de aves longevas ajustarán su esfuerzo de anidación de acuerdo a las condiciones actuales para balancear los costos y beneficios de la reproducción actual con sus necesidades de largo plazo en relación con la supervivencia y la reproducción futura. Sin embargo, las respuestas a las mismas condiciones del hábitat pueden diferir entre especies, aún en el mismo ecosistema, para producir diferentes patrones de anidación y poblacionales. Examinamos las diferencias en la ecología de anidación de dos especies simpátricas de aves vadeadoras (*Ardea alba* y *Eudocimus albus*) entre años con disponibilidad de presas alta (2006) e inferior al promedio (2007) en los Everglades de Florida. El tamaño de la nidada de *E. albus* disminuyó en cerca del 19% entre 2006 y 2007, mientras que el de *A. alba* se mantuvo constante. La selección de modelos identificó a la lluvia, la profundidad del agua, la fecha juliana, el año y la biomasa de presas como los parámetros que más influenciaron las tasas de supervivencia diaria (TSD) de los nidos de *E. albus*, mientras que el estadío del nido, la región, la fecha juliana, la profundidad del agua y la forma cuadrática de la tasa de recesión del agua fueron los factores que más influenciaron las TSD de los nidos de *A. alba.* La supervivencia diaria de los nidos de *A. alba* y de *E. albus* fue mayor en 2006 (TSD = 0.992 y 0.999, respectivamente) que en 2007 (TSD = 0.981 y 0.979). Nuestros resultados apoyan la hipótesis de que la disponibilidad de presas y factores hidrológicos desempeñan papeles cruciales regulando las poblaciones de aves vadeadoras en los Everglades de Florida. Los resultados también demostraron que la reproducción de *E. albus* fue más sensible a los cambios en condiciones hidrológicas y en la disponibilidad de presas que la de *A. alba*.

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Food availability is considered one of the primary limitations to avian populations during the breeding season (Lack 1948, 1954; Ricklefs 1968; Martin 1987). Food may become a limiting factor during the breeding cycle because of increased adult physiological demands for egg production (Drent and Daan 1980, Bolton et al. 1993), incubation (Heaney and Monaghan 1996, Reid et al. 2000), and rearing of young (Erikstad et al. 1998). Many species of birds have evolved specific responses to food limitations, including the ability to regulate behavior and body condition when faced with high energy demands (Blem 1990, Hahn 1998, Wingfield 2004), food scarcity (Stuebe and Ketterson 1982, Wingfield 2004), or food unpredictability (Cuthill et al. 2000, Wingfield 2004). Most species also time their breeding cycle to coincide with maximum food availability (Perrins 1991, Houston 1997, Thomas et al. 2001). Life-history theory predicts that adults should balance investment in their offspring against their own prospects for survival and future reproduction (Williams 1966, Stearns 1976). Because tradeoffs generally occur only when food is limited (Stearns 1992), highly variable environments should favor the selection of an elastic breeding effort (Erikstad et al. 1998).

The proximate effects of food limitation can include smaller clutch sizes, slower nestling growth rates, and decreased daily survival estimates. Within the nest of species whose young hatch asynchronously, passive brood reduction (starvation) may eliminate smaller and later-hatched young when food is limited because the first-hatched and larger young often receive more food from the parents (Mock and Parker 1986, 1997). Alternatively, active aggression and eventual siblicide can occur when older and larger brood mates attack younger and smaller siblings (Mock and Parker 1986, 1997). In response to food limitation, parents may increase foraging rates, select lower-quality but more abundant prey items (Hahn 1998), or travel farther to higher-quality foraging patches (Kacelnik 1984).

Declines in the annual breeding success and populations of colonial-nesting wading birds (Ciconiiformes) in the Florida Everglades system are believed to be linked to food limitation (e.g., reduced prey availability) as a result of historical water-management practices (Kahl 1964, Kushlan 1986, Kushlan and Frohring 1986, Frederick and Collopy 1989, Powell et al. 1989, Frederick and Spalding 1994, Ogden 1994, Gawlik 2002). Tests of the prey-availability hypothesis at foraging sites (Gawlik 2002) showed that vulnerability and density of prey did not result in a similar foraging response or strategy across a suite of wading species. Furthermore, not all species of wading birds in the Everglades have declined (Crozier and Gawlik 2003), which suggests either that species are limited by different environmental factors or that they have responded in a species-specific manner to the same limiting factors. From the 1930s to 2001, White Ibis (*Eudocimus albus*; hereafter "ibis") nest numbers declined by ~87% in the Everglades, whereas numbers of Great Egret (*Ardea alba*; hereafter "egret") nests increased by 270% (Crozier and Gawlik 2003). A key difference between these two species is their individual foraging strategies. Ibises are "searchers" that tend to select high-quality patches that they then abandon relatively quickly once prey availability drops, whereas egrets are "exploiters" that tend to stay at foraging sites even when prey densities are low (Gawlik 2002). Because they use different foraging strategies, we expected ibises and egrets to respond differently to changes in prey availability across the landscape.

Given contrasting temporal trends in the numbers of nesting egrets and ibises (Crozier and Gawlik 2003) and differences in foraging strategies (Gawlik 2002), we expected that the productivity of ibises was constrained by habitat conditions to a greater extent than that of egrets. We therefore hypothesized that during periods when foraging conditions were good (e.g., suitable hydrologic conditions that produce predictable patches of concentrated prey), both species would exhibit high nest success. However, during poor habitat conditions (unfavorable hydrologic conditions that fail to produce predictable patches of concentrated prey), we predicted that ibises would have lower nest success than egrets. To that end, we contrasted clutch size and daily survival rates (DSR) of the two sympatric species between two years that, serendipitously, differed greatly in hydrologic conditions and prey availability. We used this natural experiment to compare reproductive success of an exploiter (egret) and a searcher (ibis) between years with high and low prey availability.

Methods

Study site.—Egret and ibis nests were monitored in 2006 and 2007 in colonies in the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Lox; $n = 8$ colonies) in Palm Beach County, Florida, and in Water Conservation Areas 2A (WCA2A; $n = 2$ colonies) in Broward County and 3A (WCA3A; $n = 5$ colonies) in Broward and Miami-Dade counties (Fig. 1). Nesting colonies of both species were located by using a combination of ground and aerial surveys, by tracking radiotagged adults (Beerens 2008, Herring 2008), and by visiting known colony sites (e.g., South Florida Wading Bird Reports, South Florida Water Management District). We attempted to identify and use colonies in which both species nested, but some colonies contained only one or the other species.

Habitat conditions.—Hydrologic conditions in the 2006 dry season were near optimal for the nesting of wading birds (Gawlik 2002). At the start of the dry season, water levels were above average; they later receded, unobstructed by substantial water-level reversals. In the Everglades, water reversals redistribute concentrated prey and reduce available foraging patches because water levels are increased (Gawlik et al. 2008). The steady, prolonged recession in 2006 fostered relatively high dry-season prey densities (Gawlik et al. 2008) and a high level of nest effort by wading birds. The wet season that followed the prolonged recession of 2006 was delayed and had below-average rainfall. Consequently, this led to a drought during the 2007 dry season. Like that of 2006, the 2007 dry season had few hydrologic reversals and a relatively uninterrupted recession. However, the average water depth was lower, the amount of time that habitat was inundated with water was shorter, and mean prey density and biomass at random sites were low (Gawlik et al. 2008). This led to the characterization of 2006 as a year with favorable habitat conditions and 2007 as a year with poor habitat conditions.

Colonies were selected for the study if they were associated with adults from our radiotracking study (Beerens 2008, Herring 2008). Individual nests were selected from those that were accessible for study, except in 5% of cases, in which they were determined to be from one of our radiotagged adults. All nests within specific colonies were within ~400 m of one another, but depending on the colony configuration, they did not always occur on the same
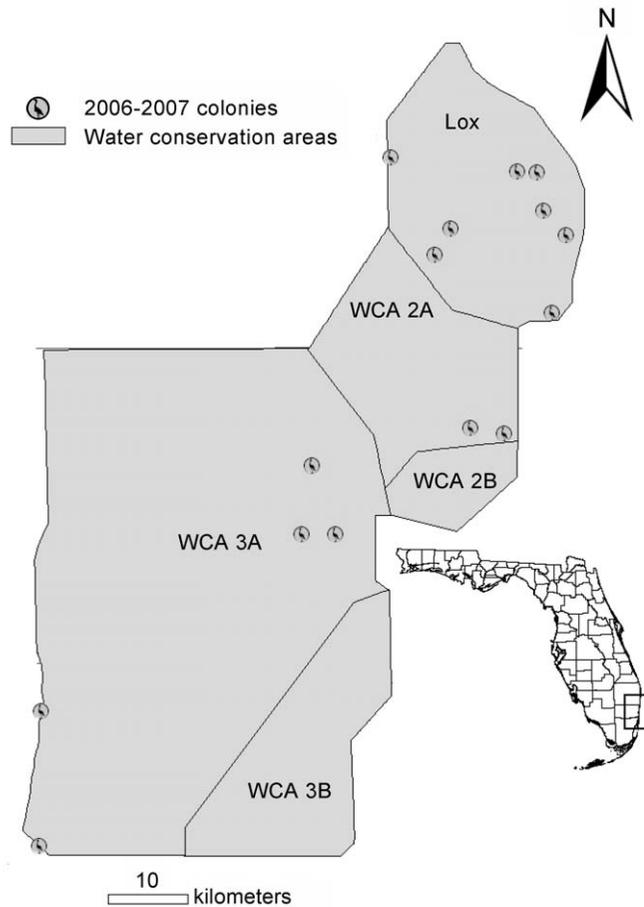
FIG. 1. Wading bird colonies in the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Lox) and Water Conservation Areas 2A (WCA2A) and 3A (WCA3A), Florida, that were included in our study during 2006 and 2007.

nesting island. Nests were individually numbered with flagging tape, and their global-positioning-system coordinates were recorded. We discovered nests at various stages of embryo development, so clutch size was defined as the maximum number of eggs observed for each clutch. All nests were visited approximately every 3–7 days until young fledged or the nests failed. A nest survived between visits if at least 1 egg or young was present, and a nest was successful if at least 1 young survived to 15 days of age.

We used the Everglades Depth Estimation Network (EDEN; Telis 2006) to estimate all water depths and recession rates adjacent to nesting colonies. The EDEN is a network of real-time water-level monitoring, water-surface modeling, and ground-elevation modeling that is used to model water depth for the entire freshwater portion of the Greater Everglades. It calculates stage levels at daily time steps to account for daily changes associated with evapotranspiration, rainfall, and sheet flow. The model estimated water depths, accurate to within 5 cm (Liu et al. 2009), in 400×400 m grid cells across the entire landscape. Negative depth values indicate that the water surface was below average ground elevation. In such cases, standing water will still be present in small areas within the cell.

To estimate recession rates and water depths associated with each nesting colony, we used ARCGIS, version 9.1 (ESRI, Redlands, California), to establish fixed-radius buffers (hereafter "foraging range") around colonies based on mean (+ SE) distances flown by radiotagged egrets and ibises. The latter data came from a contemporaneous companion study on habitat selection by individuals of the two species that nested in the same colonies (Beerens 2008). Beerens (2008) located radiotagged egrets ($n = 144$) and ibises ($n = 220$) during the 2006 and 2007 breeding seasons using a left–right control box and two side-view directional yagi antennas. A random subset of radiotagged egrets and ibises were aerially tracked to foraging sites during the morning on 3–4 days per week (Beerens 2008). Individual birds were located no more than two times per week, with a minimum of 3 days between locations. All sites were verified visually as foraging sites when a radiotagged egret or ibis was located. Mean distances flown were 12.5 ± 0.4 km ($n = 227$) and 7.4 ± 0.5 km ($n = 178$) for ibises and 8.1 ± 0.7 km ($n = 60$) and 4.6 ± 0.3 km ($n = 163$) for egrets during 2006 and 2007, respectively (Beerens 2008). The EDEN grid cells within foraging ranges were identified for specific colonies by year and species. We then used SAS, version 9.1 (SAS Institute, Cary, North Carolina), to extract water depth for each grid cell. For each day that we could estimate DSR, we calculated recession rate as the mean recession rate for the preceding week.

We estimated weekly rainfall for each colony's foraging range using rainfall data collected from gauges within the Everglades by the U.S. National Weather Service. Weather conditions were recorded at 15-min intervals at a scale of 2×2 km by the National Weather Service's Next Generation Radar system. We expected a delay in the response between rainfall and nest failure (Frederick and Collopy 1989). Thus, for each day for which we had an estimate of nest survival, we calculated a corresponding rainfall value as the mean rainfall of the preceding week within the foraging range for each species of a colony. For each colony's foraging range, we used an average ($\pm$ SE) of 7.3 ± 1.5 gauges (range: 3–16) to estimate mean rainfall per week.

Estimates of local prey biomass associated with colonies were obtained from Beerens (2008). The authors located foraging radiotagged egrets and ibises and, within 1 day, sampled those sites to estimate prey biomass using 1-m^2 throw traps (Kushlan 1981). At each foraging site, two replicate throw-trap samples were conducted within the exact area where birds were observed foraging the previous day. We used the mean of those two throw-trap samples in subsequent analysis. Throw traps provide an accurate means to assess both fish and crayfish (*Procambarus* spp.) densities (Kushlan 1981, Petrik and Levin 2000, Dorn et al. 2005). Foraging-site locations were mapped in ARCGIS, version 9.1, and prey biomass estimates from sites within the foraging range of each species around nesting colonies were used to index local prey biomass for each colony. Prey biomass estimates were used only if they were collected within a foraging range within 7 days of an estimate of nest survival at a colony. We averaged all estimates of prey biomass during the 7-day period to provide a mean estimate of landscape-level prey biomass for each weekly time step. For each colony, we used an average ($\pm$ SE) of 3.1 ± 0.1 prey biomass samples (range: 2–10) for each estimate of mean biomass per week.

Statistical analyses: Clutch size.—We used an information-theoretic approach and PROC MIXED in SAS to specify the

maximum-likelihood variance estimator (Littell et al. 1996) and determine which parameters most influenced clutch size for each species (Akaike 1974, Burnham and Anderson 2002). We built and ranked competing models (Burnham and Anderson 2002) for combinations of the main effects (year and region) and their interaction. We included the parameter for region because the Everglades are divided into distinct hydrological units with different management regimes. We did not explore relationships between clutch size and hydrologic or prey conditions because we lacked sufficient data from the time before clutch initiation.

We used Akaike's information criterion adjusted for small samples sizes (AIC_c) in all models (Burnham and Anderson 2002). We calculated delta AIC (Δ_i) and AIC weights (w_i) from AIC_c values. Models with the lowest AIC_c value were considered to be the best explanatory models, although additional competing models with $\Delta AIC_c < 2$ were considered equally plausible, given the data (Burnham and Anderson 2002). Models with $\Delta AIC_c > 4$ were considered to have little to no support (Burnham and Anderson 2002).

Statistical analyses: Nest success.—We used a logistic-exposure approach in a mixed-model setting to model nest survival (Shaffer 2004). The model is based on a binomial distribution of nest fate (0 = failed, 1 = successful) and uses a logit link function to estimate DSR and identify parameters that influence DSR (Shaffer 2004). We used the modified logit link function ($g(\theta) = \log_e(\theta^{1/t}/[(1 - \theta^{1/t}])$, where θ = nest interval survival rate and t is the interval length) to account for differences in duration of time between nest visits (Shaffer 2004). A benefit of using the logistic-exposure approach for simple models is that the appropriateness of those models can be evaluated by comparing them with more complex models via information-theoretic techniques (Shaffer 2004, Rotella 2007). Logistic-exposure models also do not require assumptions about when nest losses occur, and they allow for categorical parameters and random and fixed effects (Shaffer 2004, Rotella 2007).

We used PROC GENMOD to build and rank competing models (Burnham and Anderson 2002). Competing models were developed on the basis of a biologically meaningful understanding of the nesting responses of wading birds in previous studies (see Frederick and Collopy 1989). We included year as a parameter in the model because habitat conditions (e.g., hydrology and prey availability) differed greatly during the study. Nest stage (egg or young) was included because nest failure rates often differ between incubation and nestling periods. We included a parameter for mean prey biomass (biomass) during the week before a DSR estimate because food abundance is considered one of the most important determinants of nesting effort (Lack 1954, Ricklefs 1968) and may be linked to the size of wading-bird populations in the Everglades (Kahl 1964, Kushlan 1977, Gawlik 2002). Julian date was included because date has been shown to be an important determinant of the likelihood of nest success (Frederick and Collopy 1989). The Everglades are divided into distinct hydrological units (regions) with different management regimes that may influence DSR. Recession rate (recess) and the quadratic form of recession rate (recess + recess^2) during the week before an estimate of DSR were included in the model because they have been linked to nesting in colonial-nesting wading birds in the Everglades (Frederick and Collopy 1989) and to the distribution of foraging wading birds

(Bancroft et al. 2002, Russell et al. 2002, Beerens 2008). Rainfall (rain) and water depth (depth) measured during the week before an estimate of DSR were included because rainfall has been observed to play an important role in the failure of wading birds' nests (Frederick and Collopy 1989) and because water depth can limit foraging (Kushlan 1976, Gawlik 2002). Lastly, we included all possible interactions among main effects, and our global model included all main effects and two-way interactions. We evaluated the goodness-of-fit of the global models and verified that the models fit the data before proceeding with additional model analyses. Prior to model selection, we visually examined the residuals of model parameters to identify outliers or other patterns that might require transformation; none were required. We used PROC CORR in SAS to evaluate correlations between all parameters included in modeling efforts; we found no signs of correlations between model parameters (all $r \leq 0.25$).

We ran separate models for each species because of their different foraging strategies (Gawlik 2002) and because differences in pattern of nest success (e.g., Frederick and Collopy 1989) suggest that different variables may contribute to variation in DSR. All model building and analysis followed the procedures described for clutch size. We calculated the unconditional estimates for coefficients and unconditional standard error terms for each parameter across all models (Burnham and Anderson 2002) on the basis of all models with AIC_c weights ≥ 0.001.

Daily survival rates of nests were calculated on the basis of model-averaged coefficients from our best-fitting model using the equation $S(x) = e^{\beta_0 + \beta_1 x}/1 + e^{\beta_0 + \beta_1 x}$. Model-averaged coefficients were calculated by using only the exponentiated AIC_c values from models that contained the parameter. The exponentiated values were then summed and the original exponentiated AIC_c value was divided by the new sum to get new Akaike weights. Lastly, we multiplied the raw (individual model) parameters by the new weights and summed the products. The DSRs were raised to a species-specific power to allow for comparisons of nest success. Given the large differences in the time that egret and ibis young spend at nests before fledging, we used a conservative fledging age of 15 days. Fledging age was added to the 21- and 25-day incubation periods for ibises and egrets, respectively (Kushlan and Bildstein 1992, McCrimmon et al. 2001), giving a total nesting period of 36 and 40 days, respectively. Although our "fledging age" is not the age at which young disassociate themselves from their nest or become independent of their parents, it is typically the maximum age that young can be reliably associated with a nest (Frederick and Collopy 1989). In addition, most offspring mortality occurs within the first 2 weeks of hatching (Rubolini and Fasola 2008). This fledging age is also similar to those used in other studies of colonial-nesting wading birds (e.g., Frederick and Collopy 1989).

Results

We marked and recorded clutch size for 491 nests (ibis: $n = 73$ in 2006, $n = 263$ in 2007; egret: $n = 57$ in 2006, $n = 98$ in 2007). Eighteen nests could not be relocated, and it was uncertain whether they failed or were simply overlooked; thus, we determined nest success for 473 nests. Mean prey biomass at foraging sites within the foraging range of colonies was generally higher for both species during 2006 (Table 1). Rainfall within the foraging range of

Table 1. Habitat conditions within the mean (+ SE) foraging range of Great Egret and White Ibis breeding colonies in the Arthur R. Marshal Loxahatchee National Wildlife Refuge (Lox) and Water Conservation Areas 2A (WCA2A) and 3A (WCA3A), Florida, during 2006 and 2007. No White Ibis colonies were surveyed in WCA2A.

	Biomass (g m^{-2})			Recession (cm day^{-1})		
	Lox	WCA2A	WCA3A	Lox	WCA2A	WCA3A
Great Egret						
2006	22.42 ± 1.20	43.65 ± 1.25	7.01 ± 2.18	0.15 ± 0.03	0.31 ± 0.20	0.08 ± 0.25
n	16	28	16	162	5	20
2007	7.04 ± 0.31	10.64 ± 0.88	6.60 ± 0.34	0.34 ± 0.07	−0.12 ± 0.14	0.56 ± 0.06
n	32	8	12	241	18	90
White Ibis						
2006	15.2 ± 0.80		13.98 ± 1.0	0.60 ± 0.06		−0.41 ± 0.24
n	49		12	208		38
2007	5.57 ± 0.14		5.85 ± 0.35	1.63 ± 0.05		0.25 ± 0.12
n	46		14	672		78
	Depth (cm)			Rain (cm day^{-1})		
	Lox	WCA2A	WCA3A	Lox	WCA2A	WCA3A
Great Egret						
2006	10.80 ± 0.50	8.85 ± 2.34	−4.84 ± 1.81	0.13 ± 0.02	0.26 ± 0.05	0.10 ± 0.02
n	162	5	20	162	5	20
2007	−9.52 ± 1.11	−7.70 ± 1.30	13.11 ± 1.0	0.11 ± 0.01	0.20 ± 0.03	0.07 ± 0.01
n	241	18	90	241	18	90
White Ibis						
2006	7.43 ± 0.31	—	4.52 ± 1.21	0.1 ± 0.01	—	0.13 ± 0.02
n	208	—	38	208	—	38
2007	2.93 ± 0.40	—	8.07 ± 0.92	0.13 ± 0.01	—	0.15 ± 0.02
n	672	—	78	672	—	78

colonies of egrets and ibises were generally similar between years, whereas water depths tended to be shallower and recession rates were higher during 2007 (Table 1).

Clutch size.—Three of the models adequately described egret clutch size. The first model included only the intercept (i.e., a null model), the second included only year, and the third included year and region (Table 2). The similarity in ΔAIC_c values between the intercept-only and intercept-plus-year models suggested that year added little or no unique information regarding clutch-size variation. The weight of the evidence suggested that the intercept and year models were 2.6× and 2.1× more plausible, respectively, than the year and region model (Table 2). Egret clutch size was similar between years (2006 and 2007 means = 2.7 ± 0.1 and 2.6 ± 0.06, respectively; results are presented as means ± SE). Ibis clutch size was best described by two models with identical AIC_c values; model 1 included year, region, and year * region, and model 2 included the year * region interaction (Table 2). A third model that included the parameters year and region was also plausible with a ΔAIC_c value below 2; however, the weight of the evidence for the first two models was 2.2× greater (Table 2). Ibis clutch size decreased by 19% overall from 2006 to 2007 (means = 2.5 ± 0.07 and 2.2 ± 0.04, respectively). The largest decrease in clutch size occurred in WCA3A, and the smallest decrease occurred in Lox from 2006 to 2007 (WCA3A means = 2.75 ± 0.05 and 1.93 ± 0.06, respectively; Lox means = 2.6 ± 0.06 and 2.35 ± 0.03, respectively).

Table 2. Mixed model analysis for Great Egret and White Ibis clutch size with corresponding number of parameters (K) and Akaike's information criterion (adjusted for small sample sizes; AIC_c) scores and weights (w_i). Nests were monitored in Water Conservation Areas 2A and 3A and the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Florida, during 2006 and 2007. Model parameters included year and region. Models presented include only those that were within 4 AIC_c values of the top model ($\Delta AIC_c = 0$), the global model, and the null (intercept) models.

Model	K	AIC_c	ΔAIC_c	w_i
Great Egret clutch size				
Null	1	234.600	0	0.360
Year	3	235.000	0.4	0.295
Year, region	5	236.500	1.9	0.139
Region	4	237.000	2.4	0.108
Global model: Year, region, year * region	6	238.600	4	0.049
Year * region	3	238.600	4	0.049
White Ibis clutch size				
Global model: Year, region, year * region	5	493.200	0	0.408
Year * region	3	493.200	0	0.408
Year, region	4	494.800	1.6	0.183
Null	1	532.600	39.4	0.000

Table 3. Logistic exposure models for nest success of Great Egrets and White Ibises in the Florida Everglades during 2006 and 2007, with corresponding number of parameters (K) and Akaike's information criterion (adjusted for small sample sizes; AIC_c) scores and weights (w_i). Nests were monitored in Water Conservation Areas 2A and 3A and the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Florida, between 22 March and 6 July in 2006 and 2007. Model parameters included Julian date, mean biomass 1 week before survival estimate (biomass), mean water level recessions rate 1 week before survival estimate (recess), the quadratic function of water recession rates 1 week before survival estimate (recess + recess²), and rainfall during the 1 week before survival estimate (rain). Models presented include only those that were within 4 AIC_c values of the top model ($\Delta AIC_c = 0$), the global model, and the null (intercept) models, and are ranked by Δ_i values.

Model	K	AIC_c	ΔAIC_c	w_i
Great Egret daily nest survival				
Year, stage, region, Julian, depth, biomass, recess + recess²	9	358.054	0.000	0.201
Stage, region, Julian, rain, depth, biomass, recess + recess²	9	358.230	0.177	0.184
Stage, region, rain	5	358.317	0.263	0.176
Year, stage, region, Julian, rain, depth, biomass, recess + recess²	10	358.554	0.500	0.157
Year, stage, region, Julian, rain, depth, recess + recess²	8	358.837	0.784	0.136
Stage, region, Julian	5	360.792	2.739	0.051
Global	33	412.512	54.459	0.000
Null	1	591.728	233.675	0.000
White Ibis daily nest survival				
Year, region, Julian, rain, depth	7	906.219	0.000	0.327
Year, region, Julian, rain, depth, biomass	8	907.402	1.183	0.181
Year, stage, Julian, rain, depth	6	908.099	1.881	0.128
Year, stage, Julian, rain, depth, biomass	7	909.295	3.076	0.070
Year, region, Julian, rain, depth, biomass, recess + recess²	9	909.309	3.091	0.070
Year, stage, region, Julian, rain, depth	8	909.388	3.169	0.067
Global	33	926.586	20.367	0.000
Null	1	958.881	52.662	0.000

Egret daily nest survival.—We monitored 140 egret nests (2006: Lox, $n = 29$; WCA2A, $n = 5$; WCA3A, $n = 11$; 2007: Lox, $n = 58$; WCA2A, $n = 9$; WCA3A, $n = 28$) for a total of 536 nest intervals (AIC_c sample size = 1,397; Rotella et al. 2004); 79 were successful and 61 failed. The model selection process identified five competitive models ($\Delta_i = 0–2$) and one additional plausible model ($\Delta_i = 2–4$; Table 3). All competitive and plausible models included combinations of year, nest stage, region, Julian date, rain, depth, biomass, and the quadratic form of recession rate. The parameter-importance weights were highest and equal for nest stage and region; moderate for Julian date, water depth, and recession rate; and lowest for year and biomass (Table 4). The odds-ratio confidence interval (CI) for rain included 1.0, which suggests a weak effect (Table 4). Daily survival of egret nests was higher in 2006 (0.992 ± 0.002) than in 2007 (0.981 ± 0.002). When DSRs were raised to a constant exposure (e.g., fledging age), nest success was 0.738 (95% CI: 0.653–0.831) and 0.473 (95% CI: 0.435–0.512) during 2006 and 2007, respectively.

The DSR of egret nests increased by 7% from the egg to young stage, 3% with each Julian day, and 5% with every increase in prey biomass of 1 g m⁻² (Table 4). Great Egret nest survival was 10% higher in Lox than in WCA3A (Table 4). The DSR decreased by 4% with every 1-cm increase in water depth over the depth range −45.0 to 28.0 cm. Because the relationship between DSR and recession rate was not linear, we could not directly interpret the odds ratio. A plot of the predicted DSR as a function of recession rate showed that DSR was highest when recession rate was around 0.5 cm day⁻¹

(Fig. 2). The DSR decreased at lower and higher recession rates, especially when recession rate was positive, which meant that water level was increasing. Confidence intervals around the odds ratios for region comparisons between Lox and WCA2A and between WCA3A and WCA2A, and for rain, all included 1.0, which indicates little evidence of an effect (Table 4). Numbers of egret young fledged per nest decreased by 22% between 2006 and 2007, from 2.18 (95% CI: 2.00–2.35) to 1.69 (95% CI: 1.55–1.83).

Ibis daily nest survival.—We monitored 333 ibis nests (2006: Lox, $n = 72$; WCA3A, $n = 19$; 2007: Lox, $n = 208$; WCA3A, $n = 34$) for a total of 996 nest intervals (AIC_c sample size = 4,187); 136 nests were successful and 97 nests failed. The model selection process for nest survival identified three equally competitive ($\Delta_i = 0–2$) and three plausible models ($\Delta_i = 2–4$; Table 3). Nearly all the competitive and plausible models contained the parameters year, region, Julian date, rain, water depth, and biomass (Table 3). The parameter-importance weights were highest and near equal for Julian date, rain, water depth, and year; moderate for region and biomass; and low for nest stage (Table 3). The quadratic form of recession rate was observed in one of the plausible models (Table 3), but it was not included in the competitive models. The DSR of ibis nests was higher in 2006 (0.999 ± 0.003) than in 2007 (0.979 ± 0.003), and this translated into a nest success of 0.933 (95% CI: 0.838–1.0) and 0.479 (95% CI: 0.414–0.555) during 2006 and 2007, respectively.

The DSR of ibis nests increased by 12% from egg to young stage, was 49% higher in Lox than in WCA3A, and increased by 4% with every increase in prey biomass of 1 g m⁻² (Table 4). The

Table 4. Summary of parameter-importance weights and odds ratios for parameters in competitive models explaining variation in nest success for Great Egrets and White Ibises nesting in Water Conservation Areas 2A and 3A and the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Florida, between 22 March and 6 July in 2006 and 2007. Values calculated as the summed weights of all models that include the parameter.

Parameter	Parameter importance weight	Odds ratio[a]	95% CI
Great Egret			
Year	0.51	0.700	0.52–0.82
Stage	0.92	1.070	1.01–1.13
Region (Lox vs. WCA2A)	0.92	1.230	0.66–1.80
Region (Lox vs. WCA3A)	0.90	1.100	1.02–1.18
Region (WCA3A vs. WCA2A)	0.91	1.130	0.63–1.63
Julian day	0.75	1.030	1.01–1.05
Rain	0.64	0.660	0.03–1.50
Depth	0.68	0.960	0.94–0.99
Biomass	0.55	1.050	1.01–1.09
Recess + recess[b]	0.68	0.860	0.76–0.96
White Ibis			
Year	0.9	0.650	0.32–0.98
Stage	0.33	1.120	1.01–1.23
Region (Lox vs. WCA3A)	0.67	1.490	1.01–1.97
Julian day	0.9	0.980	0.78–0.99
Rain	0.91	0.720	0.62–0.83
Depth	0.91	0.920	0.85–0.99
Biomass	0.37	1.04	1.01–1.07

[a]Odds ratios >1 indicate a positive relationship; those <1 indicate a negative relationship.
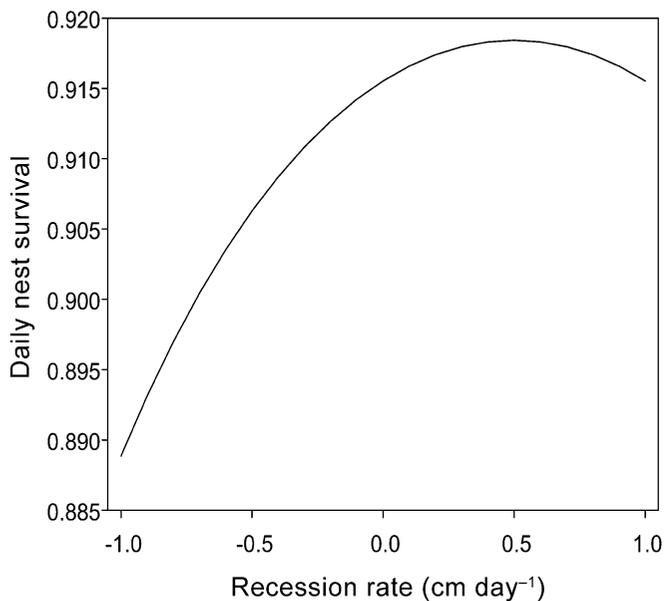[b]Confidence intervals that do not include 1 indicate evidence of effects.

Fig. 2. Variation in daily survival probability of Great Egrets in relation to recession rate within the foraging flight range of nesting colonies during the 2006–2007 breeding seasons in the Arthur R. Marshall Loxahatchee National Wildlife Refuge and Water Conservation Areas 2A and 3A, Florida. Positive values indicate decreasing water levels.

DSR decreased by 2% with each Julian day during the breeding season, by 28% with each 1 cm of rain, and by 8% with each 1-cm increase in water depth over the range −31.36 to 18.58 cm (Table 4). Numbers of ibis young fledged per nest decreased by 32% between 2006 and 2007, from 1.89 (95% CI: 1.72–2.06) to 1.28 (95% CI: 1.17–1.39).

Discussion

Several aspects of the nesting ecology of the ibises and egrets were related to landscape variables that affected the predictability of prey availability (e.g., deeper water was associated with decreased nest survival). However, ibises responded more acutely than egrets, which was consistent with our hypothesis that ibises would experience poorer nest success during years with poor habitat conditions. For instance, ibis clutch size decreased by 19% during the year of poor prey availability (2007), whereas egret clutch size remained constant. Both species had elevated estimates of daily survival during the year with favorable habitat conditions (2006), but egret nest success decreased by ~30% in the year with poor habitat conditions, compared with ~45% for ibises. Furthermore, ibises fledged 24% fewer young than egrets during the year with poor habitat conditions.

We also found support for different nest-survival responses by ibises and egrets to habitat and environmental parameters (e.g., hydrology, prey biomass, rainfall). Egret daily nest survival

increased 1% more than ibis nest success with relatively small (+1 g m⁻²) changes in landscape prey biomass during the week before a nest-survival estimate. This difference, when scaled up to an estimate of nest success over the entire nesting period, could account for a difference of ≤20% between the two species, which suggests that ibises may be more food-limited than egrets. Giving-up densities at foraging sites suggest that foraging costs increase less for egrets than for ibises as water depths at foraging sites move farther from an optimal depth (Gawlik 2002). Thus, egrets seem to exploit a wider variety of habitat conditions (e.g., depths; Gawlik 2002, Beerens 2008) than ibises, for the same foraging costs. Indeed, telemetry data show that egrets foraged closer to colonies than ibises despite large differences in weekly water levels in the area (Beerens 2008).

Contrary to previous studies that have found that birds increase their foraging distances during poor years or when resources are depleted (see Kacelnik 1984, Elliot et al. 2009), both egrets and ibises foraged closer to colonies during the year with poor habitat conditions (Beerens 2008). This was contrary to our expectations but not unprecedented in the literature (Strong et al. 1997). We cannot explain this pattern, but we raise the possibility that the foraging distance was affected by the distribution of colonies between the 2 years. Birds were concentrated in a few large colonies in 2006, whereas they were dispersed in more numerous small colonies in 2007. Thus, even if birds foraged at the same sites in both years, the foraging distance would likely be shorter in 2007.

The two species differed in sensitivity to hydrologic conditions. In particular, nest survival of ibises was more negatively affected by reduced water depth than that of egrets. The same was not true of recession rate, which mostly influenced egret DSR. Neither Kushlan (1986) nor Gawlik and Crozier (2007) detected an effect of recession rate on foraging-site selection for ibises. Recession rate may be especially important for piscivorous egrets, which benefit from increased fish concentrations as water levels fall, whereas ibises often feed on crayfish that are less sensitive to water levels (Frederick and Spalding 1994).

Our study is the first to identify the response function of DSR to recession rate, although numerous studies have suggested that a threshold of recession rate must be exceeded for successful nesting (e.g., Kushlan et al. 1975, Frederick and Collopy 1989, Frederick and Spalding 1994). Effects of low recession rates or negative parameter estimates (i.e., water level increases) on nesting of wading birds are well known (Frederick and Collopy 1989, Frederick and Spalding 1994). Our study confirms previous findings but also adds support to the weaker evidence for negative effects of an exceedingly high recession rate on wading-bird nesting (Bancroft et al. 1994).

An exceedingly high recession rate can reduce prey availability and, ultimately, DSR by either increasing the distance to foraging patches or reducing the quality of individual patches. In the gradually sloping Everglades landscape surface, high-quality foraging patches tend to occur in bands perpendicular to the plane of the landscape's slope. At any point in time, areas above the bands are too dry for foraging and areas below the bands are too deep for foraging. Bands of foraging habitat move down the slope as the dry season progresses. If the bands of foraging habitat move too rapidly across the landscape, they can move beyond an energetically profitable distance from a colony, as was the case when a colony was abandoned in 1989 (Bancroft et al. 1994). A second

hypothesized mechanism by which excessive recession rates can affect wading birds is by moving the band of foraging habitat so quickly that birds are able to capture only a small portion of the concentrated aquatic prey within a patch before it dries. The net result is that the quality of an individual patch is lower than what its prey density would indicate.

Frederick and Collopy (1989) suggested that rainfall events that trigger hydrologic reversals were the most important parameter associated with egret nest failure. Interestingly, egret nests in Frederick and Collopy's (1989) study took more than a week to fail after major rainfall events, whereas ibis nests were typically abandoned very soon (1–2 days) after a major rainfall event. We also found that ibis nests were abandoned soon after heavy rainfall events that increased water depth (G. Herring and M. I. Cook pers. obs.) and likely decreased prey availability (Gawlik et al. 2008). We did not find support for the effect of rainfall on egret DSR in our study, although greater water depths had a moderately negative influence on egret DSR. This result, coupled with the fact that ibis DSR was influenced by both rainfall and water depth, suggests that the two species may respond within different temporal frames to rainfall and subsequent hydrologic reversals that affect water depths and prey availability. Egrets may not respond to rainfall directly because they follow the exploiter foraging strategy. When conditions decline at foraging patches, egrets remain there rather than expend the energy to search for a new and more profitable patch (Gawlik 2002). Their relatively long legs allow them to continue to forage in deeper water (Gawlik 2002, Beerens 2008). By contrast, ibises are short-legged, tactile foragers that use a narrower range of water depths than egrets (Gawlik 2002, Beerens 2008). If rainfall increases water depth so much that it precludes foraging or disperses prey to the point that the profitability of the patch decreases to a bird's giving-up density, ibises move on to search for a new, more profitable patch (Gawlik 2002). Indeed, ibises foraged ~50% farther from colonies than egrets (Beerens 2008).

Tactile-searcher species appear to be less able to withstand changes in hydrologic conditions (e.g., depth) and lower levels of prey availability than exploiter species like egrets. Below-average prebreeding prey availability may be a cue for ibises to lower their clutch size in preparation for increased costs of locating suitable high-quality foraging patches to provision young. Alternatively, ibises may be physiologically constrained during the egg-production stage during below-average prebreeding periods. We hypothesize that it is advantageous for egrets to maintain a rather constant clutch size regardless of annual differences in habitat conditions because their capacity for brood reduction permits them to eliminate young that are destined to die and to produce young even in poor years (Lack 1948, 1954). Furthermore, a constant clutch size allows them to increase their reproductive output during average to above-average years, which we suspect occur less often than historically.

Critical to the nesting responses of egrets and ibises are the distinctly different means of brood reduction. For egrets, brood reduction generally occurs in the nest and is based on size hierarchies when brood sizes average 2–3 young (Mock and Parker 1986, 1997). Egret brood reduction can occur as either obligate or facultative fratricide (Edwards and Collopy 1983). When clutch sizes increase, egret nestlings become more violent and first-hatched nestlings often kill siblings (Mock and Parker 1986, 1997). By

contrast, brood reduction in ibises occurs through scramble competition among siblings (Krebs 2002), often when they are outside the nest at ≥10 days of age (Kushlan and Bildstein 1992). Thus, the relatively inefficient brood-reduction system of the ibis, which spreads food stress more equally among siblings, may have favored the evolution of greater sensitivity to poor foraging conditions and the ability to adaptively reduce clutch size when conditions for raising young are poor.

Our results add to the growing evidence that there is a link between avian reproductive investment and foraging conditions (see Frey-Roos et al. 1995, Erikstad et al. 1998, Elliot et al. 2009, Mainwaring and Hartley 2009). The hypothesis that such a relationship exists among wading birds in the Everglades, and that foraging conditions are driven by hydrologic patterns, is a foundation of the Everglades restoration project (Trexler and Goss 2009). Indeed, there is good empirical evidence that restored hydrologic patterns will increase biomass of fish and crustaceans to the size consumed by wading birds (Trexler and Goss 2009). Moreover, foraging-habitat experiments (Gawlik 2002), modeling (Fleming et al. 1994), and observational studies that rely on an indirect hydrologic index of prey availability (Kushlan 1986, Frederick and Collopy 1989) give us reason to believe that there is indeed a relationship between foraging conditions and wading-bird reproduction. The present study and that of Kahl (1964) provide some of the only direct evidence that prey availability affects wading-bird reproduction in the Everglades.

Searcher species like the ibis are known to be restricted to a narrower range of foraging habitats than exploiters like the egret (Gawlik 2002). Our results demonstrated that reproduction of searcher species is also more sensitive to hydrologic conditions and prey availability than reproduction of exploiter species. The different responses of ibises and egrets to the same level of prey availability during a year with poor habitat conditions is an important finding because it illustrates how ecosystem changes could have led to different population trends among sympatric wading birds (Crozier and Gawlik 2003). A better understanding of the long-term costs and benefits of reproduction between species that use searcher and exploiter foraging strategies may provide further insight toward better management or restoration of wetland ecosystems to meet the needs of all wading-bird species.

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