

Predicting effects of water management on breeding abundance of three wading bird species

David A. Essian¹ | Rajendra Paudel² | Dale E. Gawlik¹

¹Florida Atlantic University, 777 Glades Road, Boca Raton, FL 33431, USA

²The Everglades Foundation, 18001 Old Cutler Road, Palmetto Bay, FL 33157, USA

Correspondence

David A. Essian, Florida Atlantic University, 777 Glades Road, Boca Raton, FL 33431, USA.

Email: dessian2015@fau.edu

Present address

Dale E. Gawlik, Harte Research Institute for Gulf of Mexico Studies, Texas A&M University Corpus Christi, 6300 Ocean Drive, Corpus Christi, TX 78412, USA.

Funding information

Engineer Research and Development Center, Grant/Award Number: Task Order: W912HZ-19-2-0040

Abstract

Wetland conservation often involves creating hydrological regimes that maximize habitat and resources for wildlife. In the greater Everglades ecosystem in Florida, USA, where wading birds are food-limited in some years, models predicting the influence of hydropatterns on foraging habitat availability are used to guide the management of water levels for wading bird nesting populations. These models are useful but do not consider that nesting wading birds are central place foragers, and thus resource availability is a colony-level measure. We examined long-term nest abundance patterns of the great egret (*Ardea alba*), snowy egret (*Egretta thula*), and white ibis (*Eudocimus albus*) to determine effects of hydropatterns on wading bird nest abundance in a 400-km² littoral marsh in Lake Okechobee, Florida. We developed 2 sets of statistical models for each species: 1 examining variation in nest abundance (1977–1992, 2006–2019) and 1 predicting colony-level nest abundance (2006–2019). Models of nest abundance predicted that great egret nesting will peak when March–April lake stage is 4.3–4.5 m, coinciding with the peak in area of available foraging habitat. Neither recession rate nor stage explained total snowy egret or white ibis nest abundance, though snowy egret nest abundance has increased since the 1990s, when the water management schedule favored higher lake stages for longer duration. For all species, colony-level models predicted that nesting increased with increased habitat availability, faster water-level recession rates, and greater number of days dry in the previous 2 years at nest sites. When applied to simulated hydrological data representing changes to water-level



regulations in Lake Okeechobee, our models predicted that management regimes allowing extreme flooding (stage > 5.18 m) in <220 days per 5.0 years and Carolina willow (*Salix caroliniana*) recruitment (stage < 3.9 m) >3.0 years per 5.0 years resulted in the highest nest abundance for snowy egret and white ibis. Snowy egret and white ibis nesting decreased by 575 nests/year and 465 nests/year, respectively, when regulation schedules increased the management envelope by 0.46 m, whereas great egret nest abundance increased modestly (149 nests/year). Operational rules that allow intermediate drought disturbance in dry years and prioritize increased habitat availability at short-hydroperiod colonies in wet years should result in overall benefits to the wading bird community at Lake Okeechobee.

KEYWORDS

Florida, Lake Okeechobee, nest abundance, pulsed wetland, resource availability, wading birds, wetland management

Wetlands are increasingly engineered and managed for flood control, agriculture, storm water treatment, and ecosystem restoration (Zedler and Kercher 2005, Junk et al. 2013). Such practices alter natural flow regimes and disrupt spatiotemporal patterns of resource availability on which wildlife populations depend (Junk et al. 1989, Bayley 1995, Kingsford 2000, Middleton 2002). A core objective of water management in pulsed wetland systems is to maintain hydropatterns that balance human and ecological demands (i.e., environmental flow; Pahl-Wostl et al. 2013). This is often achieved by using water management infrastructure to manipulate surface water levels to restore ecological functions (e.g., prey production) that were degraded when hydropatterns changed. For instance, in the western United States, water managers manipulate water levels in agricultural wetlands to maximize shorebird foraging habitat at important migratory stopover sites (Elphick and Oring 1998, Reynolds et al. 2017, Schaffer-Smith et al. 2018). Similarly, species-specific models of nesting probabilities under different flow regimes have been used to help optimize water management strategies for colonial waterbird conservation in the Macquarie Marshes, Australia (Bino et al. 2014). Developing models that link water flow with wildlife responses is an important first step for optimizing hydropatterns to meet wildlife management goals.

Wildlife in pulsed wetlands are adapted to exploit ephemeral resources made available by flooding-drying regimes (Junk and Wantzen 2007). Spatiotemporal heterogeneity in resource availability is a common feature of large flood plains, and can benefit wildlife by protracting the availability of foraging opportunities (Fleming et al. 1994, Armstrong et al. 2016); furthermore, it can foster coexistence by dampening the negative effects of competition among species with similar prey requirements (Høberg et al. 2002, DeAngelis et al. 2005, Davidson et al. 2012). Because some species may be more sensitive to changes in hydropatterns than others (Swartz et al. 2020), an understanding of species-specific responses to hydropatterns is required for multispecies management. Species-specific models can also help managers determine if it is possible to optimize water levels for all species concurrently or if it is necessary to adopt management regimes that balance tradeoffs over the long term.

Long-legged wading birds (Ciconiiformes and Pelecaniformes) are used as indicators of ecosystem restoration in managed wetlands worldwide, such as Camargue, France (Hafner et al. 1994), Murray-Darling Basin, Australia



(Kingsford 2000), and the Florida Everglades, USA (Ogden et al. 2014). Restoration of wading bird populations is a core goal of the Comprehensive Everglades Restoration Plan, a massive, publicly funded effort to restore the greater Everglades ecosystem (Restoration Coordination and Verification RECOVER 2014). Nest abundance is a useful proxy for overall wading bird productivity in this system and is a key target for restoration (RECOVER 2014). For instance, Gawlik et al. (2020) demonstrated at Lake Okeechobee that overall estimated breeding productivity of great egrets (*Ardea alba*) and small herons was correlated with nest abundance but not nest survival or number of chicks fledged/successful nest. Prey availability, which is influenced by water-level fluctuations, is the primary limitation on nest abundance in the greater Everglades ecosystem (Figure S1, available online in Supporting Information; Kushlan 1986, Frederick and Spalding 1994, Gawlik 2002, Herring et al. 2011). Flooding during the wet season increases wetland surface area, allowing small fish and macroinvertebrates to disperse and exploit newly available resources. This results in higher prey recruitment and biomass of aquatic prey, which is subsequently concentrated into topographic depressions as water levels recede during the dry season (Loftus and Eklund 1994; Trexler et al. 2001, 2005; Ruetz et al. 2005; Botson et al. 2016). Wading birds cannot typically access prey where water depths exceed their leg length (<30 cm), although there are some examples of snowy egrets (*Egretta thula*) foraging in deeper areas by standing on emergent and floating vegetation (Smith 1995). Thus, spatiotemporal patterns of prey availability is thought to follow the drying edge of the wetland, in isolated ponds that are <30 cm deep (Yurek and DeAngelis 2019). Ideally, the drying edge will move across the foraging range of wading bird colonies during the nesting period, creating new foraging opportunities throughout the period of highest energetic demand. If the foraging range completely dries or floods before chicks are fledged, it can result in a lack of foraging opportunities and nest failure. Wading bird responses to hydropatterns may differ greatly among colonies because of differences in topography and vegetation, which mediate the concentrating effect of receding water levels. Another important factor for some species may be the distance to alternate food sources, such as urban or agricultural wetlands and human refuse (Dorn et al. 2011, Evans and Gawlik 2020).

Because large portions of regional nesting populations are concentrated at a few nesting colonies, the influence of hydropatterns on nesting will be most apparent if measured at the colony level. The ability of breeders to track newly available resources is limited by the distance they can travel from the colony before energy losses outweigh gains (Briscoe et al. 2018), or by the maximum amount of time they can spend away from the nest during a given stage of parental care (Thometz et al. 2016). Furthermore, to support nesting, colonies must provide protection from predators and access to suitable foraging habitat. These conditions may be met more frequently at certain colonies depending on their physical characteristics and location within the landscape. For instance, recolonization rates for wood storks (*Mycteria americana*) are highest at manmade spoil islands, which are islands formed out of dredged spoil from canals and shipping channels. Spoil islands are surrounded by deep channels and thus provide greater protection from mammalian predators (Tsai et al. 2016). This may make spoil island nesting populations less sensitive to variation in water management regimes, particularly in systems where other resources, such as prey and foraging habitat, vary independently of nest substrate availability. Colony-level effects of hydropatterns within a managed area may also vary because of heterogeneity in mediating factors such as vegetation, topography, and floodplain connectivity (Zeug et al. 2005, Jin et al. 2019). Knowledge of how hydrological effects vary among colonies can help managers narrow their focus to optimize hydropatterns for colonies that are especially sensitive to degradation in hydro-ecological processes.

A precursor to wading bird recovery under the Comprehensive Everglades Restoration Plan is to maintain hydropatterns that increase prey availability; however, most of the research linking hydropatterns, prey availability, and wading bird breeding aggregations has been in the Everglades. Lake Okeechobee is an important nesting area in the greater Everglades ecosystem, particularly for snowy egrets. For instance, Lake Okeechobee supported 44% of snowy egrets nesting in the greater Everglades ecosystem from 2006 to 2019 despite the littoral zone only composing <2% of the total area of the Water Conservation Areas, Everglades National Park, and lake littoral zone combined. This makes Lake Okeechobee an important refuge for snowy egrets, which have declined in the Water Conservation Areas and Everglades National Park during the same period (Cook and Baranski 2020). Unlike other



parts of the system, Lake Okeechobee is highly eutrophic and has a large ratio of permanently flooded area relative to pulsed marsh area. Efforts to develop water management strategies and plan restoration projects within the Lake Okeechobee watershed are currently underway, yet there are no species-specific models of wading bird responses to hydroperiods at Lake Okeechobee. Analyses that highlight differences in species responses to hydrological variation will be useful for managers because they can provide a better understanding of mechanistic effects of hydrological variation on wading bird communities. For instance, increased habitat availability during the breeding season had greater influence on species with longer nesting periods, such as the great egret, whereas prey densities had a greater influence on small herons, which have shorter nesting periods and should be better able to synchronize nesting with peak prey concentrations (Klassen et al. 2016).

In this study, we used long-term wading bird nest abundance data of nesting great egret, snowy egret, and white ibis (*Eudocimus albus*) at Lake Okeechobee to examine historical and colony-level restrictions on nest abundance. The first objective of this study was to examine the nesting responses of 3 wading bird species to hydroperiods. We predicted that species responses to foraging habitat availability, prey density, or the multiplicative benefit of both would depend on species traits such as nesting phenology and foraging strategies. The second objective was to model the relationship between hydroperiods and nest abundance for each species at the landscape and colony level. We tested the hypothesis that hydrological variables that regulate foraging habitat availability, prey densities, and nest substrate availability would act as constraints on wading bird nest abundance at the landscape level. Furthermore, we predicted that the effects of foraging habitat and nest substrate availability would vary among colonies depending on their physical characteristics. We also predicted that no nesting would occur at colonies where the surrounding marsh was dry (<0 cm), and no nesting should occur where nest substrate was flooded to the bottom of the canopy (roughly >2 m for Carolina willow [*Salix caroliniana*]). We predicted the effect of depth would be more important at marsh colonies because spoil islands are rarely inundated enough to stress nesting trees, and they are permanently surrounded by deep water, preventing nest predation by mammalian predators. Our third objective was to apply the colony-level nest abundance models to simulated hydrological data for 4 proposed changes to the water management schedule at Lake Okeechobee, and to identify the one that maximizes long-term nest abundance for each species while supporting important hydro-ecological processes in the littoral zone.

STUDY AREA

This study took place in the littoral zone of Lake Okeechobee, central Florida (bounding coordinates: -81.121759, -80.611432, 27.207778, 26.682535) from 1977–1992 and 2006–2019. The littoral zone comprises an extensive wetland (~400 km²). Water levels (National Geodetic Vertical Datum of 1929 [NGVD29]) ranged from 2.69 m in July 2007 to 5.57 m in March 1983, which represents the elevation range of wading bird habitat at Lake Okeechobee. Topography slopes from west to east such that the western portion of the littoral zone is composed mainly of short-hydroperiod wet prairies, dominated by torpedo grass (*Panicum* spp.), and the eastern edge of the littoral zone is composed mainly of long-hydroperiod marshes, dominated by floating emergent vegetation, like water lilies (*Nymphaea* spp.) and cattails (*Typha* spp.). Littoral vegetation communities exhibit high interannual variability influenced by flood pulses, fire, and rare freezes (Richardson et al. 1995). The small fish population is numerically dominated by Poeciliidae and Fundulidae, particularly eastern mosquitofish (*Gambusia holbrooki*), sailfin molly (*Poecilia latipinna*), and least killifish (*Heterandria formosa*; Chick and McIvor 1994). Lake Okeechobee is a eutrophic system that supports high secondary production relative to the vast wetlands of the Water Conservation Areas and Everglades National Park (Aumen 1995).

Rainfall, evapotranspiration, and water management determine water surface elevation in the littoral marsh. The wet season typically occurs between June and October, and the dry season occurs between November and May, resulting water accession (increasing lake stage) in June–October, relatively stable water levels in

November–February, and water recession (decreasing lake stage) in March–May. An earthen dike with gated channels surrounds the perimeter, giving managers control over inflow and outflow (Shih 1980). Water regulation schedules are implemented as a water surface envelope (Lake Okeechobee Regulation Schedule; U.S. Army Corps of Engineers 2007), which is essentially the upper and lower bounds for target lake stages (water surface elevation [m NGVD29]) on a given day of the year. When lake stage is outside of the envelope, water managers take actions to bring lake stages back inside. The long-term data set used in this study encompassed 3 different regulation schedules at Lake Okeechobee (Figure 1A, C, and D), each with different priorities for water management. Lake stage decreased and variability in stage (SD) increased with each change in regulation schedule since 1978 (Figure 1A–D). This reflects a shift from a command and control strategy that prioritized water supply during 1978–2000, to one that attempts to prioritize multiple uses by preventing prolonged periods of extremely high water levels and allowing interannual variation that is consistent with rainfall patterns in the region (Vedwan et al. 2008).

METHODS

The South Florida Water Management District (SFWMD) conducted monthly (Feb–Jun), systematic aerial surveys to monitor wading bird nest abundance at Lake Okeechobee from 1977 to 1988, University of Florida conducted the survey from 1989–1992, and Florida Atlantic University began the survey again in 2006. Flight routes from 1977 to 1987 covered the major breeding colonies for wading birds but did not follow systematic transects. Thus, it covered a slightly smaller area than the 1988–1992 and 2006–2019 surveys (Zaffke 1984, Smith and Collopy 1995), and may have missed small breeding colonies outside of the core breeding area. Because the 1977–1987 survey route would have included all colonies with >100 nests of any species during the 2006–2019 survey, we treated data from both surveys the same in our model. Crews conducted flights from 1988 to 1991 weekly (Smith and Collopy 1995), whereas they conducted monthly surveys in all other years. Since 1988, flights have followed east-to-west transects spaced ≤ 3 km apart to cover the entire littoral zone at a speed of approximately 298 km/hour and altitude of 393 m. Two trained observers (not always the same 2) were present on each flight (personnel

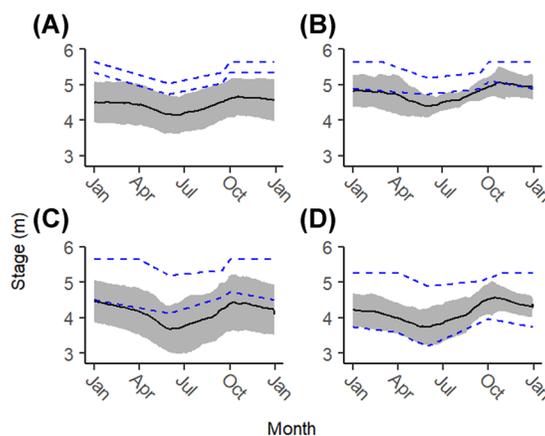


FIGURE 1 Water surface management envelope and lake stage (m) during 4 management periods at Lake Okeechobee, Florida, USA: 1978–1993 (A), 1994–1999 (B), 2000–2007 (C), and 2008–2019 (D). The black line denotes the mean, and the gray bands represent the standard deviation during 4 periods with different regulation schedules. Regulation schedules set the daily upper and lower bound for lake stage (blue dashed lines). When water levels move outside of these bounds, water managers take action to move lake stage back into the desired envelope



changed several times throughout the study period). Once observers detected a colony, the aircraft circled down to an altitude of 120 m to allow each observer to estimate the number of nests. We defined colonies as any assemblage of ≥ 2 nests that were separated by ≤ 200 m (Smith and Collopy 1995).

Crews sampled prey using throw traps (Kushlan 1974, Jordan et al. 1997) at randomly selected sites in the littoral zone. The sampling period lasted from February through June during the 2011–2013 and 2015–2019 nesting seasons. We sampled 968 traps (484 sites) in the littoral zone during the 2011–2013 and 2015–2019 breeding seasons. We sampled 44–80 sites each year and collected samples every 3.32 ± 4.18 (SD) days during each sampling season. Sampling was restricted to sites where water was 0–30 cm deep, roughly the maximum foraging depth for wading birds in this study (Powell 1987). Throw trapping is an unbiased method for sampling prey, in which 1-m² frames with an open top and bottom are thrown into the water to trap small fish (Jordan et al. 1997). We threw 2 traps at each site, separated by a random distance (5–50 m) and bearing. We removed fish from the trap using a mesh seine until there were 5 consecutive passes with no fish. We immediately placed all prey items in 250-mg/L tricainemethane sulfonate (MS-222) to be euthanized. We identified, measured, and weighed (nearest mg wet weight) fish in a lab.

We tested the relationship between nest abundance and prey and habitat availability by fitting linear regressions between species-specific nest abundance and area of available habitat during the breeding season, prey density (fish/m²), and their multiplicative effect (habitat availability \times prey density). Klassen et al. (2016) reported great egret nest abundance in the Everglades proper was correlated with foraging habitat availability but not prey density during the breeding season, and the opposite was true for snowy egret. The authors hypothesized that this was related to nesting phenology because small herons have shorter incubation and fledging periods, allowing them to synchronize peak energetic demand with peak prey availability during the breeding season. Conversely, species with longer nesting periods, like the great egret, should benefit more from increased habitat availability because a greater area of available habitat correlates with a longer duration over which foraging opportunities appear throughout the breeding season. The multiplicative effect of habitat and prey availability may explain supranormal nesting events better than either univariate effect (Cocoves et al. 2021), though this has not yet been tested. We estimated area of available habitat by counting 30.48 m \times 30.48 m cells in the littoral zone, excluding polygons classified as woody vegetation in the SFWMD Lake Okeechobee Littoral Vegetation (2007) map. We counted each cell where the estimated depth was 18–83 cm during the breeding season (Feb–May). This depth range corresponds with the 5–95% quantiles estimated at throw trap sites using the Lake Okeechobee bathymetry digital elevation model. We estimated depth by subtracting ground elevation, based on the digital elevation model, from daily lake stage (average across 4 SFWMD gauges L005, L006, L001, and LZ40). Because prey sampling was only conducted from 2011 to 2019 (excluding 2014), sample size was small ($n = 8$). We performed linear regressions using the `lm()` function in R (R Core Team 2017).

Lake-level models (1977–1992, 2006–2019)

Annual nest abundance was reported from 1977 to 1992, whereas colony-level estimates were reported from 2006 to 2019. We aggregated colony-level counts to produce monthly estimates of nest abundance for each species. We estimated annual nest abundance as the maximum monthly nest abundance reported in each year. This prevents double counting that can arise when birds abandon colonies and reneest elsewhere in the system. Because this is a conservative method for estimating nest abundance and there is a tendency for observers to undercount nests on aerial surveys (Frederick et al. 2003), our estimates are likely low.

We identified the important hydrologic variables affecting species-specific nest abundance by fitting generalized linear models in which annual (1977–1992, 2006–2019), lake-level nest abundance was the response and hydrological parameters were predictors. We fit models with a negative binomial distribution to account for overdispersion in annual nest counts. We included lake stage, recession rate, and Carolina willow (*Salix caroliniana*)



availability index as fixed effects that represent foraging habitat availability, prey availability, and nest substrate availability, respectively (Havens and Gawlik 2005, Chastant et al. 2017, Chastant and Gawlik 2018, Gawlik et al. 2020). We included lake stage (March–April) and water level recession rate as linear and quadratic terms and included the linear terms in an interaction term. We obtained lake stage from the South Florida Water Management District's DBHYDRO database. The lake stage data used in this study is the average daily water level (NGVD29) from 8 water level gage stations that were active during the study period (S135 [or S7], S308, S133, S127, S129, S77, S2, and S4). We derived daily recession rates from daily lake stage estimates by subtracting lake stage on each day from lake stage on the previous day (positive values indicate that water levels decreased). We used average daily recession rates during March–April as a covariate in the models. The willow availability index, which is an index of nest substrate availability, included 3 categories: high willow availability, which occurs when lake stages are ≤ 3.9 m NGVD for ≥ 170 days in the previous 2 water years (1 Jun through 31 May of the subsequent year); moderate willow availability, which occurs when lake stages are neither ≤ 3.9 m NGVD for ≥ 170 days nor ≥ 4.7 m NGVD for ≥ 540 days in the previous 2 water years; and low willow availability, which occurs when lake stages are ≥ 4.7 m NGVD for ≥ 540 days in the previous 2 water years. These categories are modified from Chastant et al. (2017). Because the willow index is based on multiyear hydropatterns, it is possible that the willow availability index covaries with other factors that affect wading bird nest abundance. For instance, prolonged flooding that results in low index values may also result in negative effects on foraging habitat or prey availability. We tested for multicollinearity among variables using a Pearson's correlation test, removing any variable with an $r > 0.8$. To further verify, we checked the variance inflation factor scores and removed any variables with variance inflation factor values > 4 . We included a categorical variable representing 2 management regimes implemented during the monitoring period. The management categories are based on the regulation schedules that were in place during the sample years. During 1978–1992, the regulation schedule was characterized as high (max. envelope = 5.32–5.63 m) and during 1977 and 2006–2019 the regulation schedule was characterized as low (max. envelope = 3.73–5.26 m; Figure 1).

We examined models with all combinations of variables to test the effect of water level fluctuations on lake-level nest abundance and used an information-theoretic approach to determine which hypotheses the data best supported (Burnham and Anderson 2002). We considered a model to be informative if Akaike's Information Criterion corrected for small sample size (AIC_c) was within 4 AIC_c units of the top model. If > 1 model was informative, we used weighted model averaging to calculate parameter estimates and confidence intervals. Furthermore, we examined coefficients and 95% confidence intervals to determine whether parameters in supported models had a positive or negative effect on nest abundance, and whether the confidence intervals overlapped zero. We performed all analyses in R (R Core Team 2017). We used the MASS package (Venables and Ripley 2020) to run negative binomial GLMs and we used the MuMIn package to perform model selection and model averaging (Barton 2020). We validated lake-level nest abundance models using leave-one-out cross-validation.

Colony-level models (2006–2019)

We fitted colony-level models to investigate the influence of hydrological variation on annual nest abundance from 2006 to 2009. We included only relatively large colonies (> 100 nests in ≥ 1 season) for which the frequency of colonization exceeded 3 of 14 years with nesting to avoid difficulty in interpreting nest abundance patterns for small colonies that are used infrequently. Ten colonies met these criteria for the great egret and snowy egret and 5 met them for white ibis. There were 4 distinct colony types: spoil islands (Clewiston Spit and Little Bear Beach, Bird-Rock Islands, Lakeport), short-hydroperiod marsh colonies (Liberty Point, Moore Haven, Moore Haven East), long-hydroperiod marsh colonies (Moonshine Bay, Indian Prairie), and colonies in the Eagle Bay region and various colonies north of Eagle Bay, collectively called Eagle Bay (Figure 2). This definition allowed us to group colonies that

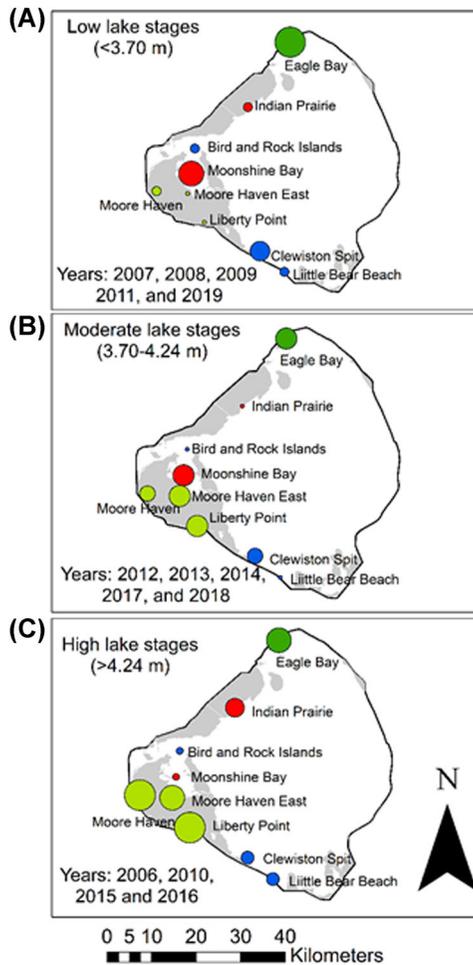


FIGURE 2 Locations of colonies of nesting great egret, snowy egret, and white ibis during years with low (A), moderate (B), and high (C) lake stages at Lake Okeechobee, Florida, USA, 2006–2019. Mean January–May lake stage was considered low if it was <3.96 m, moderate if it was $3.96\text{--}4.24$, and high if it was >4.24 m. Long-hydroperiod colonies are colored red, short-hydroperiod colonies are light green, Eagle Bay is dark green, and spoil islands are blue. Point size is scaled proportional to the aggregate number of birds nesting at each colony. Shading inside the perimeter of Lake Okeechobee represents the littoral marsh and the white area inside the perimeter represents open water

are likely to respond similarly to changes in hydropatterns because of their elevation and where they are situated in the landscape.

We analyzed the influence of hydropatterns on colony-level nest abundance using hierarchical generalized additive mixed (Pedersen et al. 2019), which we fit using the *mgcv* package in R (Wood 2017). To account for overdispersion in the nest counts, we ran the models with a quasi-poisson error distribution (Ver Hoef and Boveng 2007). We included explanatory variables that integrate hydropatterns over multiple spatiotemporal scales (Table 1). We estimated area of available habitat during March–April by counting the number of cells with water depth 18–83 cm, within 10 km of the colony. We included recession rate as an indicator of prey concentrations because fish density in the greater Everglades increases with water recession rates (Botson et al. 2016). We included days that the mean estimated water depths in cells <50 m from the colony center fell below 0 cm in the previous 2 water years, as a surrogate for nest substrate availability because prolonged flooding results in willow mortality and prolonged dry

**TABLE 1** Predictor variables used in generalized additive models of colony-level nest abundance for great egret, snowy egret, and white ibis from 2006–2019 at Lake Okeechobee, Florida, USA. We included descriptions of how we estimated predictor values and hypotheses regarding their effects on nest abundance

Predictor	Description	Hypothesis
Available foraging habitat	Total area of habitat (<10 km from the colony) in which water depths were 18–83 cm during peak nesting season (Mar–Apr). We excluded cells with dense woody vegetation or dense cattail.	Nest abundance will increase with the total amount of habitat (km ²) that becomes available within a 10-km ² range of the colony region. Because the littoral marsh slopes toward the nearshore zone, the amount of habitat that becomes available can be low when water levels are high (i.e., short-hydroperiod cells only become available toward the end of the breeding season), or when water levels are low (i.e., long-hydroperiod cells are available at the beginning of the season, but then dry). Years with the highest habitat availability within the foraging range are those in which the drying edge of the marsh moves from short hydroperiod to long hydroperiod.
Recession rate	Mean Mar–Apr recession rate (cm/day)	Receding water levels concentrate prey (Botson et al. 2016), so nest abundance will increase with recession rate.
Water depth in the colony	Mean estimated water depth within a 50-m radius of the colony center	Colonies must offer some protection from mammalian predators. Thus, colonies that have dried out and are not surrounded by deep channels will not be suitable for nesting. Likewise, colonies that have flooded >2 m will not be suitable because water will reach the bottom of the canopy.
Days dry in the previous 2 water years	Mean number of days in which 30.48 m × 30.48 m cells, within 200 m of the colony, were dry in the previous 2 water years.	Number of days dry in the last 2 water years is a willow index, based on the premise that willow mortality occurs during periods of prolonged flooding, and recruitment occurs when colony sites dry. Water year is defined as 1 June through 31 May of the subsequent year. This index assumes that willow recruitment in the previous 2 water years will increase with the number of days that a site was dry, and thus nest abundance will increase. There are other potential ecological effects of the number of days dry in the previous 2 water years, such as phosphorous release from sediments upon reflooding (Frederick and Ogden 2003), but this would only directly influence wading birds if it resulted in increased secondary productivity, which it does not.

periods allow willow recruitment (David 1994a, Chastant et al. 2017). We used average March–April water depth within 200 m of the colony center (0.13-km² buffer) as a surrogate for nest substrate suitability during the nesting season because colonies that are surrounded by standing water are better protected from mammalian predators. We could not use the digital elevation model to estimate elevation in the 200 m surrounding spoil islands because it is



based on LiDAR imagery from dry land. Because spoil islands are permanently surrounded by deep channels, we set the elevation surrounding colonies to 2.4 m, which is low enough that depth surrounding the colony was >0 m under any realistic hydrological scenario.

We included hierarchical terms to allow the effect of habitat availability to vary with colony type, and the effect of water depth to vary with colony (Pedersen et al. 2019). We specified hierarchical models by including global smoothers (i.e., smooth terms that do not interact with colony or colony type) for habitat availability and water depth, and factor smoothers where the effects are allowed to vary by group. These are analogous to random slope generalized linear mixed models because group-level effects are estimated, but groups that are too far from the average effect are penalized (Pedersen et al. 2019). We allowed the effect of water depth to vary by colony because we assumed that there is a suitable water level window for each colony, outside of which the colony is too dry or too flooded to support nesting.

With rare exceptions, differences in rainfall in the wet and dry seasons of subtropical systems are pronounced, resulting in high accession rates during the wet season and high recession rates during the dry season. In 2010, in one of those rare exceptions, heavy rainfall in March–April produced an extremely high accession rate (0.79 cm/day) during the dry season. This pattern is extremely atypical and was not predicted by any of the hydrological simulations used in management scenario testing. Therefore, we excluded data from 2010 from analyses and restricted model inferences to years with hydropatterns more characteristic of subtropical wetlands.

We chose basis dimension (K) for each common smoother by fitting models with a modest K ($K = 6$) and using the `gam.check` function to check for suspicious K indices and P -values (Wood 2017). If the K index and P -value suggest a missed pattern in the residuals, we doubled K to see if the model results changed substantially. We used maximum likelihood as the criterion and performed model selection on models with all combinations of fixed effects structures by comparing quasi-AIC values corrected for small sample sizes (QAIC_c; Burnham and Anderson 2002, Wood 2006) because we fit models using a quasi-Poisson distribution. We performed model selection using the MuMIn package in R, and used model-averaged parameter estimates for prediction. We validated the top colony-level model using k -fold cross-validation ($k = 13$; i.e., 1 fold/year) and examined the linear relationship between predicted and observed annual nest abundance by pooling cross-validated predictions from each fold and aggregating them by year. We examined root-mean squared errors (RMSE) of colony-level and annual nest abundances aggregated across colonies to better assess the predictive performance of our models. This was an important step because our colony-level approach was intended to improve predictions of annual nest abundance by accounting for ecological and physical differences among colony types that result in local responses to water management. Finally, we predicted nest abundance for 2020 and plotted it along annual k -fold predictions to see whether the predictive performance of our models held in an out-of-sample year.

Management scenario testing

We applied our models to simulations of hydrological data representing potential changes to operational rules for water management at Lake Okeechobee. We based simulations on daily hydrological climatic data collected from 1965–2005. We conducted hydrologic simulations with a regional simulation model (RSM; Lal et al. 2005, SFWMD 2005). The RSM is a physically based hydrologic model that simulates the coupled movement of surface and groundwater flows, hydraulic structures, and other operational rules and conditions that are common features in the greater Everglades. The RSM has 2 components: hydrologic simulation engine and management simulation engine. The hydrologic simulation engine provides an efficient and flexible computational engine that simulates a wide variety of hydrologic and hydraulic conditions. The management simulation engine uses diverse management algorithms to apply managerial decisions to the operations of water control structures (Park et al. 2007). In this analysis, we used a link-node application of the RSM that simulates several hydrologic components such as lakes, drainage basins, reservoirs, and treatment areas by physically connecting them. Such an application of RSM is specific to Lake Okeechobee and its surrounding basins.



We developed 6 management scenarios using RSM that covered a large variability in lake water levels with different management actions (Table S1, available online in Supporting Information). The existing condition baseline made no changes to the 2008 Lake Okeechobee regulation schedule, and assumed no changes in infrastructure, operational rules and conditions, and water use. Existing conditions baseline is today's condition with no modifications. The Comprehensive Everglades Planning Project scenario represents the project features of the Central Everglades Planning Project Post Authorization Change Report, which would increase storage capacity via a large reservoir to the south of Lake Okeechobee with a storage capacity of 296 million m³. The Comprehensive Everglades Planning Project scenario used the same regulation schedule of existing conditions scenario but also used its operational flexibility to slightly raise water surface levels. In the higher envelope scenario (Table S1), the upper and lower bounds of the regulation schedule were raised by 0.46 m to operate Lake Okeechobee in high water levels. In the lower envelope scenario, the upper and lower bounds were decreased by 0.30 m and environmental demand in downstream Everglades National Park was increased by 25% to operate the lake in lower levels. In the wider envelope scenario, the upper bound of the regulation schedule was raised by 0.30 m and lower bound was lowered by 0.30 m to operate the lake in a wider operational range. In the narrower envelope scenario, the upper bound of the regulation schedule was lowered by 0.30 m, and lower bound was increased by 0.30 m to keep lake levels within the ecologically desired stage envelope (RECOVER 2014). Hydrological simulations predicted daily lake stage over 41 years. We used these data to generate daily estimates of each of the environmental variables deemed important during model selection and predicted annual colony-level nest abundance under each scenario. We summed colony-level predictions to produce predicted cumulative nest abundance for each scenario.

RESULTS

In years with low and moderate lake stages, we observed high nest abundance at spoil islands, long-hydroperiod marsh colonies, and Eagle Bay. During wetter years, we observed high nest abundance at short-hydroperiod marsh colonies (Figure 2). Spoil islands had higher recolonization rates (% frequency of nesting; Table S2, available online in Supporting Information) and lower annual variation in nest abundance than natural willow colonies (2008–2019 coefficient of variation at natural willow colonies = 74%, created spoil island colonies = 50%). The proportion of birds that nested at spoil islands varied by species: 27% (2,854/10,573) for great egret, 18% (4,034/22,406) for snowy egret, and <0.01% (75/22,331) for white ibis (Table S2). Despite higher recolonization rates, spoil islands accounted for fewer nests over the study period, likely because their small size limited carrying capacity relative to natural colonies.

Linear regressions revealed that great egret nest abundance increased with the total area of littoral habitat ($F = 3.30$, $R^2 = 0.25$, $P = 0.12$), though this relationship was not significant. Snowy egret nest abundance increased with fish density ($F = 7.05$, $R^2 = 0.46$, $P = 0.04$), and white ibis nest abundance increased with greater habitat and prey availability (Figure 3; $F = 12.38$, $R^2 = 0.62$, $P = 0.01$).

Lake-level models

Mean annual nest abundance for the full sample period (1977–1992 and 2006–2019) was 810 ± 689 nests for the great egret, $1,001 \pm 962$ nests for snowy egret, and $1,220 \pm 1,283$ nests for white ibis. Lake stage (Mar–Apr) was the most important predictor of great egret nest abundance, and the categorical variable for management regime was the only important predictor of snowy egret nest abundance (Table 2). Hydrological predictors did not explain variation in white ibis nest abundance (Table 2). There was a nonlinear effect of lake stage on great egret nest abundance with peak nest abundance occurring when lake stage was approximately 4.5 m NGVD (Table 3; Figure 4). Although willow fell within 2 AIC units of the top model for snowy egret, it did not reduce model deviance enough to overcome the 2 AIC unit penalty, and thus was not included in the final model (Arnold 2010). Snowy

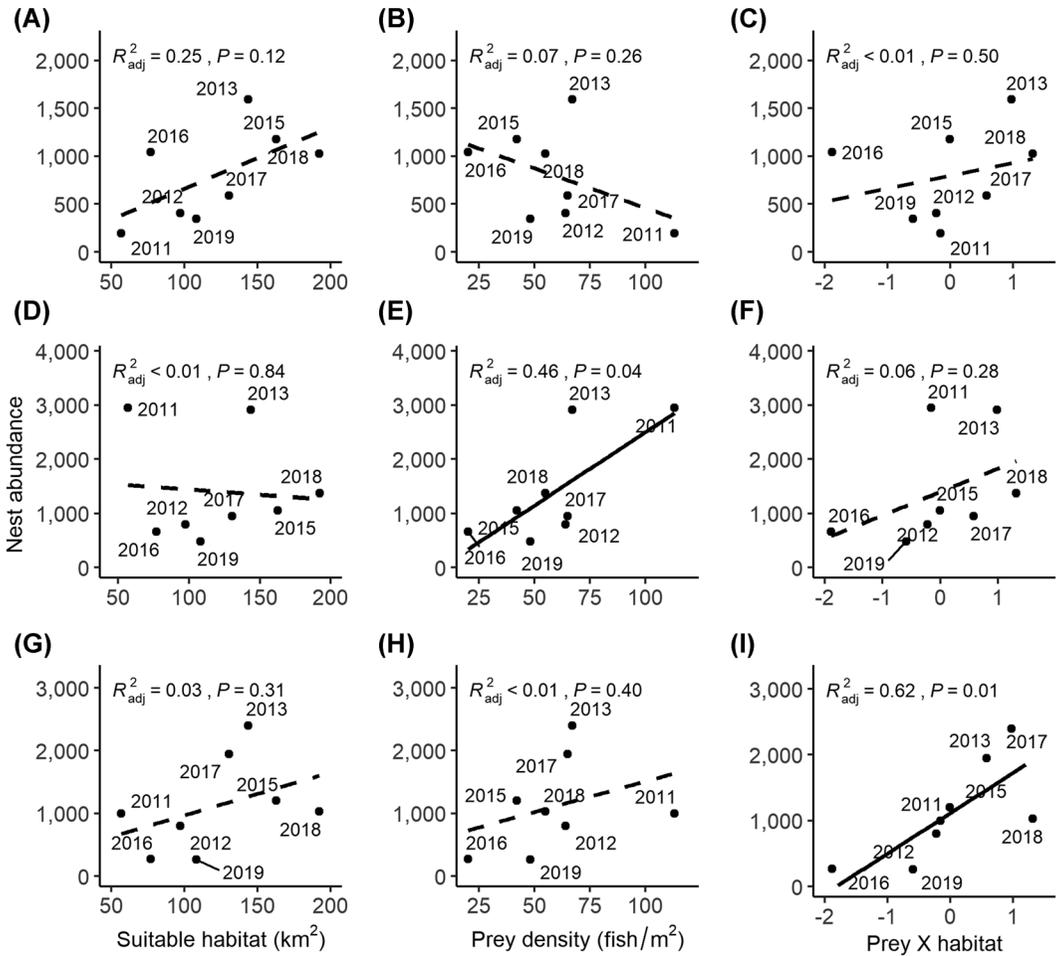


FIGURE 3 Regression plots showing the effects of habitat availability, mean prey density, and total prey available (prey density \times habitat availability), respectively, on great egret (A–C), snowy egret (D–F), and white ibis (G–I) nest abundance at Lake Okeechobee, Florida, USA, 2011–2013 and 2015–2019. Solid lines represent significant relationships and dashed lines represent insignificant relationships

egret nest abundance was higher when the regulation schedule was low (1977 and 2006–2019) than when it was high (1978–1992; Table 3). Leave-one-out cross validation resulted in predictions with reasonably low error (RMSE = 603 nests) but a weak correlation to observed values ($R^2 = 0.22$).

Colony-level models

Nest abundance generally increased with area of available habitat for great egret and snowy egret, but the effect was non-linear for white ibis (Table 4; Figure 5A, E, and I). Group level (colony type) effects of habitat availability on nest abundance were supported for great egret, but the plots of group-level responses suggest that there was no meaningful effect at the group level (Figure S2, available online in Supporting Information). One of the supported white ibis models included group-level effects for colony type, but the inclusion of the colony type effect did not improve loglikelihood estimates enough to overcome the 2-QAIC_c unit penalty imposed by including the variable; thus, it likely has no ecological effect (Table 4; Arnold 2010). There was a positive relationship between recession rate and nest abundance



TABLE 2 Model selection table showing the top-fitting models (difference in Akaike's Information Criterion corrected for small sample size [ΔAIC_c] < 4) of lake-level nest abundance (1977–1992 and 2006–2019) for the great egret, snowy egret, and white ibis at Lake Okeechobee, Florida, USA. Stage is the water surface elevation averaged across several gauges, mgmt is a factor representing the management period (high operational range or low operational range), rec is water recession rate (cm/day), and willow is an index of nest substrate availability. *K* is the number of independent parameters in the model, logLik is the maximum log(Likelihood) value, and w_i is the Akaike weight

Model	<i>K</i>	logLik	AIC_c	ΔAIC_c	w_i
Great egret					
Stage + stage ²	4	-216.1	441.8	0.0	0.4
Stage + stage ² + mgmt	5	-215.3	443.0	1.3	0.2
Stage + stage ² + willow	5	-215.8	444.1	2.3	0.1
Stage + stage ² + rec	5	-216.0	444.6	2.9	0.1
Global	7	-216.1	449.4	7.7	0.0
Null	2	-229.8	463.4	21.6	0.0
Snowy egret					
Mgmt	3	-231.9	470.6	0.0	0.4
Mgmt + willow	4	-231.4	472.5	1.9	0.2
Mgmt + rec	4	-231.7	472.9	2.3	0.1
Mgmt + stage	4	-231.7	473.0	2.4	0.1
Null	2	-237.2	477.9	8.2	0.0
Global	6	-231.2	478.0	9.1	0.0
White ibis					
Null	2	-228.6	461.7	0.0	0.2
Global	7	-226.2	471.8	10.2	0.0

TABLE 3 Model selection table showing the parameter estimates (and 95% CIs) for the top-fitting models of lake-level nest abundance for the great egret and snowy egret at Lake Okeechobee, Florida, USA, 1977–1992 and 2006–2019. Stage is the water surface elevation (m) averaged across several gauges and management is a factor representing the management period (high operational range [reference] or low operational range)

Model	β	2.5%	97.5%
Great egret			
Intercept	-25.41	-37.53	-13.28
Stage	14.04	8.17	19.87
Stage ²	-1.52	-2.21	-0.82
Snowy egret			
Intercept	6.13	4.57	7.70
Management	1.17	0.48	1.87

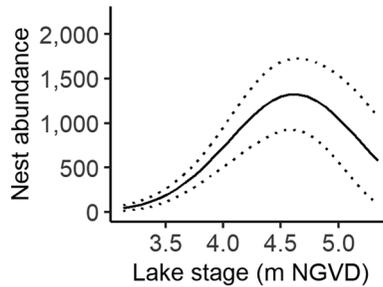


FIGURE 4 Predicted relationship between great egret nest abundance and March–April lake stage (m National Geodetic Vertical Datum) at Lake Okeechobee, Florida, USA, 1977–1992 and 2006–2019. The dotted line represents upper and lower 95% confidence intervals

for all species, although for great egret, uncertainty around model estimates increased when recession rate was low (Figure 5B, F, and J). Predicted nest abundance was approximately zero when water depth surrounding the colony was <0 m and peaked when water depth surrounding the colony was approximately 0.5–1.5 m (Figure 5C, G, and K). Nest abundance increased with the number of days dry in the previous 2 water years for all 3 species, though for snowy egret and white ibis there was a subtle decrease in nest abundance at sites that were dry for >400 days in the previous 2 water years (Figure 5D, H, and L). To rule out the possibility that increased nest abundance in years following hydrological drought can be explained by prey availability, rather than increased nest substrate availability, we performed a linear regression between days dry in the previous 2 water years and prey densities (2011–2013, 2015–2019). There was no influence of the number of days dry on fish ($F = 2.38$, $R^2 = 0.02$, $P = 0.12$) or crayfish (*Procambarus* spp.; $F = 1.08$, $R^2 = 0.00$, $P = 0.30$) density. Colony-level effects of water depth were included in supported models for all species, and generally reflect differences in suitable lake stage windows at each colony (Figure S3, available online in Supporting Information). Overall, the variables included in supported models explained a large degree of variation in nest abundance (Table S3, available online in Supporting Information).

There were large residuals for colony-level predictions for all 3 species, resulting in poor predictions of colony-level nest abundance, but colony-level prediction errors were largely mitigated within years, such that overpredictions at 1 colony were generally accompanied by underpredictions at another (Table S4, available online in Supporting Information). Predictions of annual nest abundance were excellent for great egret (RMSE = 146 nests, $R^2 = 0.95$; Figure 6A) and reasonably good for snowy egret (RMSE = 783 nests, $R^2 = 0.57$; Figure 6B) and white ibis (RMSE = 1,231 nests, $R^2 = 0.49$; Figure 6C). The large RMSE for snowy egret and white ibis suggests that predictions should be interpreted cautiously. Nevertheless, these models are promising as tools for predicting effects of future hydropatterns, particularly given the high degree of variation in nest abundance among years, and inherent variability of the number of wading birds in the system. This was demonstrated by out-of-sample predictions for the 2020 nesting season, because predictions were close to observed nest abundance for all 3 species (Figure 6).

Management scenario testing

Cumulative great egret nest abundance over the 41-year simulation length was highest (39,605 nests) under the higher envelope scenario. This scenario had the effect of increasing the frequency of extreme floods (>5.18 m) to 694 days/5.0 years and decreasing the frequency of drying events necessary for willow recruitment (3.9 m) to 292 days/5.0 years. It resulted in 149 more nests/year nests than the existing baseline scenario for the great egret but 575 fewer nests/year for the snowy egret and 465 fewer nests/year for the white ibis. Cumulative snowy egret and white ibis nest abundance were both high under the existing conditions baseline scenario and the lower envelope scenarios (Figure 7), which both resulted in extreme flooding in <0.6/5.0 years and conditions for willow



TABLE 4 Model selection table showing the parameter estimates for the top-fitting models (difference in quasi Akaike's Information Criterion corrected for small sample size [ΔQAIC_c] < 4) of colony-level nest abundance for the great egret, snowy egret, and white ibis, at Lake Okeechobee, Florida, USA, 2006–2019. Habitat area is the area of habitat that became available during March–April; colony type is a grouping factor for spoil islands, short-hydroperiod marsh colonies, long-hydroperiod marsh colonies, and colonies in the Eagle Bay region; depth is water depth at the colony; rec is water recession rate (cm/day); willow is the number of days the colony was dry in the previous 2 water years; and depth \times colony is essentially a random slope term that allows the effects of depth to vary for each individual colony, while penalizing colony-level effects that are too far from the mean effect. K is the number of independent parameters in the model, $\log\text{Lik}$ is the maximum log(Likelihood) value, and w_i is the Akaike weight

Model	K	$\log\text{Lik}$	QAIC_c	ΔAIC_c	w_i
Great egret					
Habitat area \times colony type + depth + rec + willow	14	-4,622.0	180.9	0.0	0.2
Global	24	-3,733.8	180.9	0.0	0.2
Habitat area \times colony type + depth \times colony + willow	15	-4,534.0	181.2	0.3	0.2
Habitat area + depth \times colony + willow	18	-4,290.0	181.7	0.7	0.1
Habitat area + depth \times colony + rec + willow	22	-3,929.2	182.2	1.3	0.1
Depth \times colony + rec + willow	21	-4,018.8	183.1	2.1	0.1
Depth \times colony + rec	18	-4,335.6	183.9	3.0	0.1
Habitat area + depth \times colony + rec	19	-4,304.5	184.5	3.6	0.0
Null	1	-10,753.3	345.8	164.9	0.0
Snowy egret					
Habitat area + depth \times colony + rec + willow	31	-7,653.9	197.1	0.0	0.7
Global	32	-7,382.1	198.9	1.8	0.3
Null	2	-30,000.0	-25,757.5	180.4	0.0
White ibis					
Habitat area + depth + rec + willow	13	-9,473.6	108.4	0.0	0.3
Habitat area \times colony type + rec + willow	14	-8,688.6	108.5	0.1	0.3
Depth \times colony + rec + willow	15	-8,464.0	108.9	0.5	0.2
Habitat area + depth \times colony + rec + willow	18	-7,154.9	110.0	1.7	0.1
Depth + rec + willow	12	-10,329.9	111.6	3.2	0.1
Habitat area + depth \times colony + willow	15	-8,813.9	112.1	3.7	0.0
Global	20	-6,608.6	113.5	5.2	0.0
Null	2	-32,389.9	251.0	142.7	0.0

recruitment in >3.0/5.0 years. Decreasing the upper and lower bounds of the regulation schedule by 0.30 m resulted in 220 fewer great egret nests/year, 19 more snowy egret nests/year, and 164 more white ibis nests/year than the existing baseline scenario. Though the lower and higher envelope scenarios had opposite effects on great egret and the other 2 species, the difference in nesting between the best and worst scenarios was much lower for great egret ($\pm 7,063$ nests) than for the snowy egret ($\pm 24,370$ nests) and white ibis ($\pm 19,061$ nests), suggesting that snowy egret and white ibis are more sensitive to changes to the regulation schedule.

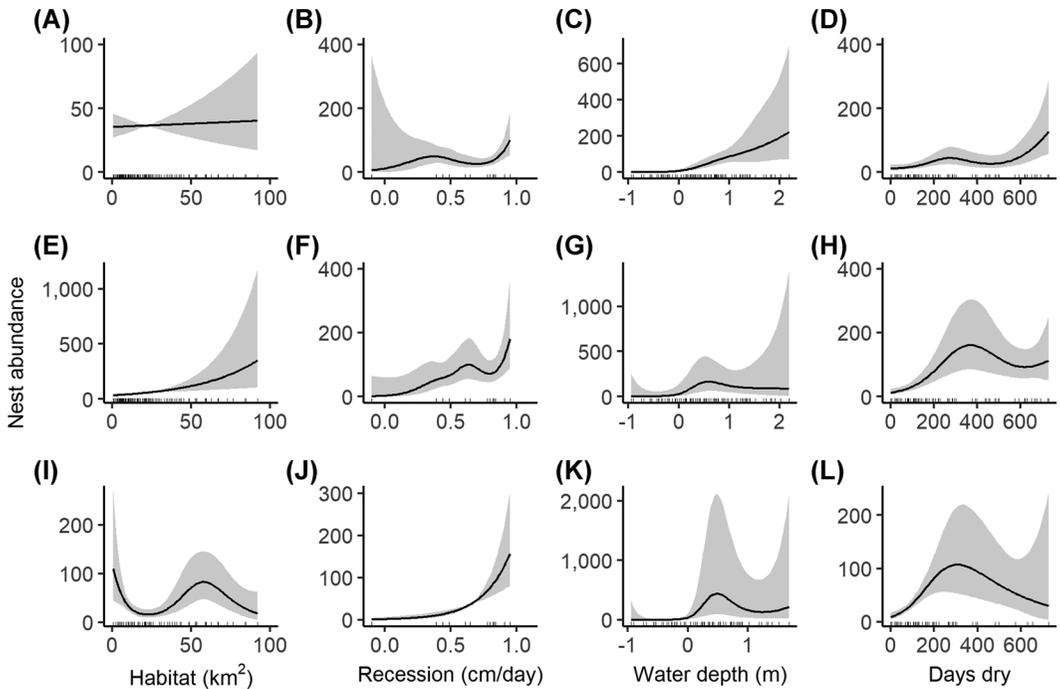


FIGURE 5 Plots showing the effects of area of available habitat (km²), water recession rate (cm/day), water depth surrounding the colony (m), and number of days the colony site dried in the previous 2 years, respectively, on great egret (A–D), snowy egret (E–H), and white ibis (I–L) nest abundance at Lake Okeechobee, Florida, USA, 2006–2019. Plots are from the top hierarchical generalized additive models in which each variable occurred. Top models were identified using Akaike's Information Criterion for quasi-Poisson models ($\Delta\text{QAIC}_c = 0$)

DISCUSSION

We modeled multiscale effects of hydrological variation on the nest abundance of the great egret, snowy egret, and white ibis in a subtropical littoral floodplain. Differences in responses reflected the different foraging and nesting ecology of each species. We used scenario testing to examine how changes to operational rules would influence cumulative nest abundances of these species over 41 nesting seasons. Snowy egret and white ibis nest abundance was highest under the existing conditions and lower envelope scenarios and lowest under the higher envelope scenario. The opposite was true for the great egret, but the potential loss in cumulative productivity was over 3 times as high for snowy egret and 2 times as high for white ibis.

Within a nesting season, water surface levels determine whether colonies are inundated, and thus suitable for nesting. They also determine the amount of available foraging habitat surrounding colonies. Wading bird responses to water depths in the habitats surrounding their colonies are documented by others (Jenni 1969, Frederick and Collopy 1989, Smith and Collopy 1995), but it is challenging to separate the effect of water depth on nesting and foraging habitat. We were able to distinguish these effects because we measured each at vastly different scales (i.e., water depth in the colony was estimated based on elevation within a 0.13-km² buffer around the center of each colony and habitat availability was estimated with a 314-km² buffer). The results of our colony-level models reflect that standing water in and around the colonies acts as an environmental constraint because predicted nest abundance decreased to zero at colonies that were completely dry. Flooding around colonies protects nesting habitats from mammalian predators. Colony-level effects of water depth were supported for all species, which supports the hypotheses that lake stage acts as

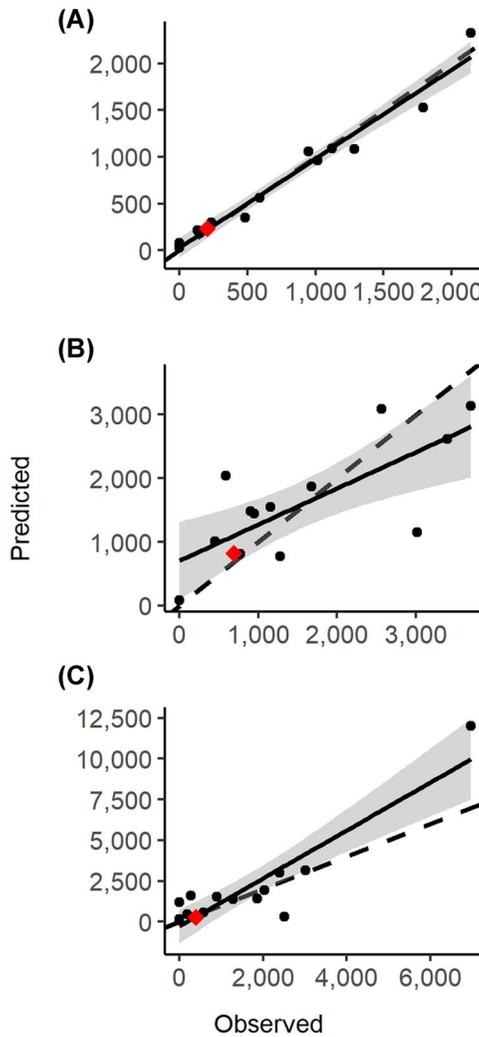


FIGURE 6 The relationship between annual great egret (A), snowy egret (B), and white ibis (C) nest abundance predictions and observed annual nest abundance at Lake Okeechobee, Florida, USA, 2006–2019. The model used to predict nest abundance was a hierarchical generalized additive mixed model that included hydrological predictors and colony-level random effects. As part of a k-fold cross validation procedure to validate the model, we predicted nest abundance of each colony using a model fitted to data that did not include samples that were being predicted. The black dots are aggregated annual nest abundance predictions from k-fold cross validation and the red diamond is an out-of-sample prediction from 2020, which was not included in the modeled data

a constraint on nesting, such that there is a window of suitable stages based on the physical characteristics of each colony. It also highlights the need to include colony-level effects in models of annual wading bird nest abundance.

Our finding that prey densities explained significant variation in nest abundance (2011–2019) for the snowy egret but not great egret or white ibis corroborate a previous study in the Everglades (Klassen et al. 2016). The authors hypothesized that the close relationship between small heron nest abundance and prey density, relative to other species, was because small herons have shorter nesting periods, and thus can synchronize nesting with ephemeral pulses in prey availability. Furthermore, the authors hypothesized that great egret nest abundance was regulated by the area of habitat that became available during the breeding season. This is because the great egret has a longer

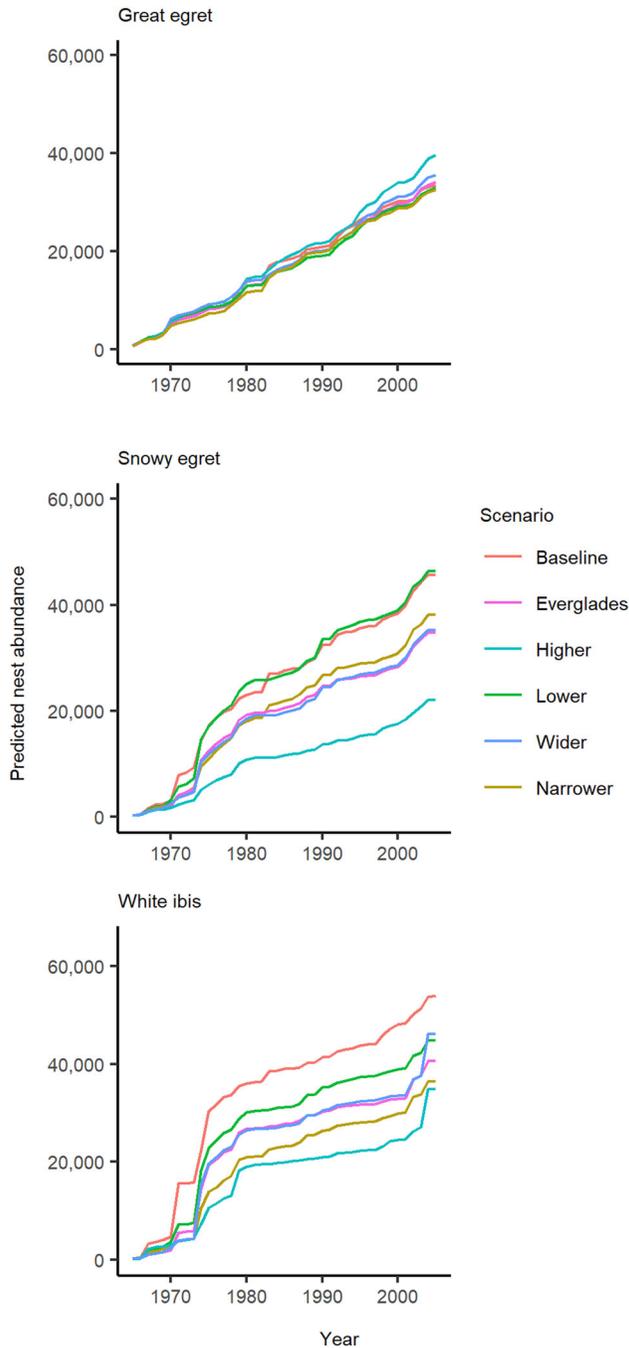


FIGURE 7 Cumulative great egret, snowy egret, and white ibis nest abundance predicted for 6 simulated water management scenarios at Lake Okeechobee, Florida, USA: the existing baseline conditions (Baseline), Comprehensive Everglades Planning Project (Everglades), higher envelope (Higher), lower envelope (Lower), wider envelope (Wider), and narrower envelope (Narrower) scenarios. The output of each simulation is daily water levels predicted over a 41-year simulation period (1965–2005). We summed colony-level predictions to estimate annual nest abundance. Line colors represent the hydrological simulation data that we used to predict nest abundance



nesting phenology and thus must initiate nesting prior to peak prey availability to avoid nest failure from rising water at the onset of the wet season. The relationship between resource phenology and nesting phenology has not been studied at the colony level in the greater Everglades and must be quantified to better examine these hypotheses. For instance, differences in foraging strategies can also explain the relative influence of prey and habitat availability because snowy egrets actively search for high-quality foraging patches and abandon them before they are thoroughly depleted, whereas great egrets exploit prey at lower densities than snowy egrets (Gawlik 2002). Great egrets are also larger, longer legged, and have a larger foraging range, and thus can exploit a greater diversity of habitat characteristics. Our results suggest white ibis nesting increases when high prey densities occur in years with a greater area of available habitat. This was not tested in Klassen et al. (2016), but it corroborates results of a recent study that suggested the combination of moderately high prey availability and high foraging habitat availability during the breeding season best explained a supranormal nesting event by white ibis in the Everglades (Cocoves et al. 2021). Despite species-specific differences revealed in our analysis of lake-wide nest abundance data from 2011–2013 and 2015–2019, the response of these species to area of available habitat and recession rate (a surrogate for prey concentrations) were roughly similar in our colony level analysis from 2006–2019.

Nest abundance was positively related to water level recession rate for all species in the colony-level models, which is consistent with the hypothesis that high recession rates result in higher nest abundance by concentrating prey into shallow isolated pools (Gawlik 2002, Botson et al. 2016). Furthermore, previous studies of non-nesting, foraging wading birds reported that abundance of great egret, snowy egret, and white ibis significantly increased with recession rate (David 1994a). In the Everglades, great egrets and white ibis selected foraging habitats with moderately high recession rates (0.5 cm/day), particularly in years when foraging conditions were poor (Beerens et al. 2011, 2015). Although nest abundance increased with water recession rates in most years, 2010 was an exception. Nest abundances were above average at Moore Haven West and Eagle Bay in 2010, which was excluded from our analysis because water accession rates were exceptionally high (0.79 cm/day). High accession rates in March–April 2010 were due to heavy rainfall events that lasted through April, which likely flooded pastures and agricultural areas just west of Lake Okeechobee. Wading birds forage in these land cover types, particularly when foraging conditions are poor in the littoral zone. The increase in habitat availability off-lake could have supported wading bird nesting at short-hydroperiod colonies that are within the typical range of foraging flights for nesting birds. Nest abundance was unaffected by recession rate in the lake-wide models, further demonstrating that recession rate may only affect nest abundance in certain ecological contexts. For instance, lake stages were extremely high for prolonged periods during 1978–1992, resulting in high willow mortality (David 1994a, 1994b). Prolonged flooding may have resulted in low prey densities within breeding seasons by allowing prey to disperse across the flooded littoral zone and by reducing the extent of submerged aquatic vegetation in the nearshore zone; prolonged and frequent flooding in the long-term might have also favored top-down control by piscivorous fish, thus increasing predation pressure on wading bird prey fish (Kushlan 1976, Dorn and Cook 2015). We hypothesize that low availability of nest substrate and low standing prey stocks were the primary limitations on wading bird nest abundance from 1978 to 1992, thus diminishing the importance of dry season recession rates in historical models.

There are several hypotheses to explain the increase in nest abundance following drought years; the predominant hypothesis emerging from research at Lake Okeechobee is that nest abundance increases because of greater availability of nest substrate, which experiences greater recruitment when marsh sediments are dry (David 1994a, Chastant et al. 2017). This hypothesis has not been tested directly because there is no direct measurement of nest substrate availability at Lake Okeechobee. Increased prey availability resulting from predator release during the drought is an important factor influencing nest abundance in the Everglades. For instance, *in situ* experiments reported that the abundance of slough crayfish (*Procambarus fallax*) at Lake Okeechobee (Hendrix and Loftus 2000) increased following the drought because of release from predation pressure (Dorn and Cook 2015). However, no such relationship was reported for fish, which are the main prey of the snowy and great egret. Furthermore, we found that neither fish nor crayfish densities increased following hydrological drought years at Lake Okeechobee. Thus, we find it unlikely that nest abundance at Lake Okeechobee increases after dry years



because of a concurrent increase in prey availability. It is possible that the mechanisms resulting in increased nesting after dry years differ between Lake Okeechobee and the Everglades proper because the 2 regions differ in spatial scale and trophic state (the Everglades are vaster and more oligotrophic). For instance, when lake stages increase above 4.5 m NGVD, the entire littoral zone floods above the level that is optimal for willow growth and recruitment, whereas the vast area of the Everglades and numerous tree islands make it unlikely that nesting substrate constrains nesting (Frederick and Spalding 1994). It is also possible that the prey release hypothesis, whereby hydrological disturbance reduces predator populations, thus reducing the influence of predators in subsequent seasons, only pertains to crayfish. Regardless, the increase in nests following drought years confirms previous studies and highlights the need for mechanistic studies focused on how prey populations affect species-specific nest abundances.

Colony-level nest abundance may be limited by the number of breeding pairs that encounter the colony, the availability of food within the foraging range of the colony, the availability of nest substrate, and the presence of nest predators. Variation in any of these required factors can limit nesting at individual colonies; however, this study reinforces the idea that the alternation of colony locations among years results in increased population stability, as birds can choose colony locations with the best nesting conditions within a given year (Wiens 1992). Except under extreme conditions (e.g., prolonged flooding resulting in widespread willow mortality), there are suitable nesting sites available in the littoral zone.

Ultimately, water management operational rules must consider ecological effects on a suite of species or habitats. For instance, Lake Okeechobee provides important nesting habitat for the Everglades snail kite (*Rostrhamus sociabilis plumbeus*). The kite's main prey species, the apple snail (*Pomacea* spp.), experiences high mortality after prolonged hydrological drought (Darby et al. 2004, 2008, 2015), leading to kite population declines with increased frequency and spatial extent of drought (Beissinger 1995, Mooij et al. 2002). Thus, a regime of lower lake stages that might benefit wading birds would seem to carry greater risk of impacts to the snail kite population at Lake Okeechobee (Sykes 1983, Beissinger 1995). The snail kite population, however, has actually increased at Lake Okeechobee since 2010 (Reichert et al. 2021), following an extreme drought period from 2007–2008. Although droughts can affect snail kites (Beissinger 1986), the recommended lake stage envelope for kites (Sykes 1983, Johnson et al. 2007) allows water levels to fluctuate between 3.96–5.03 m above mean sea level, a range that is not greatly different from recommendations for wading birds (Havens and Gawlik 2005). This suggests that lower lake stages may not be detrimental to either group of avian species in the long term if extreme drought is infrequent, a principle that is consistent with restoration of numerous ecological functions, including those outside of the littoral marsh. For instance, extreme flooding and drought can result in loss of nearshore submerged aquatic vegetation, which is important foraging and nursery habitat for economically important sport fish (Havens and Gawlik 2005). In this case too, infrequent hydrological drought may be preferable to extreme flooding, as the recovery of submerged aquatic vegetation is faster following extreme drought than after extreme flooding (Harwell and Havens 2003).

In the past, recommendations for the management of Lake Okeechobee's regulation schedule have emphasized the importance of allowing water levels to fluctuate within a moderate range of lake stages. This is a good starting point for management of pulsed wetlands because moderate levels of hydrological disturbance tend to allow higher productivity and diversity (Odum et al. 1995, Townsend et al. 1997, Goździewska et al. 2016). In contrast, stabilization of water levels resulted in a lower density and diversity of waterbirds across several large lakes in Australia (Kingsford et al. 2004). Extreme flooding (>5.1 m NGVD) degrades wetland plant communities, and severely decreases the area of submerged aquatic vegetation in the nearshore zone, which provides refuge from predators and breeding habitat for wading bird prey communities (Chick and McIvor 1994, Johnson et al. 2007). Extreme drought can have short-term negative effects on wading bird communities too, by reducing the area of available foraging habitat, resulting in low nest abundance (Smith and Collopy 1995). Water management strategies that use ecological thresholds to surface water levels, allow for natural water-level fluctuations within those bounds, and infrequently outside those bounds, will support multiple species adapted to the local environment.



MANAGEMENT IMPLICATIONS

Our results demonstrate the importance of quantifying species-specific effects of hydrological variation on wading bird responses when planning changes to water regulation schedules. Furthermore, the results highlight the benefits of managing water levels in seasonal wetlands to fluctuate within a natural range of variation. Because snowy egrets and white ibises are more sensitive than are great egrets to hydrological changes at Lake Okeechobee, management plans should prioritize avoiding negative effects on their nesting populations. Raising the upper bound of the regulation schedule could be highly detrimental to breeding snowy egret and white ibis, whereas modestly lowering the bounds, or maintaining a regulation schedule that is like the existing 2008 Lake Okeechobee Regulation Schedule, would benefit them. Managers could allow the littoral zone to dry during years when rainfall, and thus lake stage, is naturally low, to promote willow recruitment at marsh colonies. This will benefit wading birds in subsequent years, provided water levels at these colonies are suitable. During wet years, managers should aim to maintain March–April lake stages within 4.0–4.6 m NGVD to optimize nesting and foraging habitat availability at short-hydroperiod colonies. Recession rates of 0.5–1.0 cm/day in March–April would result in greater nesting abundance, although at some colonies, high recession rates can cause nesting and foraging habitat to dry before the breeding season is over; therefore, managers should balance the benefits of recession rates, foraging habitat availability, and nest substrate suitability. This could be done by promoting habitat availability in short-hydroperiod marshes during wet years and allowing long-hydroperiod willow stands to dry, and thus regenerate, in drought years. This dynamic approach is conducive to water management in a system with high interannual variation in rainfall, which is common in the subtropics. Furthermore, it is better at dealing with unpredictable events, such as drought or hurricanes, than command and control strategies, which ignore the inherent unpredictability of ecosystems.

ACKNOWLEDGMENTS

Any opinions, findings, conclusions, or recommendations expressed in this manuscript are those of the authors and do not necessarily reflect the views of The Everglades Foundation. This research stems from decades of work from personnel at multiple agencies and institutions, including Florida Atlantic University, United States Army Corps of Engineers, South Florida Water Management District, Everglades National Park, the University of Florida, Audubon Florida, and the Florida Fish and Wildlife Conservation Commission. We thank field technicians and graduate students J. D. Evans, R. C. Larson, R. Mirzadi, B. Eachus, and the many students and technicians that came before them for crucial support in the field. Critical reviews by R. Weiderholt helped improve the quality of the manuscript. Support for this research came from the Everglades Foundation, Florida Atlantic University, and through a contract to DEG from the United States Army Engineer Research and Development Center.

ETHICS STATEMENT

We conducted all research under Florida Atlantic University Institutional Animal Care and Use Committee protocol A17-05 and Florida Fish and Wildlife Conservation Commission Scientific Research Permits LSSC-18-00027 and S-20-2.

DATA AVAILABILITY STATEMENT

The data and R script that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

- Armstrong, J. B., G. Takimoto, D. E. Schindler, M. M. Hayes, and M. J. Kauffman. 2016. Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. *Ecology* 97:1099–1112.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.



- Aumen, N. 1995. The history of human impacts, lake management, and limnological research on Lake Okeechobee, Florida (USA). *Archiv für Hydrobiologie* 45:1–16.
- Barton, K. 2020. MuMIn: multi-model inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>
- Bayley, P. B. 1995. Understanding large river-floodplain ecosystems. *BioScience* 45:153–158.
- Berrens, J. M., D. E. Gawlik, G. Herring, and M. I. Cook. 2011. Dynamic habitat selection by two wading bird species with divergent foraging strategies in a seasonally fluctuating wetland. *Auk* 128:651–662.
- Berrens, J. M., E. G. Noonburg, and D. E. Gawlik. 2015. Linking dynamic habitat selection with wading bird foraging distributions across resource gradients. *PLoS ONE* 10(6):e0128182.
- Beissinger, S. R. 1986. Environmental uncertainty, and the evolution of mate desertion in the snail kite. *Ecology* 67: 1445–1459.
- Beissinger, S. R. 1995. Modeling extinction in periodic environments: everglades water levels and snail kite population viability. *Ecological Applications* 5:618–631.
- Bino, G., C. Steinfeld, and R. T. Kingsford. 2014. Maximizing colonial waterbirds' breeding events using identified ecological thresholds and environmental flow management. *Ecological Applications* 24:142–157.
- Botson, B. A., D. E. Gawlik, and J. C. Trexler. 2016. Mechanisms that generate resource pulses in a fluctuating wetland. *PLoS ONE* 11(7):e0158864.
- Briscoe, D. K., S. Fossette, K. L. Scales, E. L. Hazen, S. J. Bograd, S. M. Maxwell, E. A. McHuron, P. W. Robinson, C. Kuhn, D. P. Costa, L. B. Crowder, and R. L. Lewison. 2018. Characterizing habitat suitability for a central-place forager in a dynamic marine environment. *Ecology and Evolution* 8:2788–2801.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Chastant, J. E., and D. E. Gawlik. 2018. Water level fluctuations influence wading bird prey availability and nesting in a subtropical lake ecosystem. *Waterbirds* 41:35–45.
- Chastant, J. E., M. L. Petersen, and D. E. Gawlik. 2017. Nesting substrate and water-level fluctuations influence wading bird nesting patterns in a large shallow eutrophic lake. *Hydrobiologia* 788:371–383.
- Chick, J. H., and C. C. Mclvor. 1994. Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing a littoral zone as a landscape. *Canadian Journal of Fisheries and Aquatic Sciences* 51:2873–2882.
- Cocoves, T. C., M. I. Cook, J. L. Kline, L. Oberhofer, and N. J. Dorn. 2021. Irruption white ibis breeding is associated with use of freshwater crayfish in the coastal Everglades. *Ornithological Applications* 123:duaa072.
- Cook, M. I., and M. Baranski. 2020. South Florida wading bird report, volume 25. South Florida Water Management District, West Palm Beach, USA.
- David, P. 1994a. Wading bird use of Lake Okeechobee relative to fluctuating water levels. *Wilson Bulletin* 106:719–732.
- David, P. 1994b. Wading bird nesting at Lake Okeechobee, Florida: an historic perspective. *Waterbirds* 17:69–77.
- Davidson, T. A., A. W. MacKay, P. Wolski, R. Mazebedi, M. Murray-Hudson, and M. Todd. 2012. Seasonal and spatial hydrological variability drives aquatic biodiversity in a flood-pulsed, sub-tropical wetland. *Freshwater Biology* 57: 1253–1265.
- DeAngelis, D. L., J. C. Trexler, and W. F. Loftus. 2005. Life history trade-offs and community dynamics of small fishes in a seasonally pulsed wetland. *Canadian Journal of Fisheries and Aquatic Sciences* 62:781–790.
- Dorn, N. J., and M. I. Cook. 2015. Hydrological disturbance diminishes predator control in wetlands. *Ecology* 96: 2984–2993.
- Dorn, N. J., M. I. Cook, G. Herring, R. A. Boyle, J. Nelson, and D. E. Gawlik. 2011. Aquatic prey switching and urban foraging by the White Ibis *Eudocimus albus* are determined by wetland hydrological conditions. *Ibis* 153:323–335.
- Elphick, C. S., and L. W. Oring. 1998. Winter management of Californian rice fields for waterbirds. *Journal of Applied Ecology* 35:95–108.
- Evans, B. A., and D. E. Gawlik. 2020. Urban food subsidies reduce natural food limitations and reproductive costs for a wetland bird. *Scientific Reports* 10:14021.
- Fleming, D. M., W. F. Wolff, and D. L. DeAngelis. 1994. Importance of landscape heterogeneity to wood storks in Florida Everglades. *Environmental Management* 18:743–757.
- Frederick, P. C., and M. W. Collopy. 1989. The role of predation in determining reproductive success of colonially nesting wading birds in the Florida Everglades. *Condor* 91:860–867.
- Frederick, P. C., B. Hylton, J. A. Heath, and M. Ruane. 2003. Accuracy and variation in estimates of large numbers of birds by individual observers using an aerial survey simulator. *Journal of Field Ornithology* 74:281–287.
- Frederick, P. C., and J. C. Ogden. 2003. Monitoring wetland ecosystems using avian populations: seventy years of surveys in the Everglades. Pages 321–349 in D. E. Busch and J. C. Trexler, editors. *Monitoring ecosystems: interdisciplinary approaches for evaluating ecosystem initiatives*. Island Press, Washington, D.C., USA.



- Frederick, P. C., and M. Spalding. 1994. Factors affecting reproductive success of wading bird (Ciconiiformes) in the Everglades ecosystem. Pages 659–691 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida, USA.
- Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. *Ecological Monographs* 72: 329–346.
- Gawlik, D. E., D. A. Essian, J. D. Evans, and R. C. Larson. 2020. Wading bird colony location, size, and timing on Lake Okeechobee: 2015–2019 final report. U.S. Army Corps of Engineers, Vicksburg, Mississippi, USA.
- Goździewska, A., K. Glińska-Lewczuk, K. Obolewski, M. Grzybowski, R. Kujawa, S. Lew, and M. Grabowska. 2016. Effects of lateral connectivity on zooplankton community structure in floodplain lakes. *Hydrobiologia* 774:7–21.
- Hafner, H., O. Pineau, and Y. Kayser. 1994. Ecological determinants of annual fluctuations in numbers of breeding little egrets (*Egretta garzetta* L.) in the Camargue, S. France. *Revue d'Ecologie (La Terre et la Vie)* 49:53–62.
- Harwell, M. C., and K. E. Havens. 2003. Experimental studies on the recovery potential of submerged aquatic vegetation after flooding and desiccation in a large subtropical lake. *Aquatic Botany* 77:135–151.
- Havens, K. E., and D. E. Gawlik. 2005. Lake Okeechobee conceptual ecological model. *Wetlands* 25:908–925.
- Hendrix, A. N., and W. F. Loftus. 2000. Distribution and relative abundance of the crayfishes *Procambarus alleni* (Faxon) and *P. fallax* (Hagen) in Southern Florida. *Wetlands* 20:1994–1999.
- Herring, G., M. I. Cook, D. E. Gawlik, and E. M. Call. 2011. Food availability is expressed through physiological stress indicators in nestling white ibis: a food supplementation experiment. *Functional Ecology* 25:682–690.
- Høberg, P., M. Lindholm, L. Ramberg, and D. O. Hessen. 2002. Aquatic food web dynamics on a floodplain in the Okavango delta, Botswana. *Hydrobiologia* 470:23–30.
- Jenni, D. A. 1969. A study of the ecology of four species of herons during the breeding season at Lake Alice, Alachua County, Florida. *Ecological Monographs* 39:245–270.
- Jin, B. S., K. O. Winemiller, B. Shao, J. K. Si, J. F. Jin, and G. Ge. 2019. Fish assemblage structure in relation to seasonal environmental variation in sub-lakes of the Poyang Lake floodplain, China. *Fisheries Management and Ecology* 26: 131–140.
- Johnson, K. G., M. S. Allen, and K. E. Havens. 2007. A review of littoral vegetation, fisheries, and wildlife responses to hydrologic variation at Lake Okeechobee. *Wetlands* 27:110–126.
- Jordan, F., S. Coyne, and J. C. Trexler. 1997. Sampling fishes in vegetated habitats: effects of habitat structure on sampling characteristics of the 1-m² throw trap. *Transactions of the American Fisheries Society* 126:1012–1020.
- Junk, W. J., S. An, C. M. Finlayson, B. Gopal, J. Květ, S. A. Mitchell, W. J. Mitsch, and R. D. Robarts. 2013. Current state of knowledge regarding the world's wetlands and their future under global climate change: A synthesis. *Aquatic Sciences* 75:151–167.
- Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Canadian Journal of Fisheries and Aquatic Science* 106:110–127.
- Junk, W. J., and K. M. Wantzen. 2007. Flood pulsing and the development and maintenance of biodiversity in floodplains. Pages 407–435 in D. P. Batzer and R. R. Sharitz, editors. *Ecology of freshwater and estuarine wetlands*. University of California Press, Berkeley, USA.
- Kingsford, R. T. 2000. Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. *Austral Ecology* 25:109–127.
- Kingsford, R. T., K. M. Jenkins, and J. L. Porter. 2004. Imposed hydrological stability on lakes in arid Australia and effects on waterbirds. *Ecology* 85:2478–2492.
- Klassen, J. A., D. E. Gawlik, and P. C. Frederick. 2016. Linking wading bird prey selection to number of nests. *Journal of Wildlife Management* 80:1450–1460.
- Kushlan, J. A. 1974. Quantitative sampling of fish populations in shallow, freshwater environments. *Transactions of the American Fisheries Society* 103:348–352.
- Kushlan, J. A. 1976. Environmental stability and fish community diversity. *Ecology* 57:821–825.
- Kushlan, J. A. 1986. Responses of wading birds to seasonally fluctuating water levels: strategies and their limits. *Colonial Waterbirds* 9:155–162.
- Lal, A. M. W., R. VanZee, and M. Belnap. 2005. Case study: model to simulate regional flow in South Florida. *Journal of Hydraulic Engineering* 131:247–258.
- Loftus, W. F., and A.-M. Eklund. 1994. Long-term dynamics of an Everglades small-fish assemblage. Pages 461–483 in S. M. Davis and J. C. Ogden, editors. *Everglades: the ecosystem and its restoration*. St. Lucie Press, Boca Raton, Florida, USA.
- Middleton, B. A. 2002. The flood pulse concept in wetland restoration. Pages 1–10 in B. A. Middleton, editor. *Flood pulsing in wetlands: restoring the natural hydrological balance*. John Wiley and Sons, New York, New York, USA.
- Mooij, W. M., R. E. Bennetts, W. M. Kitchens, and D. L. DeAngelis. 2002. Exploring the effect of drought extent and interval on the Florida snail kite: interplay between spatial and temporal scales. *Ecological Modelling* 149:25–39.
- Odum, W. E., E. P. Odum, and H. T. Odum. 1995. Nature's pulsing paradigm. *Estuaries* 18:547–555.



- Ogden, J. C., J. D. Baldwin, O. L. Bass, J. A. Browder, M. I. Cook, P. C. Frederick, P. E. Frezza, R. A. Galvez, A. B. Hodgson, K. D. Meyer, et al. 2014. Waterbirds as indicators of ecosystem health in the coastal marine habitats of southern Florida: 1. Selection and justification for a suite of indicator species. *Ecological Indicators* 44:148–163.
- Pahl-Wostl, C., A. Arthington, J. Bogardi, S. E. Bunn, H. Hoff, L. Lebel, E. Nikitina, M. Palmer, L. R. N. Poff, K. Richards, et al. 2013. Environmental flows and water governance: managing sustainable water uses. *Current Opinion in Environmental Sustainability* 5:341–351.
- Park, J., J. Obeysekera, and R. VanZee. 2007. Multilayer control hierarchy for water management decisions in integrated hydrologic simulation model. *Journal of Water Resources Planning and Management* 133:117–125.
- Pedersen, E. J., D. L. Miller, G. L. Simpson, and N. Ross. 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ* 7:e6876.
- Powell, G. V. N. 1987. Habitat use by wading birds in a subtropical estuary: implications of hydrography. *Auk* 104:740–749.
- R Core Team. 2017. R: a language and environment for statistical computing. R version 3.2.4. R Foundation for Statistical Computing, Vienna, Austria.
- Reichert, B. E., R. J. Fletcher, Jr., and W. M. Kitchens. 2021. The demographic contributions of connectivity versus local dynamics to population growth of an endangered bird. *Journal of Animal Ecology* 90:574–584.
- Restoration Coordination and Verification [RECOVER]. 2014. Comprehensive everglades restoration plan: system status report. U.S. Army Corps of Engineers, Jacksonville, Florida, USA.
- Reynolds, M. D., B. L. Sullivan, E. Hallstein, S. Matsumoto, S. Kelling, M. Merrifield, D. Fink, A. Johnston, W. M. Hochachka, N. E. Bruns, et al. 2017. Dynamic conservation for migratory species. *Science Advances* 3:1–9.
- Richardson, J. R., T. T. Harris, and K. A. Williges. 1995. Vegetation correlations with various environmental parameters in the Lake Okeechobee marsh ecosystem. *Archiv für Hydrobiologie* 45:41–61.
- Ruetz, C. R., J. C. Trexler, F. Jordan, W. F. Loftus, and S. A. Perry. 2005. Population dynamics of wetland fishes: spatio-temporal patterns synchronized by hydrological disturbance? *Journal of Animal Ecology* 74:322–332.
- Schaffer-Smith, D., J. J. Swenson, M. E. Reiter, and J. E. Isola. 2018. Quantifying shorebird habitat in managed wetlands by modeling shallow water depth dynamics. *Ecological Applications* 28:1534–1545.
- Shih, S. F. 1980. Water budget computation for a shallow lake—Lake Okeechobee, Florida. *Journal of the American Water Resources Association* 16:724–727.
- Smith, J. P. 1995. Foraging flights and habitat use of nesting wading birds (Ciconiiformes) at Lake Okeechobee, Florida. *Colonial Waterbirds* 18:139–158.
- Smith, J. P., and M. W. Collopy. 1995. Colony turnover, nesting success and productivity, and causes of nest failure among wading birds (Ciconiiformes) at Lake Okeechobee. *Archiv für Hydrobiologie* 45:287–316.
- South Florida Water Management District [SFWMD]. 2005. RSM Theory Manual—HSE v1.0. SFWMD, West Palm Beach, USA.
- Swartz, L. K., W. H. Lowe, E. L. Muths, and B. R. Hossack. 2020. Species-specific responses to wetland mitigation among amphibians in the Greater Yellowstone Ecosystem. *Restoration Ecology* 28:206–214.
- Sykes, P., Jr., 1983. Recent population trend of the snail kite in Florida and its relationship to water levels. *Journal of Field Ornithology* 54:237–246.
- Thometz, N. M., M. M. Staedler, J. A. Tomoleoni, J. L. Bodkin, G. B. Bentall, and M. T. Tinker. 2016. Trade-offs between energy maximization and parental care in a central place forager, the sea otter. *Behavioral Ecology* 27:1552–1566.
- Townsend, C. R., M. R. Scarsbrook, and S. Dolédec. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* 42:938–949.
- Trexler, J., W. Loftus, F. Jordan, J. Chick, K. Kandl, T. McElroy, and O. Bass. 2001. Ecological scale and its implications for freshwater fishes in the Florida Everglades. J. Porter, editor. *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys*. CRC Press, Boca Raton, Florida, USA.
- Trexler, J. C., W. F. Loftus, and S. Perry. 2005. Disturbance frequency and community structure in a twenty-five year intervention study. *Oecologia* 145:140–152.
- Tsai, J.-S., B. E. Reichert, P. C. Frederick, and K. D. Meyer. 2016. Breeding site longevity and site characteristics have intrinsic value for predicting persistence of colonies of an endangered bird. *Wetlands* 36:639–647.
- U.S. Army Corps of Engineers. 2007. Final supplemental environmental impact statement: Lake Okeechobee regulation schedule. U.S. Army Corps of Engineers, Jacksonville, Florida, USA.
- Vedwan, N., S. Ahmad, F. Miralles-Wilhelm, K. Broad, D. Letson, and G. Podesta. 2008. Institutional evolution in Lake Okeechobee management in Florida: characteristics, impacts, and limitations. *Water Resources Management* 22:699–718.
- Venables, W. N., and B. D. Ripley. 2020. *Modern applied statistics with S*. Fourth edition. Springer, New York, New York, USA.
- Ver Hoef, J. M., and P. L. Boveng. 2007. Quasi-Poisson vs negative binomial regression: how should we model overdispersed count data? *Ecology* 88:2766–2772.



- Wiens, J. A. 1992. Ecology of bird communities. Volume II. Processes and variations. Cambridge University Press, Cambridge, United Kingdom.
- Wood, S. N. 2006. Generalized additive models: an introduction with R (2nd edition). Chapman and Hall/CRC, Boca Raton, Florida, USA.
- Wood, S. 2017. mgcv: mixed GAM computation vehicle with automatic smoothness estimation. <https://cran.r-project.org/web/packages/mgcv/index.html>
- Yurek, S., and D. L. DeAngelis. 2019. Resource concentration mechanisms facilitate foraging success in simulations of a pulsed oligotrophic wetland. *Landscape Ecology* 34:583–601.
- Zaffke, M. 1984. Wading bird utilization of Lake Okeechobee marshes 1977–1981. South Florida Water Management District Technical Publication 84–9, West Palm Beach, USA.
- Zedler, J. B., and S. Kercher. 2005. Wetland resources: status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources* 30:39–74.
- Zeug, S. C., K. O. Winemiller, and S. Tarim. 2005. Response of Brazos River oxbow fish assemblages to patterns of hydrologic connectivity and environmental variability. *Transactions of the American Fisheries Society* 134: 1389–1399.

Associate Editor: Daniel Collins.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Essian, D. A., R. Paudel, and D. E. Gawlik. 2022. Predicting effects of water management on breeding abundance of three wading bird species. *Journal of Wildlife Management* 86: e22155. <https://doi.org/10.1002/jwmg.22155>