BioOne COMPLETE

Water Level Fluctuations Influence Wading Bird Prey Availability and Nesting in a Subtropical Lake Ecosystem

Authors: Chastant, Jennifer E., and Gawlik, Dale E.

Source: Waterbirds, 41(1) : 35-45

Published By: The Waterbird Society

URL: https://doi.org/10.1675/063.041.0105

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Water Level Fluctuations Influence Wading Bird Prey Availability and Nesting in a Subtropical Lake Ecosystem

Jennifer E. Chastant[1,2,*] and Dale E. Gawlik[1]

[1]Department of Biological Sciences, Florida Atlantic University, 777 Glades Road, Boca Raton, Florida, 33431, USA

[2]Current address: Palm Beach County Environmental Resources Management, 2300 Jog Road, West Palm Beach, Florida, 33411, USA

[*]Corresponding author; E-mail: j.e.chastant@gmail.com

Abstract.—Food availability affects the reproductive success of animal populations. However, food availability includes both prey abundance and its accessibility, which are regulated by different environmental processes. The match-mismatch hypothesis links reproductive success to annual variability in food availability, but the threshold hypothesis suggests that changes in prey abundance can reduce or intensify the effects of a mismatch event. From January-June 2011-2013, food availability and wading bird (Pelecaniformes) reproduction were measured amidst different environmental conditions at Lake Okeechobee, Florida, USA. Mean prey density was 165 ± 21 prey/m^2 (2011), 87 ± 7 prey/m^2 (2012), and 104 ± 9 prey/m^2 (2013) while 34% (2011), 36% (2012), and 77% (2013) of the landscape became available for foraging. Two generalized linear mixed models were constructed to quantify the relationship between fledging success and total productivity using prey density and foraging habitat availability as independent variables. The interaction of prey density and habitat availability was significant and positive in both models. Fledging success and total productivity increased with increasing prey density, the effects of which were more pronounced when habitat availability was low. Saturation thresholds existed for both fledging success (147 prey/m^2) and total productivity (189 prey/m^2), above which high concentrations of prey could sustain nesting when habitat availability was low. *Received 10 July 2017, accepted 29 August 2017.*

Key words.—egrets, foraging ecology, herons, hydrology, ibis, Lake Okeechobee, match-mismatch hypothesis, reservoir management, threshold hypothesis.

Waterbirds 41(1): 35-45, 2018

Variation in food supply is known to affect both fecundity and reproductive success in animal populations, likely influencing life-history traits such as the number and quality of young that an individual is capable of rearing (Lack 1968; Martin 1987; Newton 1998). Animals require sufficient resources to endure the greater energy demands associated with breeding, such as pregnancy and provisioning young. Obtaining these resources may be particularly challenging when food is limited during the breeding season (Perrins 1996; Ardia *et al.* 2006; Ward and Bryant 2006). In seasonal environments, most species time their breeding cycle to coincide with maximum food availability (Perrins 1970; Thomas *et al.* 2001; Durant *et al.* 2007). This is best documented in birds where nest initiation dates and clutch sizes shift depending on variation in food availability (Monaghan and Nager 1997; Drent 2006; Durant *et al.* 2007).

For predators, food availability depends not only on prey density but also its accessibility, or vulnerability to capture (Gawlik 2002). Concomitance of predator and prey behavior as well as characteristics of the physical environment can make apparently abundant resources inaccessible to the consumer (Boutin 1990; Gawlik 2002; Lantz *et al.* 2010). For instance, in hydrologically pulsed wetlands, water depth plays a central role in wading bird (Pelecaniformes and Ciconiiformes) selection of foraging habitat due to leg length constraints, vegetation structure, and aquatic fauna dispersal (Arengo and Baldassarre 1999; Gawlik 2002; Lantz *et al.* 2010). Additionally, the varying accessibility of food in space is critical for central-place foragers such as breeding birds that must return to the nest to feed their chicks. Increased distance and travel time to a foraging location decreases food availability by reducing spatial overlap (Durant *et al.* 2007; Burke and Montevecchi 2009; Sherley *et al.* 2013).

The match-mismatch hypothesis links reproductive success to annual variability in the temporal and/or spatial overlap between an animal's nutritional needs and its food supply (Cushing 1990). Originally

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

developed to explain recruitment variation in fish, the match-mismatch hypothesis has been applied to a wide variety of reproductive predator-prey interactions (reviewed by Durant *et al.* 2007). The hypothesis assumes that: 1) both the predator and the prey display a certain degree of seasonality; 2) recruitment of the predator is limited by its access to prey during the breeding season; and 3) natural selection favors individuals that match peak food demands (i.e., reproduction) with peak food availability. Thus, reproductive success will be greatest when the predator's requirements align with the availability of the prey. Consequently, a mismatch between food requirements and food availability will reduce the predator's reproductive success (Cushing 1990; Durant *et al.* 2007; Dunn *et al.* 2011). However, the threshold hypothesis states that the abundance of prey will only affect predator populations when availability of prey is below a certain threshold (Nager *et al.* 1997). Therefore, the match-mismatch hypothesis encompasses both spatial and temporal accessibility of prey, but the threshold hypothesis suggests the relationship also varies according to the abundance of the prey (Gotceitas *el al.* 1996; Durant *et al.* 2007). Indeed, Durant *et al.* (2005) modeled trophic interactions of match-mismatch relationships relative to prey abundance in three different ecosystems. They found that changes in prey abundance can reduce or intensify the effects of the mismatch event (Durant *et al.* 2005).

In wetlands around the world, fluctuations in water depth influence the breeding success of wading birds by altering the availability of their prey (González 1997; Canepuccia *et al.* 2007; Ma *et al.* 2010) via changes in the production, distribution, and demographics of small fish and macroinvertebrates (Loftus and Eklund 1994; Trexler *et al.* 2002; Chick *et al.* 2004). For example, declines in wading bird breeding success and population size in the greater Everglades ecosystem are thought to be the result of reduced prey availability due to anthropogenic changes in the hydrologic patterns (Frederick and Collopy 1989; Frederick and Spalding 1994; Gawlik 2002). Such changes are likely to become more widespread as half of the world's area of wetlands has been lost (Zedler and Kercher 2005) and human demand for water has increased on every continent (Kingsford 2000).

Wetland restoration in south Florida, USA, is largely based on the premise that hydrologic patterns, prey availability, and water bird use are tightly linked (Canepuccia *et al.* 2007; Cui *et al.* 2009; Ma *et al.* 2010). Quantifying the response of the wading bird prey community to different environmental conditions will improve our understanding of how wading birds will be affected by hydrologic regimes, as well as how long-term habitat conditions may regulate reproduction and nesting patterns. Water levels and hydrologic regimes, are commonly used as a proxy for the prey community (e.g., Frederick and Ogden 2001; Bancroft *et al.* 2002; Canepuccia *et al.* 2007; Causarano and Battisti 2009), requiring assumptions about how the prey community will respond to changing water levels. Our study is unusual in that we have a direct measure of prey density under different hydrologic conditions, which we quantitatively link to wading bird responses.

Our objectives were to evaluate the effects of foraging habitat availability and prey density on the nesting success of wading birds at two scales, one at the colony level (i.e., fledgling success or the number of chicks fledged/nest) and the other at the wetland level (i.e., the sum of the peak number of nests for all wading bird species breeding in the littoral wetlands of Lake Okeechobee, Florida, USA). This approach allowed us to examine local environmental conditions present when wading birds decide to nest (number of nests) and when prey availability match should occur (fledgling success). We hypothesized that wading bird fledging success would peak in years when both prey density and available foraging habitat were greatest. We also hypothesized that total productivity, a metric combining nest numbers and fledging success, would be greatest in years when prey density and foraging habitat availability were greatest.

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

METHODS

Study Area

Once a part of the vast network of wetlands that stretch across south Florida, USA, Lake Okeechobee (hereafter, lake; 26° 58′ 55.39″ N, 80° 46′ 54.42″ W; Fig. 1) is currently a multi-purpose regional reservoir (Havens and Gawlik 2005). The freshwater marshes associated with the lake, known as the littoral zone, cover ~25% (450 km²) of the lake's surface area and provide important foraging and nesting habitat for wading birds during their breeding cycle (David 1994). The littoral zone hydroperiod is a function of the overall lake level, which is managed to provide flood control and water supply to south Florida's large human population (David 1994; Aumen 1995; Havens and Gawlik 2005).

Aumen (1995) provided a detailed account of the natural and management history of the lake. Annual hydrologic conditions differed during the three years of our study, as is common in subtropical lakes (Johnson *et al.* 2007). During a normal dry season (November-May), lake levels are highest early in the season (average 4.42 m National Geodetic Vertical Datum (NGVD) in January) then recede at a mean rate of 0.05 m/month from January through March and a more rapid rate of 0.14 m/month from April through May (Fig. 2). The littoral zone is gradually sloped inward (Jin *et al.* 2000) so

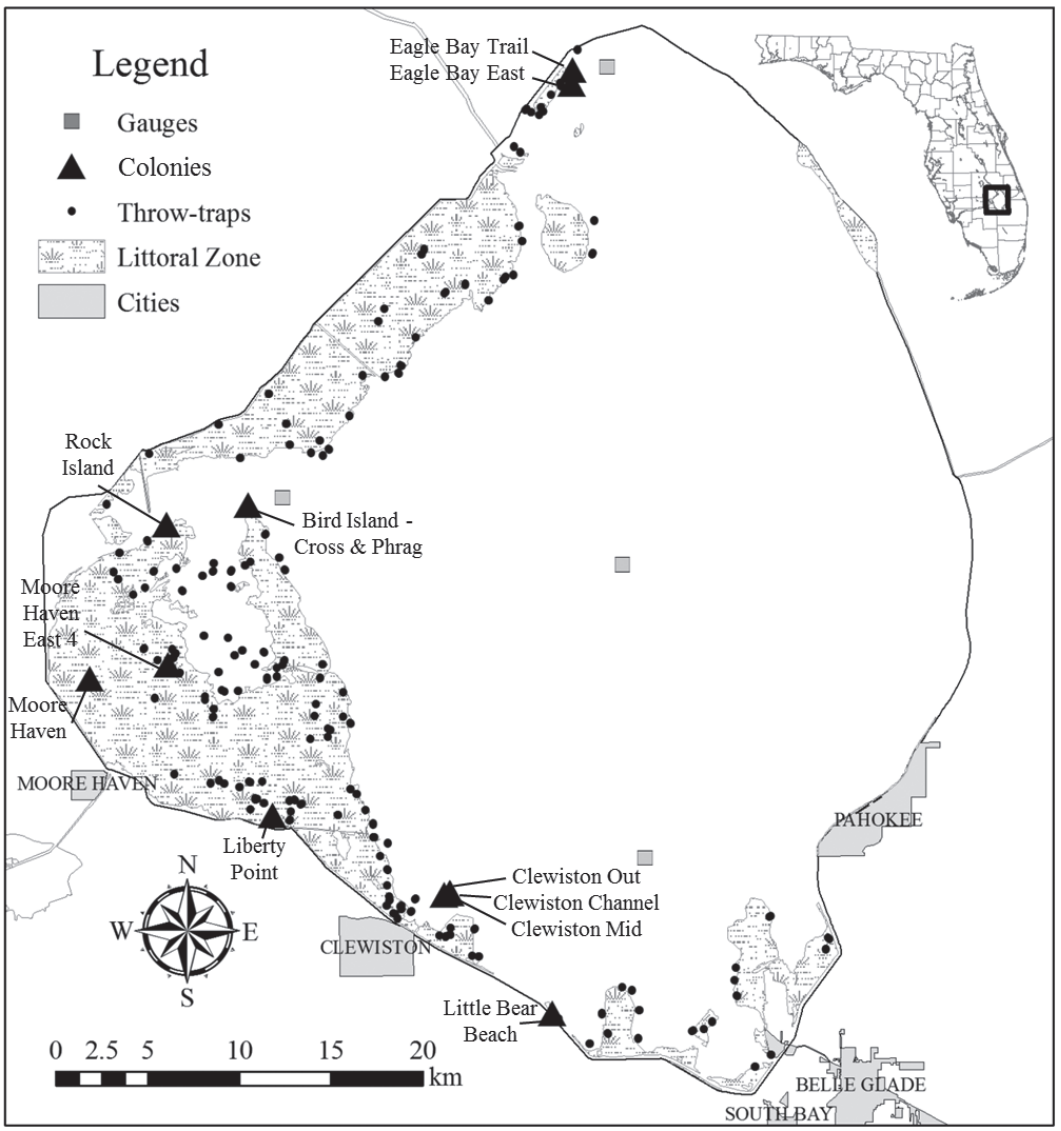


Figure 1. Map of water level gauge locations and of wading bird prey sampling locations and wading bird colonies detected in the littoral zone of Lake Okeechobee, Florida, USA, from January to June 2011-2013.

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

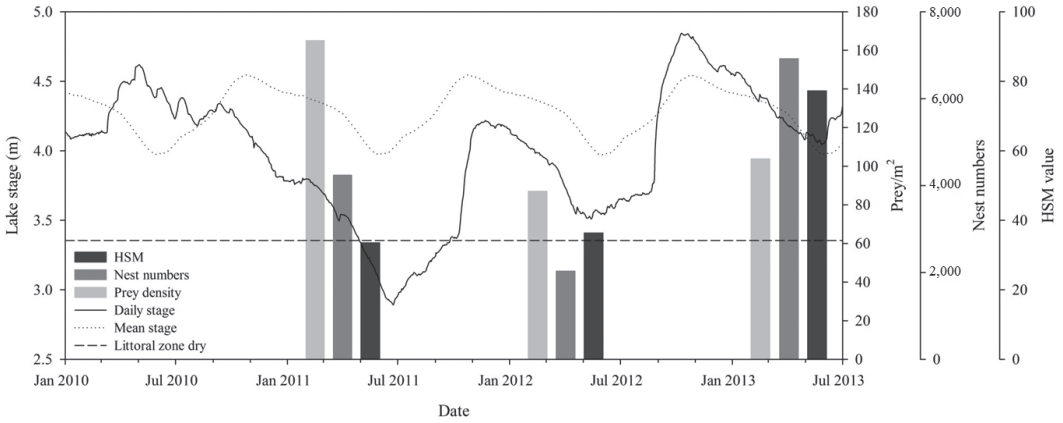


Figure 2. Lake Okeechobee hydrograph from the 2010 dry season-2013 dry season with the mean daily lake stage from 1977 to the present. The percentage of the lake's littoral zone available for wading bird foraging was estimated with a Habitat Suitability Model (HSM). Nest numbers were calculated as the sum of the peak number of nests for the Great Egret (*Ardea alba*), Snowy Egret (*Egretta thula*), Tricolored Heron (*E. tricolor*), Glossy Ibis (*Plegadis falcinellus*), and White Ibis (*Eudocimus albus*). Prey density was calculated as the mean density of fish, crayfish, and shrimp pooled from all throw-trap sites. When lake levels fall below 3.4 m, the littoral zone marsh is dry.

that a seasonal receding water level causes a window of ideal foraging depths to move across the littoral zone, with the cumulative area of good foraging habitat determined by the lake stage at the start and end of the dry season. Lake levels in the 2011 dry season were low at ~3.8 m NGVD in January and remained well below the long-term historic average throughout the nesting season (January-June; Fig. 2). Dry conditions continued in 2012, and lake levels were below average, starting at 4.15 m NGVD in January and receding at a moderate pace of 0.11 m/month during the nesting season. In 2013, lake levels were near the long-term average of ~4.6 m NGVD in January with an extended dry-down throughout the nesting season. Hereafter, we refer to 2011 and 2012 as dry years and to 2013 as an average year.

We obtained lake stage data from the DBHYDRO database (South Florida Water Management District 2013) for 1977 to 2013. This period corresponds to the period of systematic aerial surveys for wading bird nesting colonies (David 1994). We calculated lake stage as the mean of four principle gauges located in the limnetic zone of the lake (Fig. 1).

Foraging Habitat Suitability Model

We used a previously developed habitat suitability model (HSM; Botta 2014) to estimate the annual amount of foraging habitat available to wading birds in the littoral zone of the lake. The spatial extent of the model included the entire littoral region of the lake from the Herbert Hoover Dike to the inner limnetic edge at ~7.5 m North American Vertical Datum (NAVD) with a spatial grain size of 30.48 m and a total of 551,986 grid cells. The model was conducted on a daily time step for dry seasons (January 1-June 30) during 2006-2012. The suitability of a grid cell was based on factors that contribute to the accessibility, vulnerability, and abundance of wading bird prey based on functions derived from marsh elevation, lake stage, and vegetation.

Prey Community Sampling

We sampled prey density throughout the littoral zone of the lake with a 1-m x 1-m throw-trap (Kushlan 1981) during the breeding seasons of 2011-2013. Using ArcGIS (Environmental Systems Research Institute 2011) and LiDAR ground surface elevation data for the lake's littoral zone (National Oceanic and Atmospheric Administration 2007), we identified random sampling sites with depths ranging from 0-30 cm. Sites were required to be accessible by airboat. If we were unable to approach within 200 m of the site, the next closest random point was selected. We removed any vegetation by hand and used a bar seine to collect all prey items from the water column. Seining ceased after five sequential sweeps produced no prey items. Each site was sampled twice, and all contents within the traps were averaged during analyses. We chose the second sampling location by selecting a random direction and random distance 5-50 m from the original trap location. Sampled prey items were transferred to jars containing MS222, a rapid euthanizing agent, and placed on ice. In the lab, we rinsed the prey items and preserved them for 4 days with Prefer, a color fixative, and then transferred them to 70% ethyl alcohol for storage and later identification.

Nesting Colony Surveys

During the breeding seasons of 2011-2013, we surveyed wading bird nesting to determine both location and size of colonies on the lake. Each year, we conducted aerial surveys monthly from January through June with two dedicated observers, one on each side of a Cessna 182 airplane. Wading bird nests were surveyed along transects flying at an altitude of 244 m and a speed of 185 kmph. Transects were oriented east-west

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

and spaced at 3-km intervals, covering the entire littoral zone. After detecting a colony, we lowered our altitude to 122 m and circled it while estimating the number of nests of each species present within the colony, photographing the nests, and recording the colony's geographic coordinates. We subsequently verified colony counts and species composition estimates with observations from airboats. We defined colonies as any assemblage of ≥ 2 nests separated by ≥ 200 m (Smith and Collopy 1995).

Each year, within five or six of the largest and most accessible colonies, we established two 2-m x 50-m transects and counted all nests within the transects weekly. We randomized the transect origins from gridded colony maps and spaced them > 30 m apart in a loop pattern to minimize disturbance to any particular area within the colony. Within transects, we marked each nest containing an egg with numbered flagging tape. We recorded the species, nest stage, nest fate, and fledging success (number of chicks fledged/nest) for each nest monitored. To calculate a colony-specific nest density, we recorded the number of visible nests and attending adults within 5 m of each transect center and averaged the count across transects within a colony. We compared aerial surveys, low-altitude photography, and distance-derived density estimates for consistency and accuracy.

Statistical Analysis

We analyzed differences among years in prey density and fledging success pooled across species using Proc GLM in SAS (SAS Institute, Inc. 2013). We used Proc Mixed (SAS Institute, Inc. 2013) to develop generalized linear models that tested the relative effects of foraging habitat availability and prey density on wading bird fledging success and total productivity. We calculated colony-specific annual fledging success, pooled across species, from all nests present within the nest census transect lines. We calculated annual lake-wide estimates of nest numbers as the sum of the peak number of nests for the Great Egret (*Ardea alba*), Snowy Egret (*Egretta thula*), Tricolored Heron (*E. tricolor*), Glossy Ibis (*Plegadis falcinellus*), and White Ibis (*Eudocimus albus*). We included the total number of nests, summed across colonies, in our models because it is a well-established measure of general wading bird response to the hydrologic conditions of an ecosystem (Frederick and Collopy 1989; Crozier and Gawlik 2003; Frederick and Ogden 2003). We calculated total productivity by multiplying annual nest numbers for the lake by colony-specific fledging success. This metric incorporates spatial variation in colony productivity and allows for tests of local resource levels surrounding colonies. We calculated prey density as the mean density of fish, crayfish, and shrimp pooled, from all throw-trap sites within 10 km of each colony, a distance that is within the foraging range of our target species (Bancroft *et al.* 1994; Smith 1995). We used prey density instead of prey biomass because prey density can be a better indicator of prey abundance and availability to wading birds than prey biomass (Lorenz 2014). We used the annual aggregated habitat score produced by the HSM to estimate foraging habitat availability. We treated 'colony' as a random variable in the analysis because we were interested in general patterns for colonies within the lake. As part of the variable screening process, we tested for collinearity among explanatory variables with pairwise correlations, excluding one term in any pair where $r > 0.7$. The variable 'year' was excluded from all analyses due to its high correlation with the other model variables. Results are presented as means ± SE.

RESULTS

Numbers of Nests and Fledging Success

From 10 January 2011 to 25 June 2013, we detected 17 wading bird colonies (names and locations of the colonies are identified in Table 1) in the littoral zone of Lake Okeechobee (Fig. 1). Annual nest numbers for all wading bird species combined was 5,373 nests in 2011, 3,329 nests in 2012, and 7,539 nests in 2013. Despite extremely low lake levels in 2011, nest numbers were moderate (just below the long-term mean) with a mean fledging success of 1.61 ± 0.05 young/nest. Fledging success in 2012 suffered from an exceptionally dry preceding wet season, below average water levels throughout the nesting season, and storms with high winds and rain. Many colonies were abandoned before the end of the nesting season, resulting in a mean fledging success of 0.71 ± 0.03 young/nest. In 2013, nesting peaked in early April and nest numbers were supra-normal, with a mean fledging success of 1.43 ± 0.06 young/nest (Table 1). Supra-normal nesting events are those where the number of nests is > 1 standard deviation above the long-term mean (Frederick and Ogden 2001). Fledging success for all wading bird species combined varied among years (Table 1; $F_{2, 17} = 34.44$, $P < 0.001$) and was significantly lower in 2012 than in 2011 ($F_1 = 61.69$, $P < 0.001$) and in 2013 ($F_1 = 39.08$, $P < 0.001$). Fledging success did not differ significantly between 2011 and 2013 ($F_1 = 2.57$, $P = 0.13$).

Prey Density and HSM

We collected 338 throw-trap samples from 169 random sites throughout the littoral zone of the lake ($n = 64$, 62, and 43 sites

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 1. Total number of nests within colonies, mean prey density (number of individuals/m²) within 10 km of a colony, and mean number of chicks fledged per nest from 12 colonies located in the littoral zone of Lake Okeechobee, Florida, USA, during the 2011-2013 breeding seasons. Five other colonies were detected within the lake but not monitored.

	2011					2012					2013				
Colony	Colony Size (nests)	Mean Prey Density (SE)	Throw-trap (*n*)	Mean Fledged per Nest (SE)	Surveyed Nests (*n*)	Colony Size (nests)	Mean Prey Density (SE)	Throw-trap (*n*)	Mean Fledged per Nest (SE)	Surveyed Nests (*n*)	Colony Size (nests)	Mean Prey Density (SE)	Throw-trap (*n*)	Mean Fledged per Nest (SE)	Surveyed Nests (*n*)
Bird Island - Cross	150	167 (32)	52	1.7 (0.1)	100	9	—	—	N/A	N/A	—	—	—	inactive	inactive
Bird Island - Phrag	130	167 (32)	52	1.8 (0.1)	73	—	—	—	inactive	inactive	—	—	—	inactive	inactive
Clewiston Channel	167	116 (19)	26	1.5 (0.1)	127	150	109 (12)	28	1.0 (0.1)	123	—	—	—	inactive	inactive
Clewiston Mid	—	—	—	inactive	inactive	57	109 (12)	28	0.7 (0.1)	57	25	—	—	N/A	N/A
Clewiston Out	—	—	—	inactive	inactive	330	109 (12)	28	0.7 (0.1)	310	82	141 (34)	12	1.5 (0.1)	82
Eagle Bay East	4518	102 (45)	14	1.7 (0.1)	120	2,367	96 (19)	16	0.5 (0.1)	59	1,035	—	—	N/A	N/A
Eagle Bay Trail	262	129 (60)	10	1.3 (0.1)	125	92	96 (19)	16	0.6 (0.1)	66	46	—	—	N/A	N/A
Liberty Point 2	—	—	—	inactive	inactive	—	—	—	inactive	inactive	3,428	88 (13)	40	1.3 (0.2)	73
Little Bear Beach	—	—	—	inactive	inactive	325	109 (27)	10	0.9 (0.1)	277	325	217 (89)	2	1.7 (0.2)	72
Moore Haven	—	—	—	inactive	inactive	—	—	—	inactive	inactive	110	86 (10)	36	1.3 (0.1)	107
Moore Haven East 4	—	—	—	inactive	inactive	—	—	—	inactive	inactive	2402	85 (9)	46	1.5 (0.1)	163
Rock Island	34	171 (36)	46	1.7 (0.2)	25	—	—	—	inactive	inactive	—	—	—	inactive	inactive

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

during 2011, 2012, and 2013, respectively). Throw-trap sampling captured 37,392 individual animals; mosquito fish (*Gambusia holbrooki*), least killifish (*Heterandria formosa*), grass shrimp (*Palaemonetes* spp.), bluefin killifish (*Lucania goodei*), and sailfin molly (*Poecilia latipinna*) were the five most abundant prey species captured. Without regard to size, density of fish, crayfish, and shrimp pooled for the entire littoral zone varied significantly among years ($F_{2, 168}$ = 8.04, P < 0.001) and was greater in 2011 (165 ± 21 prey/m^2) than in 2012 (87 ± 7 prey/m^2); F_1 = 14.85, P < 0.001) and 2013 (104 ± 9 prey/m^2); F_1 = 7.32, P = 0.008). Prey density did not differ significantly between 2012 and 2013 (F_1 = 0.60, P = 0.44; Table 1). There was no significant correlation between prey density and water depth at the throw-trap sites (r = 0.17, P = 0.44). The estimated percent of foraging habitat that became available to wading birds was 34% (2011), 36% (2012), and 77% (2013).

Models

Fledging success of all wading bird species combined was affected significantly by prey density, foraging habitat availability, and their interaction (Prey: $F_{1, 13}$ = 26.30, P < 0.001; HSM: $F_{1, 13}$ = 18.76, P < 0.001; Prey*HSM: $F_{1, 13}$ = 14.41, P = 0.002; Table 2). The interaction indicated that predicted fledging success at the colony level increased with increasing prey density and foraging habitat availability (Fig. 3). However, fledging success increased more rapidly with increases in prey density when foraging habitat availability was low than when foraging habitat availability was high. A visual plot showed a threshold in prey density at 147 prey/m^2, above which the availability of foraging habitat had a weaker effect on fledging success than when prey density was low. In 2011, three of the six colonies we monitored had prey densities over 147 prey/m^2, whereas in 2012 no colonies had prey densities that high and in 2013 only one colony had prey densities over 147 prey/m^2 (Table 1).

Total productivity of all wading bird species combined was affected significantly by prey density, foraging habitat availability, and their interaction (Prey: $F_{1, 13}$ = 24.27, P < 0.001; HSM: $F_{1, 13}$ = 27.40, P < 0.001; Prey*HSM: $F_{1, 13}$ = 12.95, P = 0.003; Table 2). The interaction was positive, indicating that predicted total productivity increased with increasing prey density and foraging habitat (Fig. 4). Similar to our fledging success model, total productivity increased more rapidly with increases in prey density when foraging habitat availability was low than when availability was high. However, in this case the prey density threshold was 189 prey/m^2.

DISCUSSION

At both the colony and wetland scale, our models indicated that high prey density and high foraging habitat availability contributed to successful wading bird nesting. As predicted by the threshold hypothesis (Nager *et al.* 1997), the effect of prey density on wading bird nesting was greater when foraging habitat availability was low. Moreover, at extremely high prey

Table 2. Parameter estimates (β), *F*-values, *P*-values, and 95% confidence limits (LCL = lower confidence limit, UCL = upper confidence limit) for factors included in wading bird nesting models for Lake Okeechobee, Florida, USA. HSM = Habitat Suitability Model.

Model	Parameter	β	*F*-value	*P*-value	LCL	UCL
Fledging success	Intercept	-2.343			-3.77	-0.92
	Prey	0.026	26.30	< 0.001	0.02	0.04
	HSM	0.044	18.76	< 0.001	0.02	0.07
	Prey*HSM	-0.000	14.41	0.002	-0.001	-0.000
Total productivity	Intercept	-21246			-31381	-11110
	Prey	177.50	24.27	< 0.001	99.67	255.33
	HSM	378.82	27.40	< 0.001	222.47	535.18
	Prey*HSM	-2.004	12.95	0.003	-3.21	-0.80

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

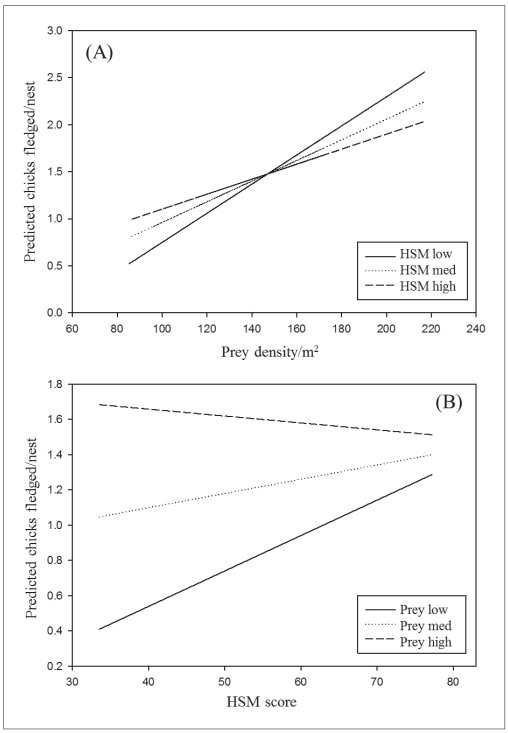


Figure 3. The relationship between predicted wading bird fledging success and (A) prey density at low, medium and high levels of foraging habitat availability (Habitat Suitability Model [HSM]) and (B) foraging habitat availability (HSM Score) at low, medium and high levels of prey density (Prey).

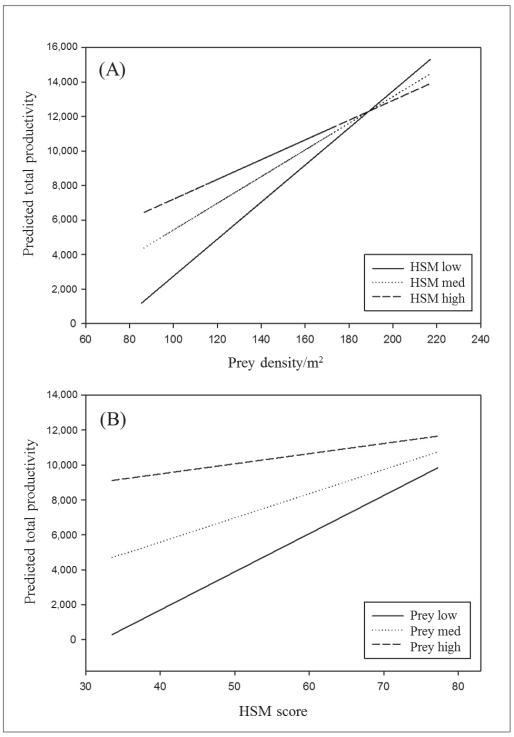


Figure 4. The relationship between predicted wading bird total productivity and (A) prey density at low, medium and high levels of foraging habitat availability (Habitat Suitability Model [HSM]) and (B) foraging habitat availability (HSM Score) at low, medium and high levels of prey density (Prey).

densities, the predicted responses were actually greater when foraging habitat availability was low, suggesting that high concentrations of prey within patches can compensate in some years for low foraging habitat availability. However, the prey density saturation threshold was greater at the wetland level, suggesting that foraging habitat availability had a stronger influence on a wading bird's decision to nest (i.e., number of nests). For example, fledging success was similar in 2011 and 2013, yet nest numbers were lower in 2011 than in 2013. In 2011, an extremely dry year, elevated prey density likely counteracted the spatial mismatch of reduced foraging habitat availability to increase fledging success. In 2013, the average water year, it is probable that despite reduced prey density, nest numbers were influenced by the extended water-level recession which allowed more of the littoral zone to become available for foraging.

Differences in the prey density threshold reveal that different mechanisms influence particular components of reproduction. Number of nests is a reflection of how adult birds perceive the environment and its potential to support nesting activities. While sufficient amounts of prey are necessary to fledge young, the chance of encountering a foraging patch increases with increasing habitat availability, likely explaining the greater influence of habitat availability on total productivity. Alternately, the greater wetland-level prey density saturation threshold could be based on the strength of the cues needed by adults to initiate nesting. A stronger cue (i.e., more prey) is more likely to be a reliable indicator of an environment's ability to sustain reproduction.

Similar to our study, evidence of prey abundance thresholds is common in other studies of avian reproduction (Nager *et al.*

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

1997; Tremblay *et al.* 2003; Crawford *et al.* 2006). Moreover, in a review of 201 experiments from 82 independent studies, Ruffino *et al.* (2014) concluded that food supplementation had no detectable effect on avian reproduction when environmental levels of food abundance were high. But unlike these studies which note that the amount of prey biomass did not equal a proportional increase in breeding success, our models related nesting success increases to increasing prey densities above the saturation threshold. Perhaps the relationship between food availability and breeding response is nonlinear resulting in a switch in limiting factors at high food availability (Frederick and Spalding 1994; Sherley *et al.* 2013; Ruffino *et al.* 2014).

A match between periods of peak energy demand and the timing and proximity of accessible prey is necessary for high recruitment of a predator species; however, the saturation threshold of prey abundance can alleviate or amplify the effects of a match or mismatch event (Tremblay *et al.* 2003; Durant *et al.* 2007). This study indicated that high prey density can compensate for a mismatch with foraging habitat availability and contribute to successful wading bird nesting. This information has important implications for water managers who set hydrologic regimes. If the hydrologic patterns that lead to high foraging habitat availability and high prey density are different, then there will be several hydrologic regimes that could meet the energetic needs of wading birds. Such flexibility is critical when water management options must balance the hydrologic needs of people against those of the surrounding ecosystems.

ACKNOWLEDGMENTS

We thank our field research crews and fellow researchers that assisted in collection of field data: R. Botta, L. Dancer, M. Dillon, B. Farmer, J. Michaud, K. Norris, and E. Plazarte. C. Callaghan and J. Klassen provided invaluable comments on earlier drafts of this manuscript. South Florida Water Management District staff generously provided data on the locations and characteristics of foraging flocks for the HSM validation. Funding for this research was provided by the U.S. Army Engineer Research and Development Center and Florida Atlantic University. All applicable ethical guidelines for the use of birds in research have been followed, including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research" (Fair *et al.* 2010). Research techniques were approved by the Florida Atlantic University Institutional Animal Care and Use Committee (Protocol A10-30) and conducted under U.S. Fish and Wildlife Service Research Permit 23354 and Florida Fish and Wildlife Conservation Commission Scientific Research Permits S-11-02, S-12-01, and S-13-01.

LITERATURE CITED

Ardia, D. R., M. F. Wasson and D. W. Winkler. 2006. Individual quality and food availability determine yolk and egg mass and egg composition in Tree Swallows *Tachycineta bicolor*. Journal of Avian Biology 37: 252-259.

Arengo, F. and G. A. Baldassarre. 1999. Resource variability and conservation of American flamingos in coastal wetlands of Yucatán, Mexico. Journal of Wildlife Management 63: 1201-1212.

Aumen, N. G. 1995. The history of human impacts, lake management, and limnological research on Lake Okeechobee, Florida (USA). Archiv fr Hydrobiologie (Special Issues, Advances in Limnology) 45: 1-16.

Bancroft, G. T., D. E. Gawlik and K. Rutchey. 2002. Distribution of wading birds relative to vegetation and water depths in the northern Everglades of Florida, USA. Waterbirds 25: 265-277.

Bancroft, G. T., A. M. Strong, R. J. Sawicki, W. Hoffman and S. D. Jewell. 1994. Relationships among wading bird foraging patterns, colony locations, and hydrology in the Everglades. Pages 615-657 *in* Everglades: The Ecosystem and its Restoration (S. M. Davis and J. C. Ogden, Eds.). St. Lucie Press, Delray Beach, Florida.

Botta, R. A. 2014. A habitat suitability model for wading birds in a large subtropical lake: linking hydrologic fluctuations and nesting. M.S. Thesis, Florida Atlantic University, Boca Raton.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Canadian Journal of Zoology 68: 203-220.

Burke, C. M. and W. A. Montevecchi. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. Journal of Zoology 278: 354-361.

Canepuccia, A. D., J. P. Isacch, D. A. Gagliardini, A. H. Escalante and O. O. Iribarne. 2007. Waterbird response to changes in habitat area and diversity generated by rainfall in a SW Atlantic coastal lagoon. Waterbirds 30: 541-553.

Causarano, F. and C. Battisti. 2009. Effect of seasonal water level decrease on a sensitive bird assemblage in a Mediterranean wetland. Rendiconti Lincei 20: 211-218.

Chick, J. H., C. R. Ruetz, III and J. C. Trexler. 2004. Spatial scale and abundance patterns of large fish

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

communities in freshwater marshes of the Florida Everglades. Wetlands 24: 652-664.

Crawford, R. J. M., P. J. Barham, L. G. Underhill, L. J. Shannon, J. C. Coetzee, B. M. Dyer, T. M. Leshoro and L. Upfold. 2006. The influence of food availability on breeding success of African Penguins *Spheniscus demersus* at Robben Island, South Africa. Biological Conservation 132: 119-125.

Crozier, G. E. and D. E. Gawlik. 2003. Wading bird nesting effort as an index to wetland ecosystem integrity. Waterbirds 26: 303-324.

Cui, B., Q. Yang, Z. Yang and K. Zhang. 2009. Evaluating the ecological performance of wetland restoration in the Yellow River Delta, China. Ecological Engineering 35: 1090-1103.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology 26: 249-293.

David, P. G. 1994. Wading bird nesting at Lake Okeechobee, Florida: an historic perspective. Colonial Waterbirds 17: 69-77.

Drent, R. H. 2006. The timing of birds' breeding seasons: the Perrins hypothesis revisited especially for migrants. Ardea 94: 305-322.

Dunn, P. O., D. W. Winkler, L. A. Whittingham, S. J. Hannon and R. J. Robertson. 2011. A test of the mismatch hypothesis: how is timing of reproduction related to food abundance in an aerial insectivore? Ecology 92: 450-461.

Durant, J. M., D. O. Hjermann, G. Ottersen and N. C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate Research 33: 271-283.

Durant, J. M., D. O. Hjermann, T. Anker-Nilssen, G. Beaugrand, A. Mysterud, N. Pettorelli and N. C. Stenseth. 2005. Timing and abundance as key mechanisms affecting trophic interaction in variable environments. Ecology Letters 8: 952-958.

Environmental Systems Research Institute (ESRI). 2011. ArcGIS v. 10.1. ESRI, Redlands, California.

Fair, J., E. Paul and J. Jones (Eds.). 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington, D.C.

Frederick, P. C. and M. W. Collopy. 1989. Nesting success of five species of wading birds (Ciconiiformes) in relation to water conditions in the Florida Everglades. Auk 106: 625-634.

Frederick, P. C. and M. G. Spalding. 1994. Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem. Pages 659-691 *in* Everglades: The Ecosystem and its Restoration (S. M. Davis and J. C. Ogden, Eds.). St. Lucie Press, Delray Beach, Florida.

Frederick, P. C. and J. C. Ogden. 2001. Pulsed breeding of long-legged wading birds and the importance of infrequent severe drought conditions in the Florida Everglades. Wetlands 21: 484-491.

Frederick, P. and J. C. Ogden. 2003. Monitoring wetland ecosystems using avian populations: seventy years of surveys in the Everglades. Pages 321-350 *in* Monitoring Ecosystems: Interdisciplinary Approaches for Evaluating Ecoregional Initiatives (D. E. Busch and J. C. Trexler, Eds.). Island Press, Washington, D.C.

Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72: 329-346.

González, J. A. 1997. Seasonal variation in the foraging ecology of the Wood Stork in the southern Llanos of Venezuela. Condor 99: 671-680.

Gotceitas, V., V. Puvanendran, L. L. Leader and J. A. Brown. 1996. An experimental investigation of the 'match/mismatch' hypothesis using larval Atlantic cod. Marine Ecology Progress Series 130: 29-37.

Havens, K. E. and D. E. Gawlik. 2005. Lake Okeechobee conceptual ecological model. Wetlands 25: 908-925.

Jin, K. R., J. H. Hamrick and T. Tisdale. 2000. Application of three-dimensional hydrodynamic model for Lake Okeechobee. Journal of Hydraulic Engineering 126: 758-771.

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.

Kingsford, R. T. 2000. Protecting rivers in arid regions or pumping them dry? Hydrobiologia 427: 1-11.

Kushlan, J. A. 1981. Sampling characteristics of enclosure fish traps. Transactions of the American Fisheries Society 110: 557-662.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, U.K.

Lantz, S. M., D. E. Gawlik and M. I. Cook. 2010. The effects of water depth and submerged aquatic vegetation on the selection of foraging habitat and foraging success of wading birds. Condor 112: 460-469.

Loftus, W. F. and A. M. Eklund. 1994. Long-term dynamics of an Everglades small-fish assemblage. Pages 461-483 *in* Everglades: The Ecosystem and its Restoration (S. M. Davis and J. C. Ogden, Eds.). St. Lucie Press, Delray Beach, Florida.

Lorenz, J. J. 2014. The relationship between water level, prey availability and reproductive success in Roseate Spoonbills foraging in a seasonally-flooded wetland while nesting in Florida Bay. Wetlands 34: S201-S211.

Ma, Z., Y. Cai, B. Li and J. Chen. 2010. Managing wetland habitats for waterbirds: an international perspective. Wetlands 30: 15-27.

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18: 453-487.

Monaghan, P. and R. G. Nager. 1997. Why don't birds lay more eggs? Trends in Ecology & Evolution 12: 270-274.

Nager, R. G., C. Ruegger and A. J. Van Noordwijk. 1997. Nutrient or energy limitation on egg formation: a feeding experiment in Great Tits. Journal of Animal Ecology 66: 495-507.

National Oceanic and Atmospheric Administration (NOAA). 2007. LiDAR dataset. Department of Commerce, NOAA, Washington, D.C. https://coast.noaa.gov/dataviewer/#/lidar/sear

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

ch/-9033328.002742128,3081711.669373451,-8967286.410303736,3151116.491056391/details/528, accessed 10 March 2009.

Newton, I. 1998. Population limitation in birds. Academic Press, London, U.K.

Perrins, C. M. 1996. Eggs, egg formation and the timing of breeding. Ibis 138: 2-15.

Perrins, C. M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

Ruffino, L., P. Salo, E. Koivisto, P. B. Banks and E. Korpimäki. 2014. Reproductive responses of birds to experimental food supplementation: a meta-analysis. Frontiers in Zoology 11: 80-93.

SAS Institute, Inc. 2013. SAS statistical software v. 9.4. SAS Institute, Inc., Cary, North Carolina.

Sherley, R. B., L. G. Underhill, B. J. Barham, P. J. Barham, J. C. Coetzee, R. J. M. Crawford, B. M. Dyer, T. M. Leshoror and L. Upfold. 2013. Influence of local and regional prey availability on breeding performance of African Penguins *Spheniscus demersus*. Marine Ecology Progress Series 473: 291-301.

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, nest success and productivity, and causes of nest failure among wading birds (Ciconiiformes) at Lake Okeechobee, Florida (1989-1992). Archiv fr Hydrobiologie (Special Issues, Advances in Limnology) 45: 287-316.

South Florida Water Management District. 2013. DBHYDRO database environmental monitoring. South Florida Water Management District, West Palm Beach, Florida. http://www.sfwmd.gov/dbhydro/, accessed 1 November 2013.

Thomas, D. W., J. Blondel, P. Perret, M. M. Lambrechts and J. R. Speakman. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291: 2598-2600.

Tremblay, I., D. W. Thomas, M. M. Lambrechts, J. Blondel and P. Perret. 2003. Variation in Blue Tit breeding performance across gradients in habitat richness. Ecology 84: 3033-3043.

Trexler, J. C., W. F. Loftus, F. Jordan, J. H. Chick, K. L. Kandl, T. C. McElroy and O. L. Bass, Jr. 2002. Ecological scale and its implications for freshwater fishes in the Florida Everglades. Pages 153-181 *in* The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: an Ecosystem Sourcebook (J. W. Porter and K. G. Porter, Eds.). CRC Press, Boca Raton, Florida.

Ward, S. and D. M. Bryant. 2006. Barn Swallows *Hirundo rustica* form eggs mainly from current food intake. Journal of Avian Biology 37: 179-189.

Zedler, J. B. and S. Kercher. 2005. Wetland resources: status, trends, ecosystem services, and restorability. Annual Review of Environmental Resources 30: 39-74.

Downloaded From: https://complete.bioone.org/journals/Waterbirds on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use