DIET AND NESTING HABITAT OF WADING BIRDS IN A SHALLOW,

EUTROPHIC LAKE

By

Jenna C. May

A Thesis Submitted to the Faculty of

Charles E. Schmidt College of Science

In Partial Fulfillment of the Requirements for the Degree of

Master of Science

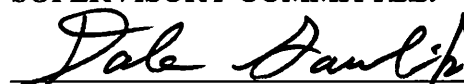Florida Atlantic University

Boca Raton, FL

August 2018

Diet and Nesting Habitat of Wading Birds in a Shallow, Eutrophic Lake

by

Jenna C. May

This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Dale E. Gawlik, Department of Biological Sciences, and has been approved by the members of her supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

SUPERVISORY COMMITTEE:

_____
Dale E. Gawlik, Ph, D.
Thesis Advisor

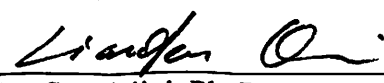_____
Kindy Anderson, Ph. D.

_____
Colin Hughes, Ph. D

_____
Dale E. Gawlik, Ph. D.
Director, Environmental Sciences Program

_____
Ata Saradejini, Ph. D.
Dean, Charles E. Schmidt College of Science

_____
Khaled Sobhan, Ph. D.
Interim Dean, Graduate College

July 24, 2018
Date

iii

ACKNOWLEDGEMENTS

ABSTRACT

Author: Jenna May

Title: Diet and Nesting Habitat of Wading Birds in a Shallow, Eutrophic
                Lake

Institution: Florida Atlantic University

Thesis Advisor: Dr. Dale E. Gawlik

Degree: Master of Science

Year: 2018

Avian reproductive success varies depending on environmental conditions, degree of predation, location, and food availability. I examined food availability and nesting habitat of wading birds in South Florida. Evaluating prey availability and prey used by two small heron species demonstrated the ability for small herons to maintain consistent diets through fluctuating environmental conditions, within and across different wetland types. Small herons may be able to cope with environmental changes by altering foraging locations and strategies. Regarding nesting habitat, man-made sites may provide habitat comparable to natural sites, at least in the short-term. The nest's position can influence its susceptibility to increased temperatures and predators, particularly for. Climatic conditions such as rainfall can also impact nesting success by altering foraging conditions and fish behavior. Understanding the effects of hydrologic regimes on biota can have practical applications since ecosystems around the world share similar problems

with competing demands for resources, and there is a concern for how use can affect the

quality of the resource.

DIET AND NESTING HABITAT OF WADING BIRDS IN A SHALLOW,

EUTROPHIC LAKE

LIST OF TABLES

LIST OF FIGURES

xiii

CHAPTER I. INTRODUCTION

Avian reproductive success varies depending on environmental conditions, degree
of predation, location, and food availability (Martin 1995). Traditionally, food
availability has been identified as a primary factor in driving reproductive processes, and
it has been shown to influence population sizes and the likelihood of additional
reproduction (Martin 1987, Simons and Martin 1990, Filliater et al. 1994). The nestling
stage, in particular, is a crucial period that requires high energy demands from the parent
(Martin 1987). Parents will increase the frequency of foraging trips to meet the food
demands of their nestlings, demonstrating the importance for adequate reserves to be
within close proximity (Bryan et al. 1995). When unable to find food resources nearby,
parents must travel farther distances and spend more time away from the nest, which can
affect incubation duration, hatch success, and nestling survival (Martin 1987). Limiting
resources have a particularly strong influence on long-lived species, which may abandon
their nest to avoid the even greater costs of losing eggs or chicks (Frederick and Collopy
1988, Yorio and Boersma 1994, Crawford and Dyer 1995, Kazama et al. 2015).
In food-rich habitats, territoriality or competition for quality nesting space has been
shown to constrain breeding densities (Krebs 1971, Huhta et al. 1997, Chamberlain and
Fuller 1999). High quality nesting sites provide structural support for nests and
protection against predators and adverse weather conditions (Minias 2014). Many bird

species build their nests in locations that are inaccessible or use vegetation to conceal nest contents to minimize the probability of nest depredation (Holway 1991, Filliater et al. 1994, Colombelli-négrel and Kleindorfer 2009). Some also exploit vegetation structure and adjust nest position to achieve favorable microclimatic conditions at nest sites. For example, hatching success of black kites was greater in nests with preferred nest orientations and, the authors attributed this to improved microclimate at the nest (Viñuela and Sunyer 1992). Nest position can be important for reducing the brunt of rainfall and prevailing winds and also meeting the metabolic demands of chicks and adults (Burton 2006).

Wading birds nesting at Lake Okeechobee, Florida, USA provide a unique opportunity for investigating some of the factors that influence nest numbers and success, specifically food availability and nesting habitat. The number of wading birds nesting at Lake Okeechobee is strongly correlated with water levels that are (1) able to slowly recede with a dry season, thereby concentrating prey and (2) low enough to promote willow (*Salix carolinensis*) regeneration for several consecutive years (Chastant et al. 2017).

Most of the understanding of prey availability and food habits of wading birds in South Florida has stemmed from studies conducted in the Florida Everglades, an oligotrophic wetland just south of Lake Okeechobee. Studies have shown small herons in this region do not exhibit taxonomic selectivity but have selectively fed on larger fish compared to what is available in the wetland (Boyle et al. 2012, Klassen et al. 2016). Exploiting high density pools and selecting larger fish are effective strategies for

achieving the energy necessary to sustain through the breeding season. In both the Everglades and Lake Okeechobee, it has been suggested, high concentrations of prey may be able to support nesting when the availability of foraging habitat is low, and high availability of foraging habitat can compensate for moderate prey concentrations (Klassen et al. 2016, Chastant and Gawlik 2018). However, it is not known whether diet composition and consistency of small herons are constant across ecosystems that may differ in the processes driving environmental variation.

Nesting substrate, specifically willow (*Salix caroliniana*), has also been linked to wading bird reproduction at Lake Okeechobee (Chastant et al. 2017). Previous studies have indicated willow is an important nesting substrate for wading birds at the lake (David 1994, Johnson et al. 2007, Havens and Gawlik 2005). However, increased willow regeneration provides a delayed benefit to wading birds since it can take up to two years for willow to become suitable nesting substrate. Therefore, the importance of nest substrate characteristics, within a nesting season, is not known.

This thesis examines the food habits and characteristics of nesting sites of wading birds at Lake Okeechobee. Chapter 2 compares the diet of two small heron species, Tricolored Heron and Snowy Egret, within and across regions and varying environmental conditions. Chapter 3 evaluates the influence of colony structure and nest position on nesting success. Chapter 4 provides a synopsis of this research and views findings through a management lens to highlight potential applications in highly productive, intensely managed systems.

CHAPTER II. CONSISTENCY IN SMALL HERON DIETS IN DYNAMIC

ENVIRONMENTS

INTRODUCTION

Food limitation is one of the primary factors influencing the reproduction of

species (Martin 1987, ODonoghue et al. 1997, Levin et al. 1997, French et al. 2007). It

has been shown to influence population sizes, the timing of reproduction, and the

likelihood of additional reproduction (Simons and Martin 1990, Filliater et al. 1994,

Ostfeld and Keesing 2000). In dynamic landscapes around the world, species must cope

with low or highly variable food availability, and it is expected that they would adopt

strategies that would increase foraging efficiency to maintain reproductive processes

(Schmidt and Ostfeld 2003, Durant et al. 2007, Kingsford et al. 2010).

Wading birds are a top-predator in wetland ecosystems, and they must contend

with food resources that vary both spatially and temporally (Kushlan 1976, Poizat and

Crivelli 1997, Kingsford 1999, Alho 2008, Taylor and Schultz 2008). Much research has

been conducted on wading bird diet, foraging, and nesting in the Everglades, an

oligotrophic and food-limited region. Wading birds in this ecosystem rely on the

availability of prey to initiate and sustain reproduction, and their breeding season

coincides with a seasonal pulse of resources (Frederick and Collopy 1989, Frederick and

Loftus 1993, Frederick and Spalding 1994). Receding water levels increase prey

availability by creating high density pools, which increases foraging success and net

energy intake (Gawlik 2002), and patterns of continuous recession during the dry season have been related to large numbers of nesting birds (Beerens et al. 2011). However, a sudden increase in water depth during the dry season, also referred to as a "reversal", can allow prey to disburse and reduce prey densities. A reduction in prey density can decrease foraging efficiency and result in nest failure (Cook and Herring 2007).

In addition to exploiting ephemeral, high density pools, small herons select larger fish, on average, than what is available in the environment (Boyle et al. 2012, Klassen et al. 2016). Larger fish can represent a higher quality prey resource if energetic content is high and handling time and foraging costs are low (Krebs and Stephens 1986). In past years, large fish (>1.9 cm) density within pools has accounted for 70% of the variation in the number of small heron nests in the Everglades (Klassen et al. 2016). The combination of exploiting high density pools and selecting larger fish provides an effective way to gain the energy reserves necessary to sustain through the breeding season.

Situated just north of the Everglades is Lake Okeechobee, a shallow, eutrophic lake. Large numbers of wading birds use this area for foraging and nesting during the dry season, much like the Everglades. The littoral zone, on the west side of the lake, is comprised of marsh habitat and provides highly productive foraging grounds for breeding wading birds (Havens and Gawlik 2005). The littoral marsh also experiences pulses of resources driven by the wet and dry season, with water recession creating high-density concentrations of prey available for wading birds during the breeding season (Chastant and Gawlik 2018).

Preliminary data has been collected on prey availability at Lake Okeechobee, and findings show prey biomass per m^{-1} at Lake Okeechobee to be substantially higher than in the Everglades (Chastant, Florida Atlantic University, unpublished data). Moreover, nesting success at Lake Okeechobee was not limited by reversals that decreased the extent of foraging habitat when prey concentrations were high (Chastant et al. 2018). These findings are contrary to what is typically observed in the Everglades and suggest mechanisms that increase foraging options for wading birds may be different in a eutrophic lake than a nearby oligotrophic wetland, and that prey abundance may be substantial enough that sudden changes in hydrological conditions do not impact foraging as strongly.

Some information exists on wading bird diet and foraging at Lake Okeechobee (Smith 1995, Smith 1997), however, relatively little is known about the relationship between prey availability and wading bird diet in a eutrophic lake. Evaluating wading bird diets in these two systems can provide a better understanding of the underlying mechanisms that make food resources available and wading bird responses to different environmental conditions and hydrologic regimes. This study aims to compare and contrast prey availability and small heron diet in eutrophic lakes and oligotrophic wetlands and across varying environmental conditions. The objectives of the study were to 1) evaluate species composition and size of prey (fish) available at Lake Okeechobee and compare findings to what has been previously documented in the Everglades, 2) compare prey composition in small heron diet with that available in the Lake Okeechobee littoral zone, and 3) compare prey consumed by small herons at Lake Okeechobee and the Everglades.

METHODS

Study Area

Lake Okeechobee is a large, shallow lake at the center of the Greater Everglades Ecosystem in Florida (26°56'28" N, 80°51'32" W). Its area is approximately 1700km^2 with a 400km^2 littoral zone, comprised of emergent marsh that supports wading bird foraging and nesting activity. An earthen dike surrounds much of the lake, separating extensive emergent marsh, submerged vegetation, and open water habitats inside the dike from diverse natural (isolated-pocket, riparian, and lacustrine wetlands) and artificial (agricultural fields and various sloughs, ditches, retention areas, and canals) wetland habitats outside of the dike. The period of this study (dry seasons of 2015-2016) included a year of moderate water levels followed by a year of high water levels. In 2015, lake stage was just over 15.0 ft at the beginning of the breeding season and receded to 13.5 ft by mid-April. Increased rainfall in early May increased lake levels to 13.8 ft, initiating the end of the nesting season. In 2016, lake stage started and remained high (>15.0 ft.) until the end of March, with a steady recession to just below 14 ft. in mid-May.

Prey Availability and Small Heron Diet at Lake Okeechobee

Prey Availability

To assess prey available to wading birds at Lake Okeechobee during the 2015 and 2016 breeding season, small fishes were sampled at random sites throughout the littoral zone (Figure 2.1). Protocol was consistent with past studies examining prey availability at the Lake (Chastant and Gawlik 2018). Random sampling points were generated in ArcGIS 9.3 (ESRI Inc., Redlands, CA, USA) using lake stage data accessed via the South

Florida Water Management District DBHYDRO database, and bathymetry data, provided

by the U.S. Geological Survey. The sampling site was determined by selecting the

closest suitable wading bird foraging habitat to the random points. Suitable foraging

habitat was defined as an area with sparse to moderate vegetation, less than 30 cm in

water depth (Lantz et al. 2011, Botson et al. 2016, Klassen et al. 2016).

When suitable habitat was detected, a random bearing and distance was used to

select the sampling location within the suitable area. A 1-m^2 throw trap and seine was

used to capture prey items (Kushlan 1981). Before sampling, all vegetation within the

trap was cleared to prevent the seine from being obstructed. Once the vegetation was

cleared, a seine was passed through the water within the trap, and prey items were

collected. The trap was considered cleared when five consecutive sweeps returned no

faunal species. All captured items were transferred to a jar containing a rapid euthanizing

agent, MS-222 (Western Chemical, Ferndale, WA). A second trap was deployed

following the same methods, using a random bearing and distance that was at least 5

meters away from the first throw trap location. In the lab, samples were poured through a

0.6µm mesh net, rinsed with water, placed in Prefer color fixative, and then later

transferred to a 70% ethanol solution for further preservation. Prey samples were sorted

and identified to species. Additionally, each item was weighed to 0.01 g and standard

and total length was measured to the nearest millimeter.

Small Heron Diet

During the 2015 and 2016 breeding season, food bolus samples were collected

from Snowy Egret and Tricolored Heron nestlings. Heron capture, handling, and bolus

collection techniques were identical to previous studies examining wading bird diet (Klassen et al. 2016) and adhered to protocols approved by the Institutional Animal Care and Use Committee at Florida Atlantic University (permit number A12-03) and the Florida Fish and Wildlife Conservation Commission (permit number LSSC-12-00012). Sampling occurred along randomly placed transects in two wading bird colonies at Lake Okeechobee. Samples were collected every 2-13 days from chicks aged 1-3 weeks.

Nestlings often regurgitate in the presence of humans, readily providing a food bolus whose contents can usually be identified. When a targeted nestling did not voluntarily regurgitate, the trachea was gently massaged to encourage regurgitation. Once the nestling regurgitated, the sample was placed in a plastic bag on ice, and a dead bait fish was left in the nest to compensate for the loss of bolus contents. In the lab, bolus contents were rinsed, preserved and sorted using the same methods as the throw trap samples, described above.

Contrasting Prey Availability at Lake Okeechobee and the Everglades

Data collected from 2011-2013 at Lake Okeechobee and the Everglades were analyzed to compare prey available in the two wetland types. Methods for site selection, prey collection, and prey sorting at Lake Okeechobee during the 2011-2013 study were identical to the methods used during 2015-2016 (Chastant and Gawlik 2018).

The Everglades sampling design was similar to Lake Okeechobee (See Cochran 1977, Philippi 2003, Klassen et al. 2016 for details), and methods for site selection, prey collection, and prey sorting in the Everglades during 2011-2013 were identical to the methods used at Lake Okeechobee.

Comparing Prey Selected at Lake Okeechobee and the Everglades

Bolus data from the Everglades was provided by a companion study that occurred concurrently with 2015-2016 bolus collection at Lake Okeechobee. The bird species and methods for collecting and sorting samples were identical to the methods employed at Lake Okeechobee. Figure 2.2 shows the locations of colonies selected for bolus sampling.

Statistical Analysis

Multivariate analyses were conducted in PRIMER v7 (Clarke and Warwick 2001, Clarke and Gorley 2015) to determine prey composition patterns within bird species across years and regions. Bolus data collected from the same nest on the same date was combined since nestlings represent diet from the same parent. To prevent over-representation of rare species, prey species that accounted for <1% of total prey composition biomass for each bird species were eliminated from the analysis. This created 1 sample point representative of the prey communities consumed by an individual of each wading bird species for each nest and date. For comparisons of species from both locations, biomasses were calculated for each prey type in each bolus before calculating a Bray-Curtis dissimilarity index. A pair-wise similarity matrix was used to assess bolus-bolus similarity and was visually inspected with non-metric multi-dimensional scaling plots (NMDS). ANOSIM tests (non-parametric permutation procedure that randomly re-identifies boluses) were employed to determine multivariate differences in prey composition between years and locations. If no statistical differences occurred ($P >$ 0.05), all bolus data was combined across sampling years for each bird species to increase

sample size and improve the ability to detect statistical differences. When statistical differences ($P < 0.05$) were detected, a similarity percentage analysis (SIMPER) was used to determine which prey types were most responsible for the dissimilarity between locations. It is important to note, when interpreting results from ANOSIM tests, the R statistic itself is a useful comparative measure of the degree of separation of sites, and its value is at least as important as its statistical significance. It is possible for R to be significantly different from zero yet inconsequentially small, if there are many samples from each site (Clark and Warwick 2001). Mean standard length of all fish in each bolus was calculated and the means were compared directly with ANOVA (R Core Development Team 2009).

The same multivariate analysis described above was used to detect differences in prey communities available in the landscape and prey composition in boluses. Only throw trap samples that coincided spatially and temporally with bolus sampling were included. Throw trap samples that occurred within 30 km of each colony were used as that is the maximum foraging distance for small herons (Strong et al. 1997).

To evaluate differences in sizes of fish available in the landscape and consumed by small herons, I performed a one-way analysis of variance (ANOVA) on ranks using R 3.3.2 (R Core Team 2017) to compare the mean length of prey items within boluses and the mean length of fish available in the landscape as determined by throw trap samples.

RESULTS

Prey Availability and Small Heron Diet at Lake Okeechobee

During the 2015 and 2016 breeding season, a total of 80 throw traps (22 traps in 2015 from 13 sites, 58 traps in 2016 from 33 sites) were used to characterize the fish available within the littoral zone (Figure 2.3). Additionally, a total of 31 boluses from Tricolored Heron nestlings (3 in 2015 and 28 in 2016) and 70 boluses from Snowy Egret nestlings (28 in 2015 and 42 in 2016) were collected at Lake Okeechobee.

Prey Availability

Mean fish length in throw traps was 1.87 ± 0.54 cm and did not differ between years ($F_{1, 44} = 2.54$, $P = 0.12$). Additionally, there was not a significant difference in species composition between years ($R^2 = 0.16$, $P = 0.99$). Mosquitofish (*Gambusia holbrooki*), flagfish (*Jordanella floridae*), and least killifish (*Heterandria formosa*) comprised >50% of fish biomass (Table 2.1).

Small Heron Diet

For Tricolored Herons, mean fish length in boluses was 2.22 ± 0.49 (SD) cm and did not differ between years ($F_{1, 29} = 0.7$, $P = 0.40$) (Figure 2.4). There was also no difference between prey composition between years ($R^2 = 0.13$, $P = 0.44$). For Snowy Egrets, mean fish length in boluses was 2.14 ± 0.88 (SD) cm and did not differ between years ($F_{1, 68} = 2.04$, $P = 0.16$) (Figure 2.4). Prey composition was statistically different between years, but the difference is negligible ($R^2 = 0.12$, $P < 0.05$), as indicated by the low R^2 value. Mean fish length in boluses from Tricolored Heron and Snowy Egret did

not differ ($F_{1,\,99} = 1.42$, $P = 0.24$), and prey composition was statistically similar ($R^2 = 0.03$, $P = 0.67$) (Figure 2.5). The fish species contributing the most to biomass, in decreasing importance, were mosquitofish, sailfin mollies (*Poecilia latipinna*), and least killifish. Mosquitofish contributing 61% and 57% of the total biomass for Tricolored Herons and Snowy Egrets, respectively (Table 2.1).

Prey Availability and Small Heron Diet

Fish present in boluses of small herons were, on average, 0.31 cm larger than those captured in throw traps ($F_{1,\,145} = 7.37$, $P < 0.05$) (Figure 2.4 and Figure 2.6). Approximately 65% of prey biomass within small heron boluses were fish <1.9cm standard length and, similarly, 70% of fish available in the landscape were <1.9cm standard length. The prey composition in boluses from Tricolored Herons and Snowy Egrets was statistically different than the fish community available in the landscape; however, the difference was negligible ($R^2 = 0.22$, $P < 0.05$) as indicated by the low R^2 value (Figure 2.5). Similar species were found in boluses and throw traps; however, boluses contained a notably larger proportion of mosquitofish (Table 2.1).

Contrasting Prey Availability at Lake Okeechobee and the Everglades

Data collected from 2011-2013 at Lake Okeechobee and the Everglades were analyzed to compare prey availability. At Lake Okeechobee, 173 sites were sampled (66 in 2011, 62 in 2012, and 45 in 2013). In the Everglades, 272 sites were sampled (156 in 2012, 57 in 2012, and 59 in 2013).

At Lake Okeechobee, average prey densities (individuals/m^{-1}) were 108, 66, and 72 for 2011, 2012, and 2013, respectively (Figure 2.7). Prey biomass (g/m^{-1}) was 9.8,

9.1, and 9.8 for 2011, 2012, and 2013, respectively (Figure 2.8). Mean fish length in throw traps at Lake Okeechobee was statistically different between years (1.5 ± 0.3 in 2011, 1.6 ± 0.2 in 2012, 1.7 ± 0.3 in 2013; $F_{2,170} = 9.6$, $P < 0.05$); however, mean wading bird prey length was below the preferred prey length (1.9 cm; Klassen et al. 2016) in all years. Species composition of fish did not differ between years ($R^2 = 0.013$, $P = 0.15$).

In the Everglades, average prey densities were 32, 14, and 14 for 2011, 2012, and 2013, respectively. Prey biomass was 5.6, 2.2, and 2.9 for 2011, 2012, and 2013, respectively. Mean fish length in throw traps in the Everglades was statistically different between years ($F_{2,269} = 6.05$, $P < 0.05$; 1.6 ± 0.4 in 2011, 1.8 ± 0.4 in 2012, 1.8 ± 0.3 in 2013). As with the Lake, mean prey length was below the preferred prey length (1.9 cm) of wading birds (Klassen et al. 2016) in all years. Species composition of fish did not differ between years ($R^2 = 0.07$, $P = 0.06$).

Average biomass was higher at Lake Okeechobee compared to the Everglades during 2011, 2012, and 2013 ($F_{1,217} = 20.79$, $P < 0.05$; $F_{1,117} = 61.88$, $P < 0.05$; and $F_{1,100} = 42.99$, $P < 0.05$, respectively). Average prey densities were notably higher at Lake Okeechobee compared to Everglades in 2011, 2012, and 2013 ($F_{1,217} = 67.72$, $P < 0.05$; $F_{1,117} = 94.42$, $P < 0.05$; $F_{1,100} = 70.5$, $P < 0.05$). Mean length of fish differed between regions in 2011 and 2012 ($F_{1,220} = 5.14$, $P < 0.05$ and $F_{1,117} = 8.83$, $P < 0.05$, respectively), but not in 2013 ($F_{1,102} = 2.88$, $P < 0.09$). Fish were 0.1 - 0.2 cm smaller, on average, at Lake Okeechobee compared to the Everglades, (Figure 2.9). Species composition between regions also was statistically different; however, the difference was negligible ($R^2 = 0.07$, $P < 0.05$), as indicated by the low R^2 (Figure 2.10). Mosquitofish and bluefin killifish (*Lucania goodie*) comprised >50% of fish biomass in the Everglades,

and mosquitofish and least killifish comprised >50% of fish biomass at Lake Okeechobee (Table 2.1).

Comparing Small Heron Diet at Lake Okeechobee and the Everglades

During the 2015 and 2016 nesting season in the Everglades, a total of 104 boluses from Tricolored Heron nestlings (52 in 2015 and 52 in 2016) and 55 boluses from Snowy Egret nestlings (36 in 2015 and 19 in 2016) were collected.

For Tricolored Herons, average fish length in boluses was 3.2 ± 1.1 cm and did not differ between years ($F_{1,\,102} = 0.88$, $P = 0.35$). There was also no difference between prey composition between years ($R^2 = 0.02$, $P = 0.12$). Mean fish length in Everglades boluses was, on average, 0.57 cm larger than fish in boluses from Lake Okeechobee ($F_{1,133} = 32.55$, $P < 0.05$) (Figure 2.11). Species composition was statistically different between the two regions; however, the differences were negligible ($R^2 = 0.10$, $P < 0.05$), as indicated by the low R^2 value (Figure 2.12 and 2.13). Differences emerged from the high contribution of biomass from mosquitofish in boluses at Lake Okeechobee (Table 2.1).

For Snowy Egrets, fish length in boluses was 2.7 ± 0.9 cm and did not differ between years ($F_{1,\,52} = 1.32$, $P = 0.26$). There was no difference between prey composition between years ($R^2 = 0.03$, $P = 0.24$). Mean fish length in Everglades boluses was, on average, 0.96 cm larger than fish in boluses from Lake Okeechobee ($F_{1,122} = 16.66$, $P < 0.05$) (Figure 2.11). Species composition was statistically different between the two regions; however, the differences were negligible ($R^2 = 0.10$, $P < 0.05$) as indicated by the low R^2 value (Figure 2.12 and 2.13). One notable difference in diets

between the two ecosystems was the high contribution of mosquitofish biomass in boluses at Lake Okeechobee (Table 2.1).

Prey size differed between bird species in the Everglades ($F_{1, 156} = 10.34$, $P < 0.05$). Prey composition was statistically similar between bird species ($R^2 = 0.03$, $P = 0.16$). The species contributing the most to biomass were mosquitofish sailfin mollies, golden topminnow (*Fundulus chrysotus*), and flagfish (Table 2.1).

DISCUSSION

The consistency in prey composition in boluses between years suggests that small heron diet was surprisingly consistent across a range of hydrologic conditions (moderate and high water conditions in this study and extreme low water conditions in Smith (1995) and Smith (1997)). Furthermore, small heron diet in this study were similar to results reported in Smith (1997), where diet was consistently comprised mostly of mosquitofish, sailfin mollies >2 cm standard length. Small herons in the Everglades, as in the Lake, exhibited a consistent diet across hydrologic conditions (average and extremely dry), selecting for similar prey sizes and species. (Strong et al. 1997, Boyle et al. 2012, Klassen et al. 2016).

The lake region provides a high diversity of foraging opportunities within a relatively limited area of birds nesting on the lake. The close proximity of such an array of choices may generally preclude the need for extensive travel to find food. Smith (1995) showed Tricolored Herons will utilize upper littoral zone transitional habitats when water levels are high. Small herons can also cope with high water levels by adjusting foraging techniques, which include utilizing aerial foraging methods and using

dense surface mats of submerged and floating vegetation for support to access prey in deep water areas (Smith 1995, Smith et al. 1995).

The consistency in small heron diet across years may also suggest prey composition at available foraging sites, on and off-lake, are fairly insensitive to hydrologic conditions. Changing hydrologic trends and habitat conditions may require nesting birds to forage in shallower off-lake habitats (Zaffke 1984, David 1994, Smith 1995, Smith et al. 1995), but they maintain a consistent diet. There is diverse assortment of natural (riparian and lacustrine wetlands) and artificial (agricultural lands) wetland habitats just outside of the dike. During a drought, agricultural field ditches and canals, in particular, may provide unnaturally persistent source of flooding habitat when many natural habitats have dried (Smith 1995). During high lake stages, habitats such as the pocket and slough wetlands interspersed with pasture land and the original Kissimmee River and Fisheating Creek floodplains, are considered important resources for wading birds that nest on or near the lake. Foraging surveys conducted during 2016 showed significantly lesser foraging flocks on the lake compared to previous years (Baranski 2017). Smith (1995) noted birds nesting at Clewiston Spit would primarily forage off-lake during high-water conditions, and Snowy Egrets frequently used off-lake agricultural habitats, primarily agricultural field ditches and canals. Foraging in off-lake sites may not require significantly extending travel distances as colonies monitored in my study were located less than 3 km from the dike.

The significant difference in prey density and biomass found at Lake Okeechobee compared to the Everglades suggest that mechanisms for creating high density pools may be more conducive to prey production and concentration at the lake. In the Everglades,

an important mechanism for creating high density pools of fish is the development of local depressions, which provide deeper water refugia for fish during the dry season (Kushlan and Kushlan 1980, Hoffman et al. 1994, Loftus and Eklund 1994). The combination of local scale abiotic factors such as recession rate and microtopography can produce high quality foraging patches (Botson et al. 2016). This mechanism is critically important in oligotrophic systems, where prey standing stocks are generally low (Turner et al. 1999). At Lake Okeechobee, the nearshore and pelagic zones and a rim canal, intersected by airboat trails and access points into the lakes interior, provide marsh fish with refugia when water levels recede. Deep water refugia allow marsh fish to escape entrapment and allow prey stocks to recharge without interruption. Additionally, legacy phosphorus coupled with agriculture and urban sources contribute to the generation of high-nutrient conditions that facilitate high secondary productivity (Havens and Gawlik 2005). At low and intermediate levels, phosphorus enrichment is known to increase fish density and biomass (Rader and Richardson 1994, Turner et al. 1999, Trexler and Goss 2008, Hagerthey et al. 2014). The combination of nutrient conditions and the accessibility to deeper water refugia likely contribute to the high production and remarkably high prey densities.

Of special note is the relatively high abundance of mosquitofish available and consumed at Lake Okeechobee (Smith 1997, Chastant et al. 2018). During 2015 and 2016, mosquitofish were the most frequently caught species at the lake, and they contributed 10% of the total biomass. Moreover, they comprised more than half of the fish consumed at Lake Okeechobee. Mosquitofish were also a dominant species in small heron diet in the Everglades, however, mosquitofish biomass comprised a relatively

lower proportion of total fish consumed. The lower abundance of mosquitofish in the Everglades may be attributed to the increasing abundance of non-native fish (Brandt et al. 2014). In the Everglades, non-native cichlids have been thought to have impacts on species composition, and anecdotal evidence suggests there has been a decline in mosquitofish in the Everglades (Harrison et al. 2013).

The consistency in small heron diet between years and across South Florida wetlands show additional support for the idea that tricolored herons and snowy egrets are diet specialists, actively seeking out larger marsh fish regardless of foraging conditions and nesting location. There has been support for similar selection for fishes in other diet studies in Puerto Rico (Miranda and Collazo 1997) and Brazil (Martinez 2010). Factors supporting diet consistency under different environmental conditions include the ability to adjust foraging techniques and access a diverse array foraging grounds that are highly productive. Heron species in Greece have also exhibited varying foraging tactics in response to varying habitat and prey characteristics (Dimalexis et al. 1997).

It should be noted that results from this study may not be applicable to all small herons in South Florida. Little blue herons (*Egretta caerulea*) have a similar body size and visual foraging strategy; however, they tend to have more of a generalist diet and select considerably more grass shrimp compared to tricolored herons and snowy egrets (Smith 1997, Klassen et al. 2016). Because only a small number of little blue herons nested at Lake Okeechobee during 2015-2016, limited data on diet is available. More research is needed across the South Florida regions to determine the consistency of their diet.

Evaluating resource selection within and across habitats provides a better understanding of how species around the world respond to different environmental conditions. Wetlands including the French Camargue, Brazilian Pantanal, and Australian Murray-Darling Basin are characterized by dynamic landscapes that have hydrological patterns that vary both temporally and spatially. Understanding resource selection of species and the critical mechanisms that control resource availability is essential for understanding natural ecosystem function and managing populations of apex predators.
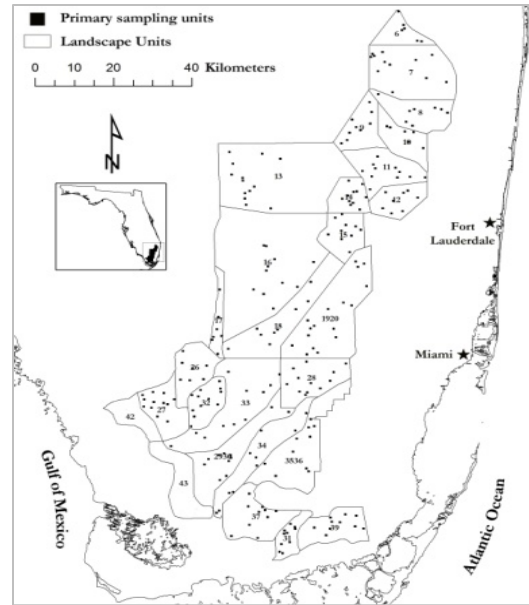
Figure 2.1. Map of throw trap sites at Lake Okeechobee (left) and Everglades (right) from 2011-2013.
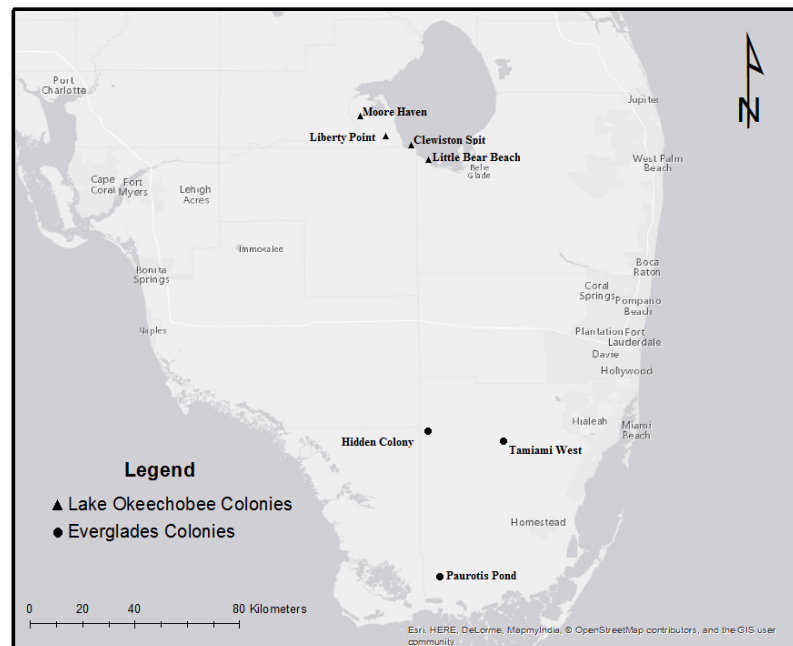
Figure 2.2. Map of colony locations for bolus collection at Lake Okeechobee and the Everglades.
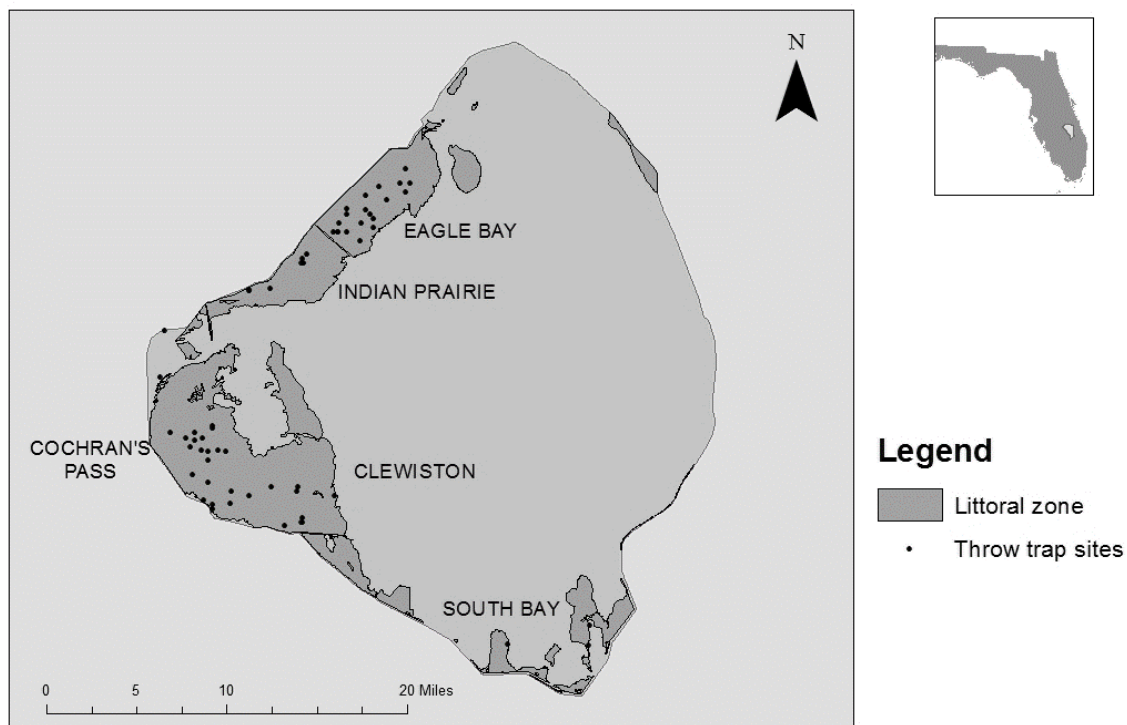
Figure 2.3. Map of throw trap sites at Lake Okeechobee (2015-2016).
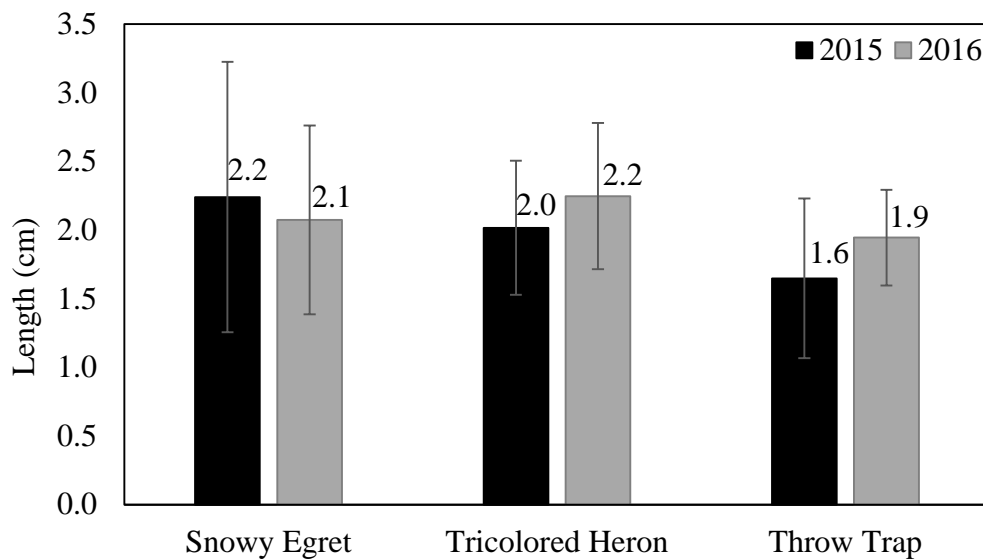
Figure 2.4. Mean fish length in Tricolored Heron and Snowy Egret boluses and throw traps at Lake Okeechobee from 2015 – 2016.

22
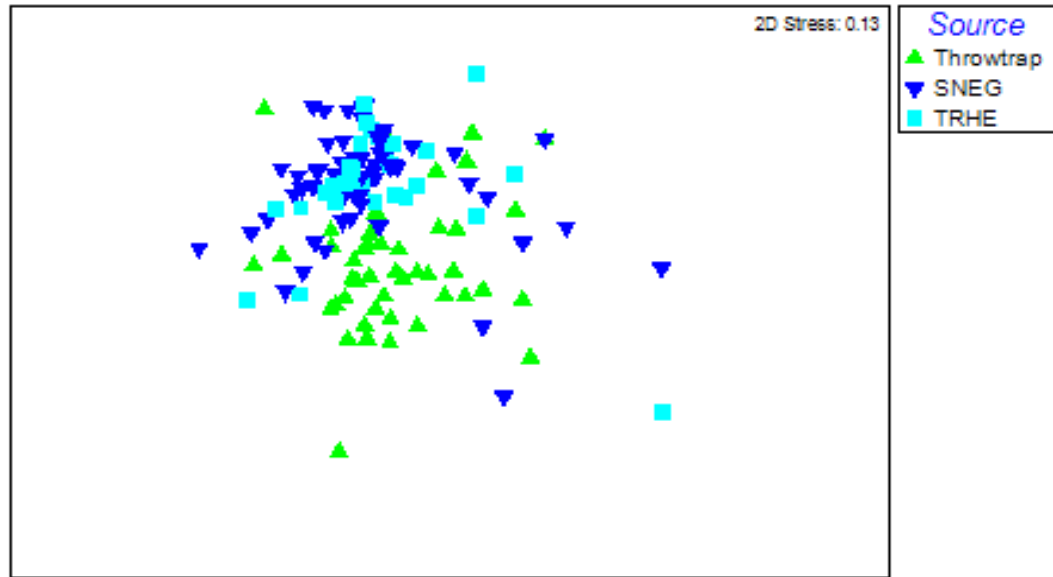
Figure 2.5. NMDS plots of Lake Okeechobee bolus and throw trap (2015-2016).
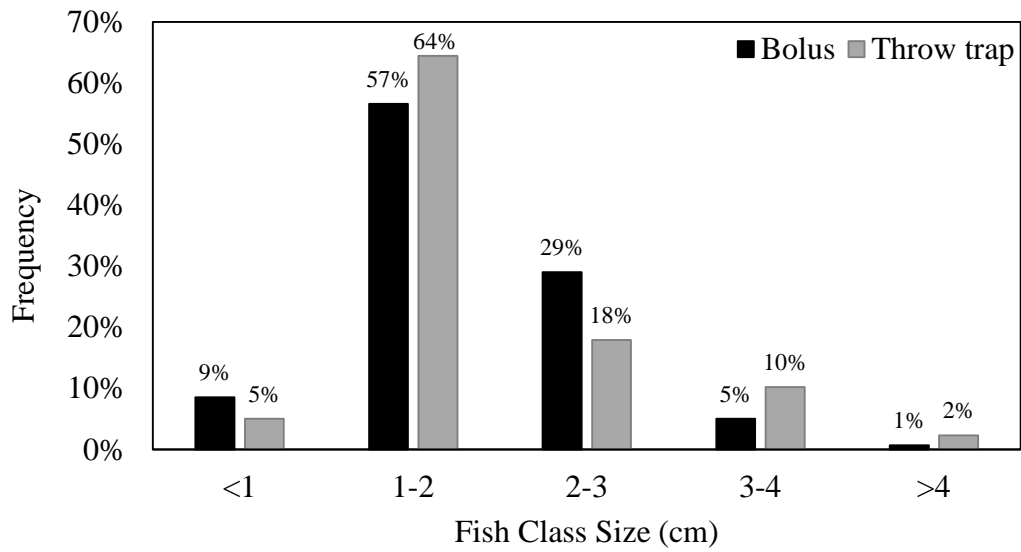
Figure 2.6. Distribution of fish sizes within small heron boluses and in throw trap samples, Lake Okeechobee, Florida USA, 2015-2016.
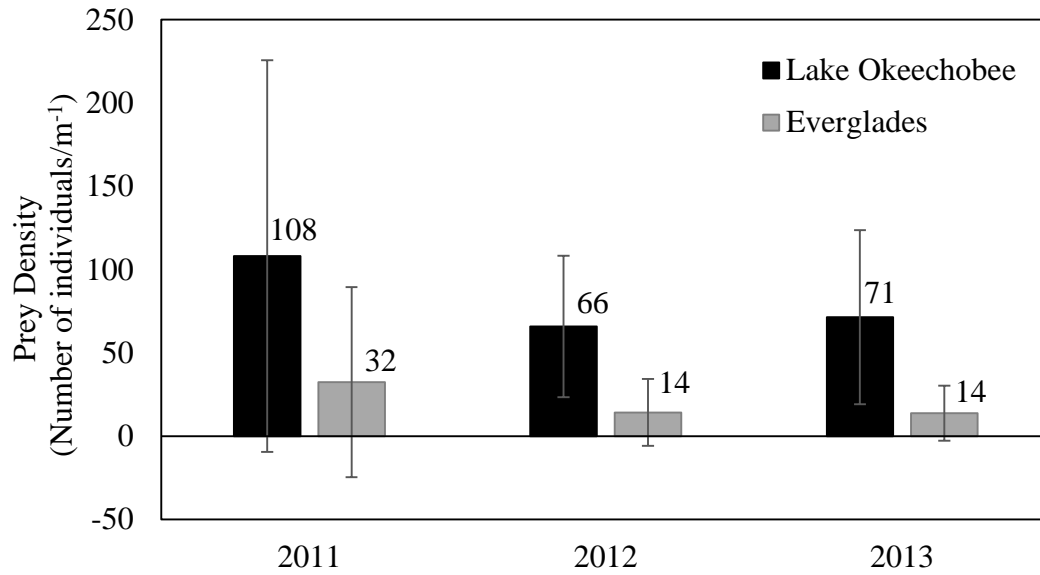
Figure 2.7. Mean fish density at Lake Okeechobee and the Everglades from 2011-2013.
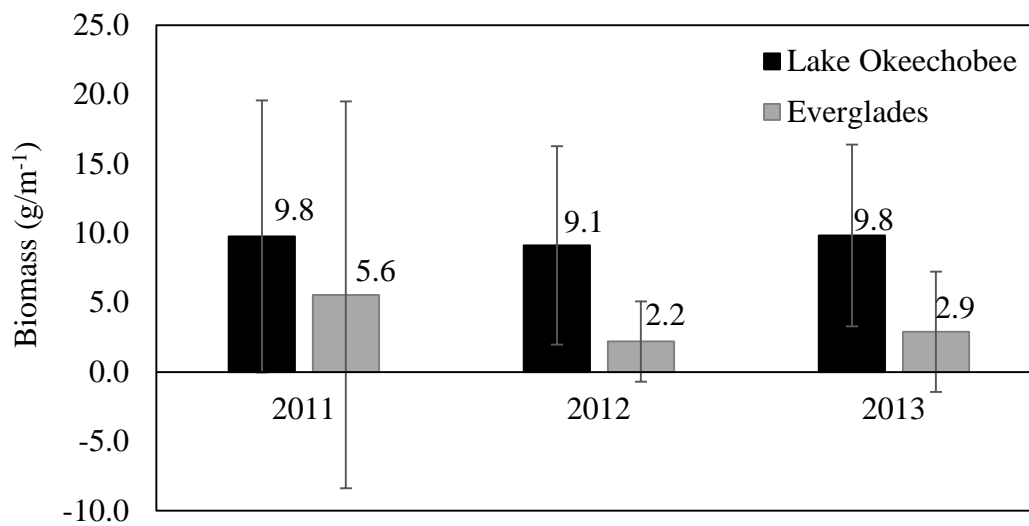
Figure 2.8. Mean fish biomass at Lake Okeechobee and the Everglades from 2011-2013.
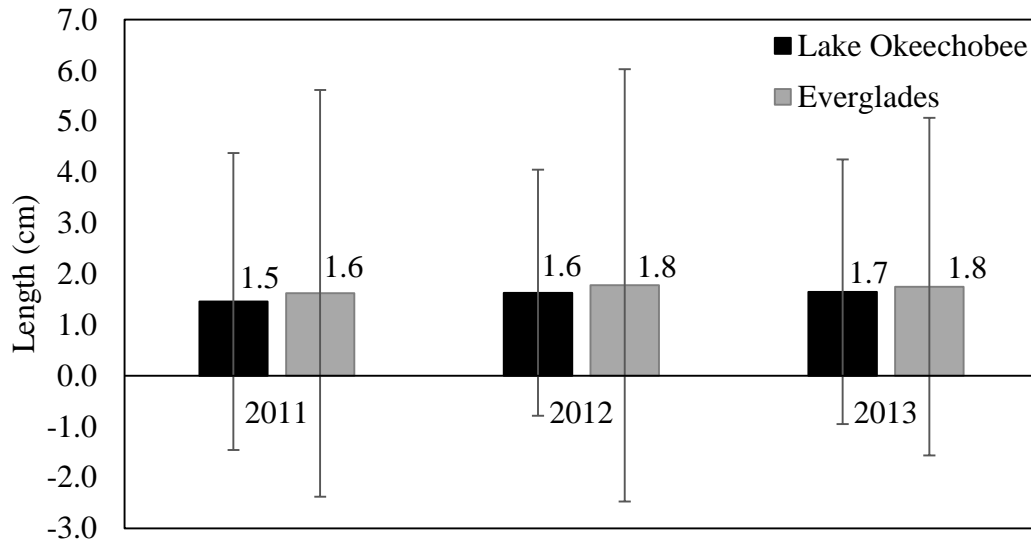
Figure 2.9. Mean standard length of fish in throw traps at Lake Okeechobee and the Everglades from 2011-2013.
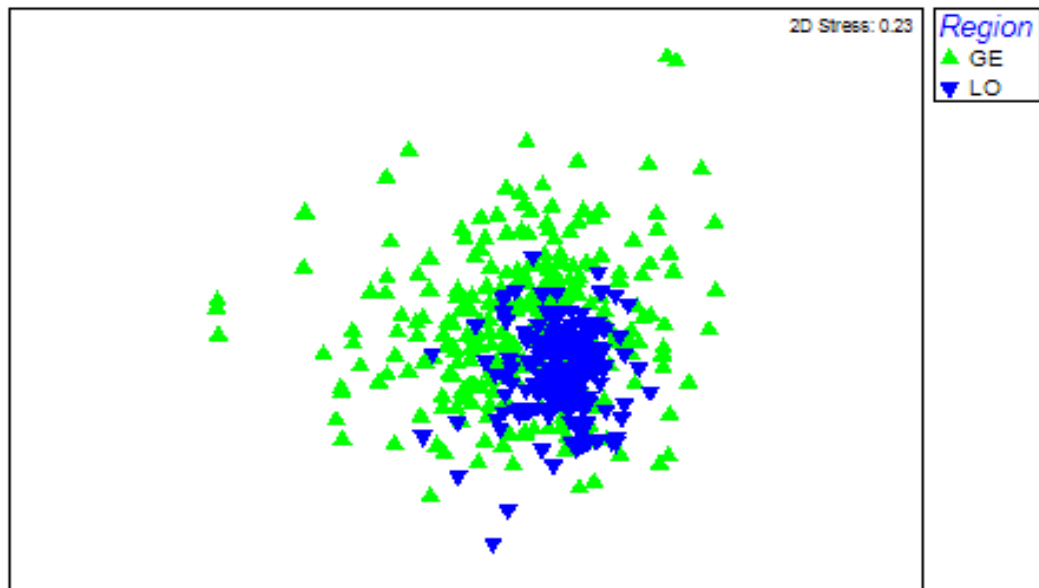
Figure 2.10. NMDS plot of throw traps at Lake Okeechobee and the Everglades from 2011-2013.
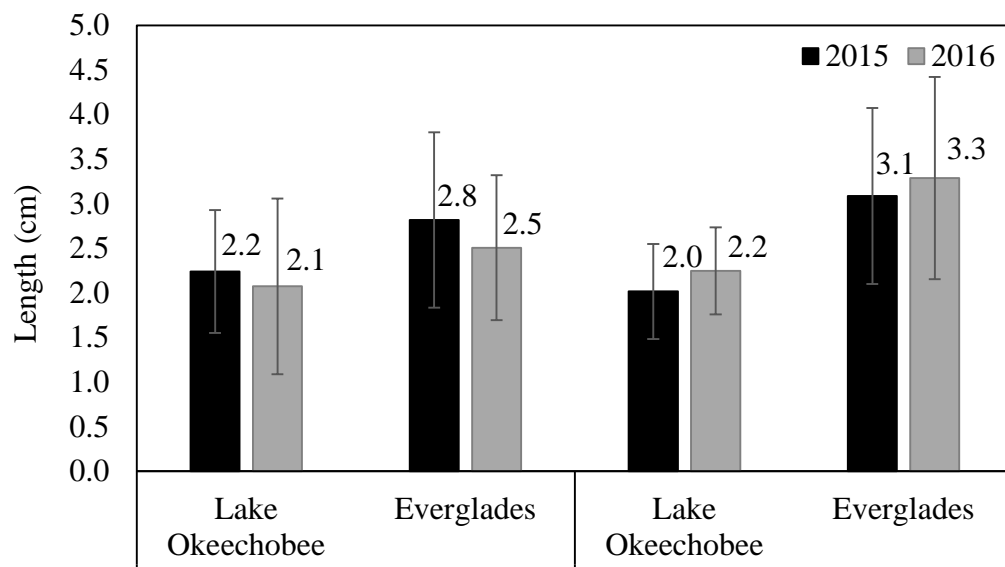
Figure 2.11. Mean fish length in Tricolored Heron and Snowy Egret boluses at Lake Okeechobee and the Everglades from 2015-2016.
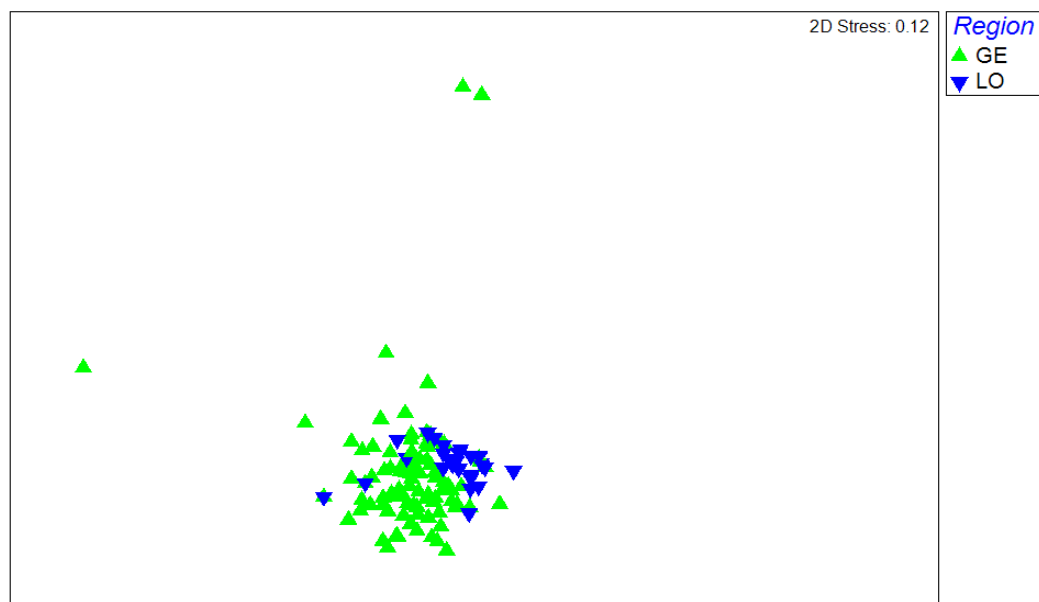
Figure 2.12. NMDS plots of Tricolored Heron bolus at Lake Okeechobee and the Everglades from 2015-2016.
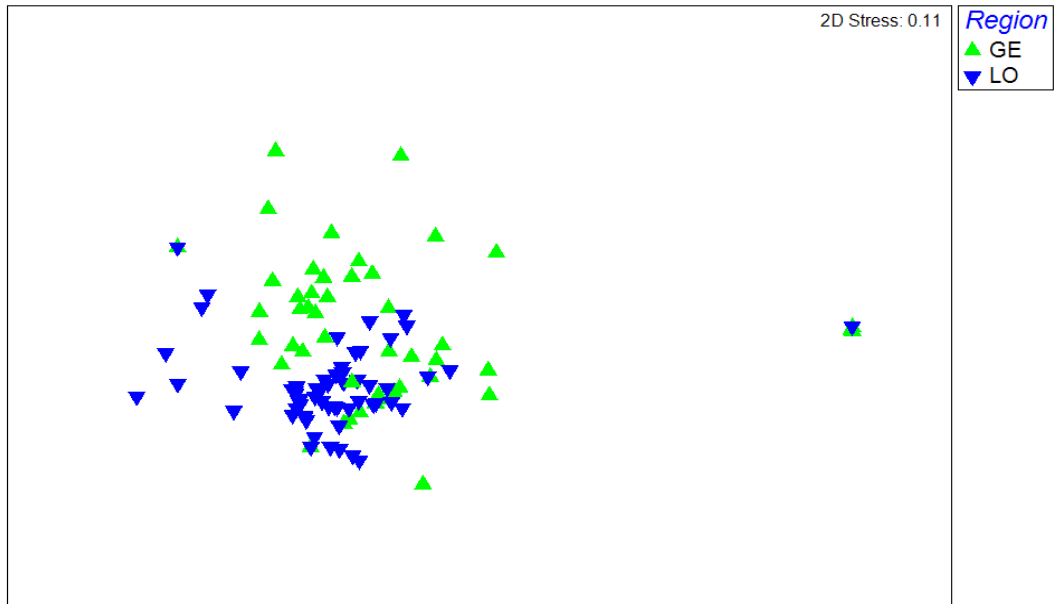
Figure 2.13. NMDS plots of Snowy Egret bolus at Lake Okeechobee and Everglades from 2015-2016.

Table 2.1. Percent biomass (% frequency) of prey species within small heron boluses and throw trap samples at Lake Okeechobee and the Everglade. The number of boluses collected from each bird species or throw trap to determine prey composition is also presented (n).

	Percent biomass (% frequency)						
	Tricolored Heron		**Snowy Egret**		**Throw Traps**		
Prey Species	**Lake Okeechobee (2015-2016)**	**Everglades (2015-2016)**	**Lake Okeechobee (2015-2016)**	**Everglades (2015-2016)**	**Lake Okeechobee (2015-2016)**	**Lake Okeechobee (2011-2013)**	**Everglades (2011-2013)**
Atherinopsidae							
Brook silverside (*Labidesthes sicculus*)		<1 (<1)	1 (<1)				
Cyprinodontidae							
Flagfish	<1 (<1)	16 (17)	<1 (<1)	10 (11)	32 (17)	11 (3)	15(8)
Fundulidae							
Golden topminnow	2 (<1)	14 (11)	1 (1)	14 (5)	7 (5)	3 (1)	8 (4)
Marsh killifish		8 (6)		6 (4)		<1 (<1)	13 (4)
Bluefin killifish	2 (1)	2 (8)	1 (1)	3 (10)	5 (9)	8 (9)	12 (18)
Poeciliidae							
Sailfin molly	19 (<7)	20 (12)	14 (4)	32 (11)	14 (12)	16 (6)	6 (3)
Least killifish (*Heterandria formosa*)	6 (12)	<1 (2)	7 (20)	1 (7)	5 (24)	20 (40)	6 (23)
Mosquitofish	61 (76)	10 (32)	57 (67)	22 (47)	10 (22)	38 (42)	22 (33)
Pike killifish (*Belonesox belizanus*)		6 (2)		4 (<1)			
Rainwater killifish (*Lucania parva*)		<1 (<1)		<1 (<1)			
Centrachidae							
Bluespotted sunfish (*Enneacanthus gloriosus*)		<1 (<1)			<1 (<1)	<1 (<1)	1 (<1)
Redear sunfish (*Lepomis microlphus*)			<1 (<1)		5 (<1)	1 (<1)	4 (<1)
Spotted sunfish (*Lepomis punctatus*)			2 (<1)		6 (<1)	<1 (<1)	3 (<1)

Dollar sunfish (*Lepomis marginatus*)			2 (<1)		2 (<1)		2 (<1)
Largemouth bass (*Micropterus salmoides*)	4 (<1)	3 (<1)	1 (<1)		1 (<1)	1 (<1)	
Warmouth (*Lepomis gulosus*)			1 (<1)		<1 (<1)	<1 (<1)	
Bluegill (*Lepomis macrochirus*)					<1 (<1)	1 (<1)	<1 (<1)
Unknown sunfish (*Lepomis spp*)	<1 (<1)		4 (<1)		1 (1)	<1 (<1)	1 (<1)
Cichlidea							
Mayan cichlid (*Cichlasoma urophthalmus*)		2 (<1)	2 (<1)	4 (<1)			
African jewelfish (*Hemichromis bimaculatus*)	3 (<1)	15 (7)		2 (1)	3 (3)		<1 (<1)
Spotted tilapia (*Pelmatolapia mariae*)		2 (<1)	4 (2)		(<1) (<1)		
Blue tilapia (*Oreochromis aureus*)			(<1) (<1)		2 (3)		
Unknown fish	1 (1)		1 (<1)	<1 (<1)			
Sparidae							
Sheepshead minnow (*Archosargus probatocephalus*)			<1 (<1)				
Percidae							
Swamp darter (*Etheostoma fusiforme*)			1 (3)				
Elassomatidae							
Everglades pygmy sunfish (*Elassoma evergladei*)				<1 (2)			4 (4)
Iclaturidae							
Brown bullhead (*Ameiurus nebulosus*)					4 (1)	<1 (<1)	1 (<1)
n	31	104	70	55	80	173	272

CHAPTER III. THE EFFECTS OF COLONY STRUCTURE AND NEST POSITION

ON THE NESTING SUCCESS OF WADING BIRDS

INTRODUCTION

Nest site can influence fitness outcomes of adult and juvenile birds (Lack 1950, Chalfoun and Schmidt 2012). Hypotheses related to predator avoidance describe various strategies for increasing fitness by limiting accessibility to predators by nesting over standing water or in thorny or thick vegetation (Ricklefs 1969, Collias and Collias 1984, Frederick and Spalding 1994) or adjusting nest position (Piper and Catterall 2004, Tabib et al. 2015). Nest position can also influence exposure to potentially harmful abiotic factors, like wind and direct sunlight, and nests placed near the canopy edge can be more susceptible. High winds can blow nest contents out of trees and lead to nest failure (Torres et al. 2010), while direct sunlight can result in higher temperatures at nests compared to those that are shaded. Temperature can have a significant impact on energy and water budgets of both parents and developing young (Ricklefs and Hainsworth 1969, Dawson et al 2005). Young raised in warmer nest sites require less nest attentiveness by incubating females, allowing for increased provisioning rates by parents (Robertson 2009). However, nests exposed to elevated temperatures can experience egg dehydration or heat exhaustion of nestlings and result in reduced fitness (Grant 1982, Cunningham et al. 2013).

Nesting in colonies can also provide a suite of protective and social benefits. In large breeding colonies, the probability of predation may be reduced because of early detection of predators, effective deterrence of predators by group mobbing and defense, or predator swamping (Wittenberger and Hunt 1985).

Wading birds (Pelecaniformes and Ciconiiformes) implement a number of the nesting strategies described above. At Lake Okeechobee, wading birds will also nest in different colony types, "tree islands" and spoil islands. Tree islands are large, discrete stands of vegetation surrounded by water. Willow is frequently used and appears to be the preferred nesting substrate; however, species have also been observed nesting in cattail, common reed (*Phragmites spp*), and smaller shrubs. Willow is an attractive nesting substrate because it is capable of withstanding extended periods of inundation, which allows for standing water to persist through the nesting period, thereby restricting access to nests by potential predators (Frederick and Spalding 1994). Because the spatial extent of willow fluctuates with hydrologic patterns, and because of its high usage by wading birds, willow is thought to be a limiting factor in the distribution of colony sites (Frederick and Collopy 1989, Havens and Gawlik 2005).

Spoil islands that support some wading bird colonies at Lake Okeechobee were created from the deposition of dredged material during the development of canal networks. From 2006 to 2016, spoil island colonies supported an average of 20% of the nesting effort on Lake Okeechobee (Fern et al. 2014). Species occupying man-made structures (e.g. spoil islands or artificial nest boxes) have been well-documented, and, in some cases, nest survival is relatively high (Erwin 1980, Parnell et al. 1986, Olah et al. 2013, Selman and Davis 2015). However, the high level of disturbance associated with

spoil islands makes communities more susceptible to non-native plant recruitment, which can improve search efficiency of predators and lead to nest failure (Borgmann and Rodewald 2004).

In addition to the development of man-made habitat, the existing, natural habitat at Lake Okeechobee has also been extensively modified since the construction of the Herbert Hoover Dike in the 1940s. Past water management schedules allowed for relatively high water levels for extended periods of time, which reduced the number of nesting wading birds and affected vegetation, including reducing the spatial extent of important nesting substrate (Havens and Gawlik 2005). Between 1973 and 1990, there was a reported 40% decrease in the areal extent of willow (Richardson and Harris 1995). In 2008, regulatory agencies implemented the Lake Okeechobee Regulation schedule (LORS 2008), which aimed to lower lake levels while dike maintenance occurred and decrease the likelihood of highly-damaging discharges to the Caloosahatchee and St. Lucie estuaries (Zhang and Sharfstein 2012). Numbers of nesting wading birds responded positively to the implementation of the new lake schedule and, based on reproductive data collected from 2009-2016, nesting effort has increased since its implementation (Fig. 3; Trimble and Marban 1988; David 1994; Smith and Collopy 1995; RECOVER 2014). Despite an improvement in breeding numbers, the spatial extent of willow remains affected, and the consequences associated with wading birds utilizing less preferred nesting substrate and altered colony structure is unknown (Havens and Gawlik 2005).

In this study, I examined the influence of nest site on the nesting success of wading birds at Lake Okeechobee during the 2015 and 2016 nesting seasons. The

objective of this study was to evaluate the effects of colony structure and nest position on wading bird nesting success and fledgling production.

METHODS

Study Area

Lake Okeechobee is a large, shallow lake at the center of the Greater Everglades Ecosystem, Florida (26°56'28" N, 80°51'32" W). It measures approximately 1700km^2 with a 400km^2 littoral zone comprised of emergent marsh. The littoral zone in Lake Okeechobee is comprised of diverse flora, including spikerush (*Eleocharis cellulosa.*), sawgrass (*Cladium jamaicense.*), white waterlily (*Nymphaea odorata*), torpedo grass (*Panicum repens*), and bulrush (*Scirpus spp.*). Species of trees and shrubs include water primrose (*Ludwigia spp.*), willow, and pond apple (*Annonna glabra*).

Anthropogenic effects have influenced vegetation composition at the lake. The development of canals and berms created upland habitat that support Brazilian pepper (*Schinus terebinthefolis*) and elderberry (*Sambucus spp.*), and the input of excess nutrients has contributed to the proliferation of cattail (*Typha spp.*) (Havens and Gawlik 2005). Lastly, water management coupled with natural climatic variation has contributed to fluctuations in water levels, which have resulted in altered hydroperiods and subsequently affected species composition.

Lake Okeechobee hosts approximately 15% of the total wading bird nests in South Florida (Cook and Baranski 2017). Large concentrations of wading birds have been consistently documented nesting in the littoral zone of Lake Okeechobee since the 1940s, and earlier accounts, recorded by game wardens, date back to the early 1900's

(David 1994). Aerial surveys during 1957-1978 showed typically 4,700 nests per year

while, in more recent years, an average of approximately 4,300 nests per year were

estimated (Havens and Gawlik 2005; Essian et al. 2016).

Hydrologic Conditions

Hydrologic conditions during the 2015 nesting season (01 January – 30 June)

were slightly higher than the 10-year average at the beginning of the season, and

gradually receded with only a few minor interruptions by water ascension (reversals). In

2016, the nesting season was characterized by the highest water levels in 10 years, and

high rainfall early in the nesting season allowed lake stages to rise outside of the

regulation envelope. Apart from remarkably high-water levels, the 2016 nesting season

followed similar hydrological trends with regard to water recession and reversals.

Field Methods

Great Egret (*Ardea alba*), Snowy Egret (*Egretta thula*), and Tricolored Heron

(*Egretta tricolor*) nests were selected for monitoring since they were common in all

survey colonies. Four colonies were selected for nest surveys; two spoil island colonies

and two natural island colonies (Figure 3.1). Colonies were selected based on the number

of nests present and the constraint that colonies must be accessible by airboat. Larger

colonies were favored over smaller colonies to allow for a larger number of nests

sampled. Colony activity level and accessibility were assessed during monthly aerial

surveys. Active colonies were circled so that the colony location and physical

dimensions could be recorded using a GPS tracklog and ArcGIS.

To determine nest success, two survey transects were established in each selected colony. Entry points into each colony were determined by choosing a random point around the colony perimeter. Starting points for transects were established by selecting a random direction and distance (20-200 m) from the colony entry point. The first transect intersected the colony and extended 50 m along a randomly selected bearing, and a second transect was initiated 30 m away from the endpoint of the first transect. The second transect was situated parallel to the first transect, looping back to the colony entry point. Based on previous colony surveys, this transect scheme seems to produce the least amount of disturbance for nesting birds because the cone of disturbance around observers (~10m radius) does not surround a given nest for more than a few minutes.

Because spoil islands tended to be narrow, less than 30 m at many points, and the vegetation used for nesting was clumped, transect locations could not be completely randomized. Instead, locations of transects were opportunistically selected to ensure the largest possible sample size was obtained and several nest substrate types were covered. Using this modified approach, approximately 55-70% of nests on the spoil islands could be surveyed. Since the purpose of randomizing transect locations in natural colonies is to obtain a representative sample of the birds, and a high percentage of the nests sampled were present at each spoil island, this approach seemed justified. The purpose of the parallel transect design in natural colonies is to minimize the area disturbed around nests. Disturbance was minimized on spoil islands by traveling along unvegetated paths between transects.

Nests within 1 m of each transect were marked using surveyor's tape and monitored. Each colony was surveyed once every 7-14 days. Species, nest stage, and

35

nest fate were recorded at each nest. Eggs of the Snowy Egret and Tricolored Heron look

similar (Hammat 1981) and were thus identified as "small heron" until chicks hatched or

the nest was confidently identified by the presence of an adult. Nest fate was categorized

as either "successful" or "failed". A successful nest was defined as at least one chick

reaching a predefined age threshold, 15 days. After this age, nestlings are highly mobile

and can intermix with neighboring nestlings, making it difficult to confidently associate

them with a nest (Frederick et al. 1992).

To evaluate the structural differences of each nest site, seven nest characteristics

were measured. A telescoping pole was used to measure tree height and nest height, and

these measurements were used to calculate distance from nest to canopy edge and nest to

ground. Distance to canopy edge was considered the distance of the nest to the edge of

the canopy directly above the nest. A measuring tape was used to measure the diameter

at breast height (DBH) of the nesting tree, and the tree species was recorded. Because

wading birds also nested in herbaceous vegetation (i.e. cattail) that wouldn't allow for

DBH measurements, a nesting substrate category was developed. Criteria for each

category was based on substrate type (herbaceous, shrub, and tree) and DBH (Table A1).

Statistical Analysis

Mean nest height and distance to canopy was calculated for each species in each

year and the means were compared directly with ANOVA (R Core Development Team

2009). If there was no significant difference detected between years, data was pooled for

each species when testing for differences between colony types. If a significant

difference was detected, differences between colony types were analyzed separately for

each year. ANOVAs were used to compare environmental factors (i.e. climatic variables

and lake stage at the start of nesting season) between years. The start of the nesting season was determined from aerial surveys.

Nest survival probabilities and daily survival rates were estimated using the logistic-exposure method (Shaffer 2004). The logistic-exposure method allows for varying visitation intervals, makes no assumptions about when nest loss occurs, and allows for categorical parameters and random and fixed effects (Shaffer 2004, Rotella 2007). A modified maximum likelihood estimation model in the bbmle package, available in R (Bolker 2014), was used.

Daily survival rates (DSR) of nests were calculated by using coefficients from the model and inserting values in the following equation:

$$s(x) = \frac{e^{\beta 0 + \beta 1 x}}{1 + e^{\beta 0 + \beta 1 x}}$$

The probability of a nest surviving through the fledging period (θ) was calculated by raising the daily survival rate (s) to an exponent equal to the length of the fledging period for each species (t):

$$\theta = s^t$$

Fledging age was considered to be 15 days because this is typically the age at which chicks can move among nests, as stated above. Total nesting period was determined by adding fledging age and incubation period, the latter of which is 21 days for small herons and 25 days for Great Egrets (Kushlan and Bildstein 1992, Parsons and Master 2000, McCrimmon et al 2001).

Fledgling production was defined as the number of chicks reaching fledging age at each nest. Generalized linear mixed models were used and based on a Poisson distribution for counts. Because the eggs of small herons are indistinguishable, and for purposes of comparing DSR at varying nest stages, data for Tricolored Heron and Snowy Egret nests were combined for the analysis and are hereinafter referred to as "small herons".

An information-theoretic approach was used to investigate competing models of factors predicting DSR and fledgling production (Table 1), and the Akaike's information criterion was used for model selection (Burnham and Anderson 2002, Akaike 1973). The relative importance of covariates representing ecological hypotheses was assessed by comparing Akaike information criterion values for small sample sizes (AICc). Model-averaged parameter estimates were used to estimate DSR during the median nesting period, and the probability of survival during that period was estimated following Shaffer (2004). Predictor and response variables are summarized in Table A2.

Separate models were run for each species (Great Egret, Snowy Egret, and Tricolored Heron) and nest stage (incubation and nestling periods) because different variables may be acting at different time periods and contribute to variation in survival (Frederick and Collopy 1989). Models were also run with both nest stages combined to ensure that variables identified as important during each stage were also identified important overall.

RESULTS

Environmental Conditions

Nest initiations for each species in colonies monitored began in March each year, therefore March 1 was considered the start of the nesting season. Median nest initiation dates for Great Egrets and small herons were four and two days earlier, respectively, in 2015 than in 2016. Correspondingly, lake stage near the start of nesting was higher in 2016 compared to 2015 (15.8 ft. NGVD and 14.7 ft. NGVD, respectively). All environmental variables, including wind speed, mean rainfall, and mean temperature, measured during the nesting season were statistically different between years ($P < 0.05$; Table 3.2 and 3.3)

Nests Monitored

A total of 330 nests (Great Egret $n = 108$, small herons $n = 222$) from 4 different colonies were monitored during the 2015 and 2016 breeding seasons (Table 4). Apparent survival for Great Egrets was 66% (SE = 0.5) and did not differ among colonies in 2015 and 2016 ($F_{3, 33} = 0.93$, $P = 0.44$ and $F_{3, 67} = 1.95$, $P = 0.13$, respectively) or years ($F_{1, 106} = 1.33$, $P = 0.25$). Apparent survival for small herons was 59% (SE = 0.3) and did not differ among colonies in 2015 and 2016 ($F_{3, 74} = 1.24$, $P = 0.30$ and $F_{3, 139} = 2.60$, $P = 0.05$, respectively) or years ($F_{1, 220} = 1.18$, $P = 0.28$).

Mean nest height for Great Egrets was 1.63 ± 0.55 (SD) m and did not differ between years ($F_{1, 106} = 2.56$, $P = 0.11$), however, mean distance to canopy edge was significantly different between years ($F_{1, 106} = 18.73$, $P < 0.05$). Mean distance to canopy edge was 0.30 ± 0.41 in 2015 and 1.02 ± 0.97 in 2016. Mean nest height for small herons

was 1.47 ± 0.42 and did not differ between years ($F_{1, 220} = 3.78$, $P = 0.05$), however, mean distance to canopy edge was significantly different between years ($F_{1, 220} = 4.33$, $P < 0.05$). Mean distance to canopy edge was 1.31 ± 0.68 in 2015 and 1.53 ± 0.78 in 2016. Mean nest height was higher for Great Egrets than small herons ($F_{1,328} = 7.97$, $P < 0.05$) and mean distance to canopy edge was shorter for Great Egrets than small herons, ($F_{1,328} = 50.92$, $P < 0.05$).

Great Egrets

Of the 108 Great Egret nests monitored, 47 occurred in natural island colonies ($n = 15$ in 2015 and $n = 32$ in 2016) and 61 occurred in spoil island colonies ($n = 23$ in 2015 and $n = 38$ in 2016). Mean distance to canopy edge was lower in 2015 compared to 2016 ($F_{1, 106} = 250.8$, $P < 0.05$; Table 3.5 and 3.6), however, it did not differ between colony types in 2015 or 2016 ($F_{1, 106} = 0.4$, $P = 0.53$ and $F_{1, 106} = 0.2$, $P = 0.65$, respectively; Table 3.5 and 3.6). Mean nest height was not significantly different between years ($F_{1, 106} = 2.6$, $P = 0.11$) or between colony types in 2015 ($F_{1, 35} = 0.1$, $P = 79$), but there was a difference in 2016 ($F_{1, 69} = 82.5$, $P < 0.05$) respectively; Table 3.5 and 3.6).

Estimated DSR for Great Egrets during the incubation stage was 0.987 (95% CI = 0.987 - 0.998), equating to a 0.58 (95% CI = 0.57 - 0.59) probability of survival through the 40-day nesting period (Table 3.7; Figure 3.2). The best-approximating model for nest survival during the incubation period included an interaction between distance to canopy edge and temperature ($w_i = 0.15$) (Table 3.8). The effect of temperature was strongest when nests were closer to the canopy edge (<1 m). Likewise, the effect of temperature was small when nests were far from the canopy edge (>1 m). Other plausible models included temperature and substrate category, but the model-averaged

parameter estimates had confidence intervals that overlapped zero, indicating these variables were unimportant.

During the hatchling period, estimated DSR was 0.998 (95% CI = 0.997 - 0.998), equating to a 0.94 (95% CI = 0.93-0.95) probability of survival through the 40-day nesting period. The top-fitting model included nest height ($\beta_{Nest\ Height}$ =1.87, 95% CI = 0.40 – 4.28), rainfall ($\beta_{Rainfall}$ =-0.58, 95% CI = 0.01 – 1.66), and distance to canopy edge (β_{Canopy} = 0.51, 95% CI = -1.28 – 2.81) (Table 3.7; Figure 3.3). In terms of parameter importance weight, nest height (w_i = 0.80) ranked highest, while rainfall and distance were comparable (w_i = 0.69 and w_i = 0.66, respectively; Table 3.8).

The top-fitting model for fledgling production of Great Egrets included temperature ($\beta_{Temperature}$ = 0.28, 95% CI = -0.02 – 0.57) and wind (β_{Wind}=0.11, 95% CI=-0.09 – 0.31) (Table 3.7; Figure 3.4). The other plausible model also included distance to canopy (β_{Canopy} = 0.22, 95% CI = -1.86 – 2.29). Parameter importance weights showed temperature (w_i = 0.65) was ranked the highest, followed by distance to canopy (w_i = 0.42) and wind (w_i = 0.35) (Table 3.8).

Small Herons

Of the 222 small heron nests monitored, 69 occurred in natural island colonies and 153 occurred in spoil island colonies. Mean distance was shorter in 2015 compared to 2016 ($F_{1,\ 219}$ = 4.3, $P < 0.05$; Table 3.5). Mean distance to canopy was shorter at natural islands compared to spoil islands in 2016 ($F_{1,\ 141}$ = 4.8, $P < 0.05$; Table 3.5), but distance did not differ between colony types during 2015 ($F_{1,\ 76}$ = 0.3, $P = 0.58$; Table 3.5). Mean nest height did not differ between years ($F_{1,\ 219}$ = 3.6, $P = 0.58$), but it was significantly different between colony types in 2015 and 2016 ($F_{1,\ 219}$ = 47.4, $P < 0.05$

and $F_{1,\,219} = 47.4$, $P < 0.05$, respectively; Table 3.6). Nest height was lower in natural islands compared to spoil islands (Table 3.5)

Estimated DSR for small herons during the incubation stage was 0.997 (95% CI = 0.996 - 0.997), equating to a 0.46 (95% CI = 0.44-0.45) probability of survival through the 35-day nesting period. The best-approximating model for small herons during the incubation period included an interaction between rainfall and distance to canopy edge (Table 3.4; Figure 3.7). The parameter importance weight was higher for rainfall (w_i = 0.88) compared to distance to canopy (w_i = 0.62; Table 3.8). Daily survival rates during the incubation period were negatively associated with rainfall ($\beta_{Rainfall}$ = -0.16, 95% CI = 0.38 - 0.04) and positively associated with distance to canopy edge (β_{Canopy} = 0.31, 95% CI = -1.61 – 2.23). The effect of canopy edge was particularly strong when rainfall was high. Likewise, the negative effect of rainfall was strongest when nests were near the canopy edge.

Estimated DSR for small herons during the hatchling stage was 0.979, equating to a 0.48 probability of survival through the 35-day nesting period. The null model was the best-approximating model for nest survival during the hatchling period (Table 3.7), indicating that none of the model terms affected nest survival. The evidence ratio suggested that the null model was at least 1.1x more plausible than the other competitive models.

The top-fitting model for fledgling production for small herons included temperature, rainfall, and distance to canopy edge (Table 3.7; Figure 3.6). Fledgling production was positively affected by temperature and distance to canopy edge ($\beta_{Temperature}$ = 0.33, 95% CI = 0.05 - 0.60; β_{Canopy} = 0.03, 95% CI = -2.95- 3.00), and it was

negatively associated with rainfall ($\beta_{Rainfall}$ = -0.20, 95% CI = -0.34- -0.06) (Table 3.7).

Parameter importance weight was highest for the temperature (w_i = 0.99) and rainfall (w_i = 0.97) and slightly lower for distance to canopy edge (w_i = 0.86) (Table 3.8).

Colony Type and Nesting Substrate

Colony type and nesting substrate were considered in the analyses for DSR and fledgling production, however, there was no evidence of effects. Because these components were a central theme to the study, further investigation seemed necessary. A post-hoc analysis was conducted to compare apparent survival and fledgling production at both colony types. Apparent survival and fledgling production did not differ between the two colony types for Great Egrets ($F_{1, 106}$ = 1.37, P = 0.25 and $F_{1, 106}$ = 0.7, P = 0.40, respectively) or small herons ($F_{1, 76}$ = 0.6, P = 0.46 and $F_{1, 141}$ = 0.7, P = 0.40, respectively). Furthermore, apparent survival and fledgling production did not differ between vegetation type (native vs. non-native) for Great Egrets ($F_{1, 76}$ = 0.6, P = 0.46 and $F_{1, 141}$ = 0.1, P = 0.93, respectively) and small herons ($F_{1, 219}$ = 0.4, P = 0.53 and $F_{1, 219}$ = 2.7, P = 0.10, respectively).

DISCUSSION

Nest Position

Distance to canopy edge was the most important parameter as it was consistently present in almost all top-fitting models, except for Great Egret fledgling production and small herons during the hatchling period. When present, canopy edge generally comprised a large part of the model weight. Increased distance from the canopy edge may offer additional protection against aerial predators and can provide nests with a

buffered microclimate. Although wind was important in only one of the plausible models, collapsed nests were commonly observed during nest surveys that followed storms, especially during the 2016 season. In fact, the highest number of nest failures for Great Egrets during the hatchling period occurred after a storm event characterized by high wind speeds and increased rainfall that resulted in increases in water depths.

Great Egret nest survival during the incubation period was negatively correlated with distance to canopy, which could be related to decreased efficiency in thermoregulation as the nest moves away from the canopy edge. Though increased distance from the canopy edge could provide protection from high winds and avian predators, lower lying nests may be shaded and not receive the same temperature benefits as higher nests. This observation illustrates that distance to canopy edge may impact nests differently depending on nest stage. For small herons, survival during the incubation period and fledgling production was positively correlated with distance to canopy edge, suggesting there was a benefit to being closer to the canopy edge. Increased nest height benefitted Great Egrets during the hatchling period. Increased distance from the ground can decrease the susceptibility of nest depredation by mesopredators, like snakes or raccoons.

Wading birds exhibit patterns of vertical stratification when selecting nest sites. Larger species, like Great Egrets, will typically nest towards the top of the tree, while smaller species will fill in spaces below (McCrimmon 1978, Beaver et al. 1992). Therefore, it is not surprising that responses differed among species.

Nesting Substrate and Colony Type

Invasive and non-native species, like cattail (*Typha spp*) and Brazilian pepper (*Schinus terebenthifolus*), were commonly used as nesting substrate in both natural island and spoil island colonies. Surprisingly, the support and structure provided by invasive and non-native species had no apparent effect on nesting success and fledgling production. Similar results were found for Everglade Snail Kites (*Rostrhamus sociabilis plumbeus*) nesting at nearby Lake Tohopekaliga. There, snail kites will use similar nesting substrate (e.g. giant bulrush, cattail, willow) as wading birds at Lake Okeechobee. In the snail kite study, there was no significant difference in the daily survival rates of nests built in bulrush, cattail, or willow (Olbert 2013).

There was also little evidence for colony type explaining DSR or fledgling production for wading birds. This suggests that spoil islands can provide nesting habitat comparable to natural tree islands, at least in the short-term. Previous studies that compared fledging rates of wading birds nesting at different colony types at Lake Okeechobee found spoil islands produced fewer fledglings per nest compared to natural islands (Chastant et al. 2017). Differences in fledgling production at colonies may be affected by environmental conditions experienced during the nesting season. Spoil islands can be particularly important during drought events since they are built along deep canals and maintain surrounding water for a longer period. Past surveys show during years when lake stage was extremely low, spoil island colonies were used exclusively, which demonstrates the flexibility in their utility in a highly variable system.

45

Despite the lack of evidence for differences in survival or fledgling production between the two colony types, it is important to consider the more obvious constraints associated with spoil island colonies. Because of their larger spatial extent, natural island colonies can support a significantly higher number of nests, assuming the area surrounding the colony remains inundated. During this study, approximately 150-200 nests were detected at spoil islands each year, while up to 2,800 nests were detected at the largest natural colony. Therefore, the larger natural island colonies can produce a higher total of young. This illustrates the importance of maintaining the extant area of naturally-occurring nesting habitat.

Environmental Conditions

The positive relationship between temperature and fledgling production for both Great Egrets and small herons provides support for the importance of warmer temperatures that may facilitate prey activity and physiological processes of chicks. However, it is more likely that the effects of low prey activity are more impactful to nests than physiological stress. Great Egrets nesting farther north regularly incubate successfully during periods of much colder temperatures than those experienced in the Everglades. A study on marsh fish in the Everglades showed fish species fed, courted, and schooled more readily during warmer temperatures. During colder temperatures, fish would aggregate around and within dense vegetation, which is unfavorable foraging habitat for wading birds. (Frederick and Loftus 1993, Lantz et al. 2011).

Unexpectedly, a positive relationship was observed between rainfall and Great Egret nest success during the nestling stage. Increased rainfall resulting in slight

46

increases of water levels may potentially benefit nesting Great Egrets if the deeper waters

support larger-sized prey or exclude competition from short-legged waders. However,

too much rainfall during the dry season can increase water levels and allow prey to

disburse, which reduces prey concentrations and affects food availability for wading birds

(Gawlik 2002). Evidence for this consequence was revealed in the model output for

small herons, which showed a decrease in DSR with increased rainfall. Increased rainfall

could also make thermoregulation more energetically expensive. If prey availability also

declines, these factors could compound the negative effect on DSR.

Nest Depredation

Although weather seemed to be the most significant cause of nest failure for

wading birds at Lake Okeechobee, it should be noted that predators such as rat snakes

(*Elaphe spp*.) and cottonmouths (*Agkistrodon piscivorus*) were observed in colonies on a

few occasions. Additionally, nest depredation on Lake Okeechobee has been observed for

other avian species during 2015 and 2016. For example, nest depredation was attributed

to approximately 25% of the nest failures of the snail kite; a sizeable proportion of the

nest failures occurred for unknown causes (Fletcher, University of Florida, unpublished

data). The breeding season for the snail kite coincides with that of wading birds, and snail

kite nesting sites are associated with wading bird colonies (Bennetts 1997). Considering

the spatial and temporal commonalities of the breeding seasons of snail kites and wading

birds, depredation could have been contributing to a higher proportion of wading bird

nest failures than perceived.

In general, model fit appeared to be weaker as the nest matured. This is expected since more factors can impact the nest once chicks hatch and become more mobile. During the later stages, food provisioning may be more impactful on nest survival.

Management Implications

As the human population continues to increase, the degradation of natural habitats will continue to occur at a rapid rate. Man-made habitats will become increasingly important to mitigate the negative effects of human activities. Man-made spoil islands are an important management tool commonly used for the maintenance of many bird species in the United States and around the world (Pyrovetsi 1997, Spear et al. 2007, Selman 2015)

Spoil islands can support a wide variety of habitat types from clear, sandy-rocky beach, berm and open areas, to sparsely vegetated areas of grasses and low shrubs, to mature areas with trees and accompanying undergrowth. They provide sites for feeding, roosting, and loafing for resident and migratory bird species. They also provide a place for resting, preening, and other essential body maintenance activities and serve as a social gathering place especially important for courtship activities (Schreiber and Schreiber 1978).

Results from this study elucidate relationships between nest survival and nest position and environmental conditions. Managers interested in creating habitat for wading birds should consider a few factors in their design and maintenance. First, colony access by predators should be limited. This can be achieved by ensuring water surrounding islands is present and deep enough to prevent entry. Second, the growth of

taller vegetation species should be facilitated to allow for adequate distance between the

nest and canopy edge and the ground. And third, a management plan should be

developed to mitigate the negative effects of erosion, which can lead to a reduction in the

spatial extent of habitat and spoil island destruction.
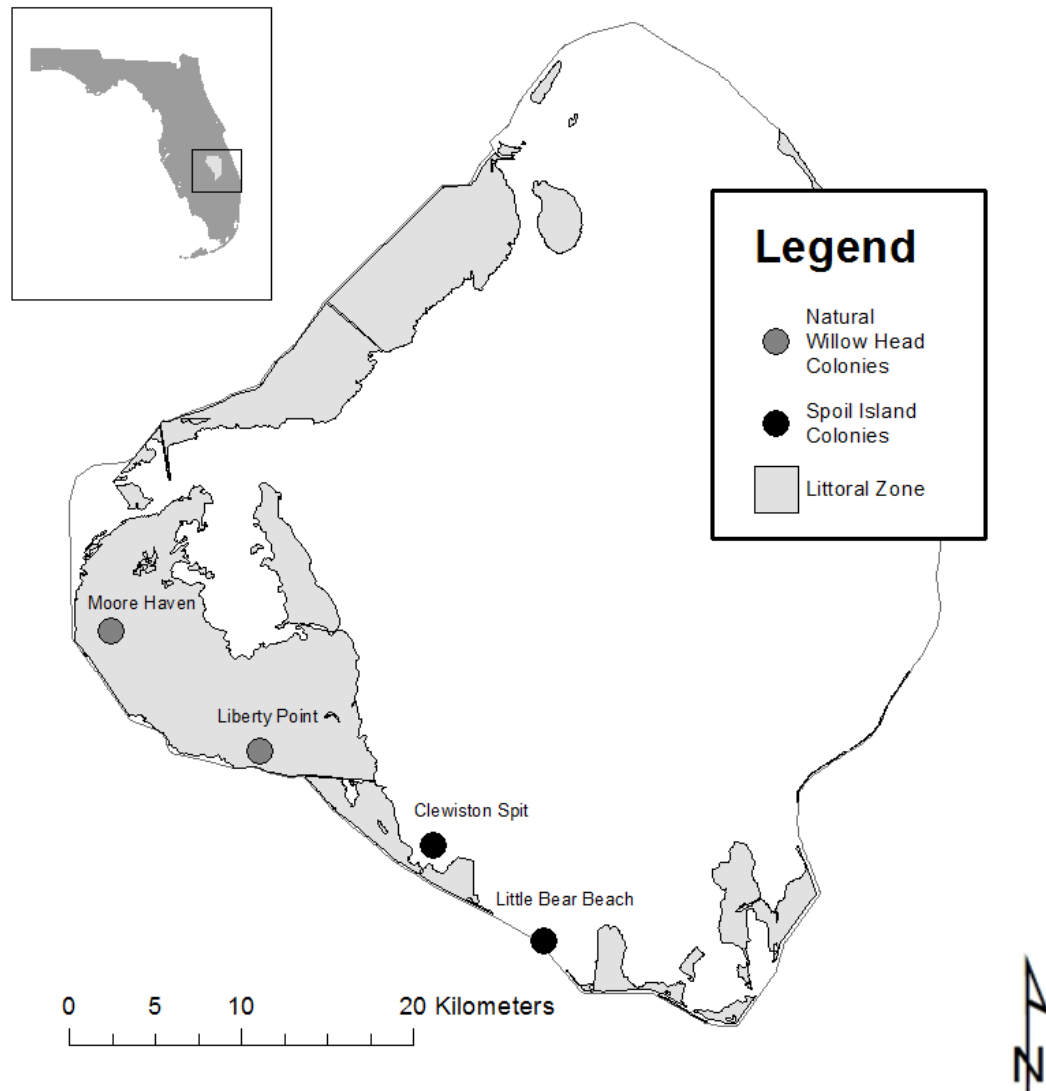
Figure 3.1. Map of the study area with locations of monitored colonies.

Table 3.1. Summary of hypotheses and model structure. A description of parameter can be found in the Appendix (see Table A2)

Hypothesis	Model Structure
Nest position hypothesis	Nest height + Distance to canopy
Colony type hypothesis	Colony type
Weather hypothesis	Rainfall + Temperature + Wind speed
Substrate type hypothesis	Substrate Category
Null	-

Table 3.2. Summary of environmental conditions experienced by each species during the 2015 and 2016 breeding season.

Great Egret	Mean Max Wind Speed (m/s)	Mean Rainfall (cm)	Mean Temperature (ºC)	March 1 Lake Stage (ft. NGVD)
2015	10.72 ± 2.33	0.94 ± 1.14	23.81 ± 2.05	14.7
2016	13.74 ± 1.90	1.97 ± 1.43	22.59 ± 1.09	15.8
Small heron				
2015	11.19 ± 2.46	1.91 ± 0.91	24.26 ± 3.87	14.7
2016	13.16 ± 2.13	1.46 ± 1.16	23.56 ± 1.05	15.8

Table 3.3. Results of ANOVAs examining annual and species differences in environmental conditions during the 2015 and 2016 breeding season

Comparison	Mean Max Wind Speed	Mean Rainfall	Mean Temperature
Great Egret – 2015 vs. 2016	$F_{1,106} = 250.8, P < 0.05$	$F_{1,106} = 5.4, P < 0.05$	$F_{1,106} = 90.5, P < 0.05$
Small heron – 2015 vs. 2016	$F_{1,220} = 66.7, P < 0.05$	$F_{1,220} = 7.2, P < 0.05$	$F_{1,220} = 102.0, P < 0.05$
2015 - Great Egret vs. Small heron	$F_{1,114} = 2.4, P = 0.12$	$F_{1,114} = 6.4, P < 0.05$	$F_{1,114} = 25.0, P < 0.05$
2016 - Great Egret vs. Small heron	$F_{1,212} = 51.3, P < 0.05$	$F_{1,212} = 0.3, P = 0.57$	$F_{1,212} = 86.5, P < 0.05$

Table 3.4. Number of samples for each species at each colony from 2015-2016. Colonies sampled during this study include Liberty Point (LP), Moore Haven (MH), Clewiston Spit (CS), and Little Bear Beach (LBB).

| | 2015 | | | | | 2016 | | | | | |
| | Natural Colonies | | Spoil Island Colonies | | | Natural Colonies | | Spoil Island Colonies | | | |
	LP	MH	CS	LBB	2015 Total	LP	MH	CS	LBB	2016 Total	Grand Total
Great Egrets	12	3	13	10	38	7	25	6	32	70	108
Small heron	6	11	17	44	78	20	32	29	63	144	222
Grand Total	18	14	30	54	116	27	57	35	95	214	330

Table 3.5. Nest height and distance to canopy for each species at each colony type from 2015-2016

| Great Egret | 2015 | | | 2016 | | | Total | |
	Natural Colony	Spoil Island Colony	Total	Natural Colony	Spoil Island Colony	Total	Natural Colony	Spoil Island Colony
Mean Nest Height (m)	1.53 ± 0.25	1.50 ± 0.37	1.51 ± 0.33	1.18 ± 0.28	2.11 ± 0.52	1.69 ± 0.64	1.28 ± 0.32	1.89 ± 0.56
Mean Distance to Canopy (m)	0.35 ± 0.44	0.26 ± 0.39	0.30 ± 0.41	1.08 ± 0.87	0.98 ± 1.06	1.02 ± 0.97	0.86 ± 0.83	0.71 ± 0.93

Small Herons

Mean Nest Height (m)	1.47 ± 0.17	1.39 ± 0.33	1.40 ± 0.30	1.13 ± 0.37	1.73 ± 0.36	1.51 ± 0.46	1.21 ± 0.36	1.59 ± 0.39
Mean Distance to Canopy (m)	1.23 ± 0.92	1.34 ± 0.61	1.31 ± 0.68	1.34 ± 0.78	1.64 ± 0.76	1.53 ± 0.78	1.32 ± 0.81	1.52 ± 0.71

Table 3.6. Results of ANOVAs examining annual and colony type differences in nest position during the 2015 and 2016 breeding season

Comparison	Mean Distance to Canopy	Mean Nest Height
Great Egret – 2015 vs. 2016	$F_{1,106} = 250.8$, $P < 0.05$	$F_{1,106} = 2.6$, $P = 0.11$
Great Egret – Natural Island vs. Spoil island (2015)	$F_{1,106} = 0.4$, $P = 0.53$	$F_{1,35} = 0.1$, $P = 0.79$
Great Egret – Natural Island vs. Spoil island (2016)	$F_{1,106} = 0.2$, $P = 0.65$	$F_{1,69} = 82.5$, $P < 0.05$
Small heron – 2015 vs. 2016	$F_{1,219} = 4.3$, $P < 0.05$	$F_{1,219} = 3.6$, $P = 0.58$
Small heron – Natural Island vs. Spoil island (2015)	$F_{1,76} = 0.3$, $P = 0.58$	$F_{1,219} = 47.4$, $P < 0.05$
Small heron – Natural Island vs. Spoil island (2016)	$F_{1,141} = 4.8$, $P < 0.05$	$F_{1,219} = 47.4$, $P < 0.05$

Table 3.7. Logistic exposure models for nest success of Great Egrets and small herons at Lake Okeechobee during 2015 and 2016. All models included an intercept term and random effect of year and nest site. Provided for each model are number of parameters (K), values of the Akaike's Information Criterion for small sample sizes (AIC_c), ΔAIC_c, and Akaike weights (w_i). Competitive models (models with $\Delta AIC_c <2$), global models, and null (intercept) models are shown.

Model	K	AIC_c	ΔAIC_c	w_i
Great Egret				
Incubation period				
Canopy*Temperature	6	136.65	0.00	0.15
Null	3	137.87	1.22	0.08
Temperature	4	138.01	1.35	0.08
Substrate Category	4	138.47	1.82	0.06
Global	16	144.34	7.69	0.00
Hatchling Period				
Canopy + Nest Height + Rainfall	6	84.61	0.00	0.42
Nest Height + Rainfall	5	86.40	1.80	0.17
Null	3	92.34	7.73	0.01
Global	16	98.98	14.38	0.00
Fledgling Production				
Temperature + Wind	5	303.22	0	0.27
Temperature + Canopy	5	304.59	1.37	0.13
Null	3	307.24	4.01	0.04
Global	16	329.39	26.16	0.00
Small Herons				
Incubation Period				
Canopy * Rainfall	6	344.36	0	0.27
Canopy + Rainfall	5	344.96	0.60	0.20
Global	16	352.23	7.87	0.01
Null	3	353.04	8.68	0
Hatchling Period				
Null	3	130.53	0	0.11
Global	16	141.73	11.19	0
Fledgling Production				
Rainfall + Temperature + Canopy	6	706.36	0	0.80
Global	16	712.84	6.48	0.03
Null	3	716.75	10.39	0

Table 3.8. Model-averaged coefficients for glmm models representing the relationship between structure and climate variables during the incubation, hatchling, and fledging production for Great Egrets and small herons. Lower and upper confidence limits (LCL and UCL) are included along with the relative importance ($\sum w_i$) of each coefficient in the model set.

Parameters	β	LCL	UCL	$\sum w_i$
Great Egrets				
Incubation period				
intercept	7.17	-3.60	17.95	--
Canopy	-4.26	-16.56	8.03	0.36
Temperature	-0.36	-0.84	0.11	0.33
Substrate Category	-0.16	-0.42	0.10	0.22
Canopy*Temperature	0.47	0.11	0.82	0.15
Hatchling Period				
Intercept	2.65	-2.19	7.49	--
Nest Height	1.87	0.40	4.28	0.80
Rainfall	0.58	0.01	1.66	0.69
Canopy	0.51	-1.28	2.81	0.66
Fledgling Production				
intercept	-4.65	-14.49	5.19	--
Temperature	0.28	-0.02	0.57	0.65
Canopy	0.22	-1.86	2.29	0.42
Wind	0.11	-0.09	0.31	0.35
Small Herons				
Incubation Period				
intercept	3.86	-0.10	7.82	--
Rainfall	-0.16	-0.38	0.04	0.88
Canopy	0.31	-1.61	2.23	0.62
Canopy*Rainfall	0.13	-0.05	0.30	0.27
Hatchling Period				
intercept	6.96	-3.74	17.65	--
Fledgling Production				
intercept	-7.96	-15.85	-0.08	--
Temperature	0.33	0.05	0.60	0.99
Rainfall	-0.20	-0.34	-0.06	0.97
Canopy	0.03	-2.95	3.00	0.86

Figure 3.2. Relationship between daily survival rates of Great Egret nests during the incubation period and temperature when nests are 0 m, <1 m, and >1 m from the canopy edge. Nests near (0 m), medium (<1 m), and far distances (>1 m) from the canopy edge are represented by dotted, dashed, and solid lines, respectively.
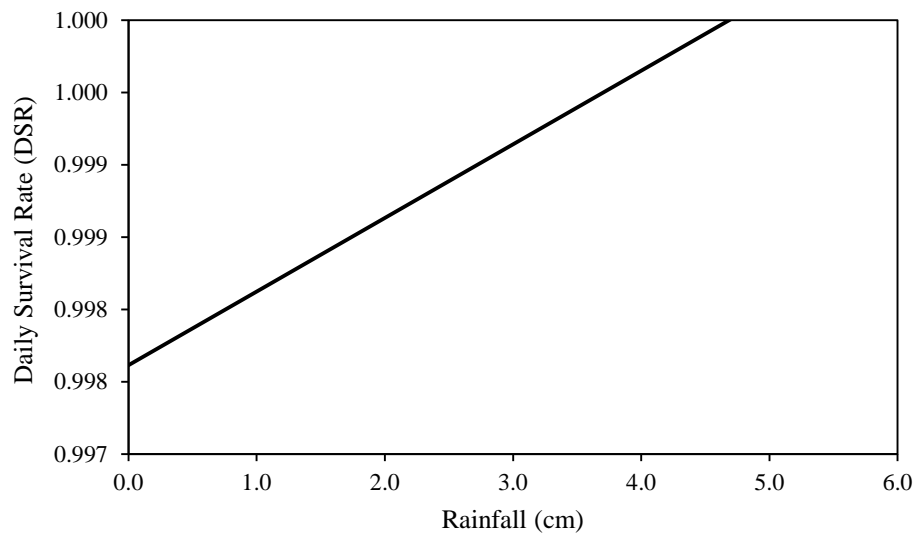
Figure 3.3. Relationship of covariates to daily survival rates of Great Egret nests during the hatchling period in 2015 and 2016.
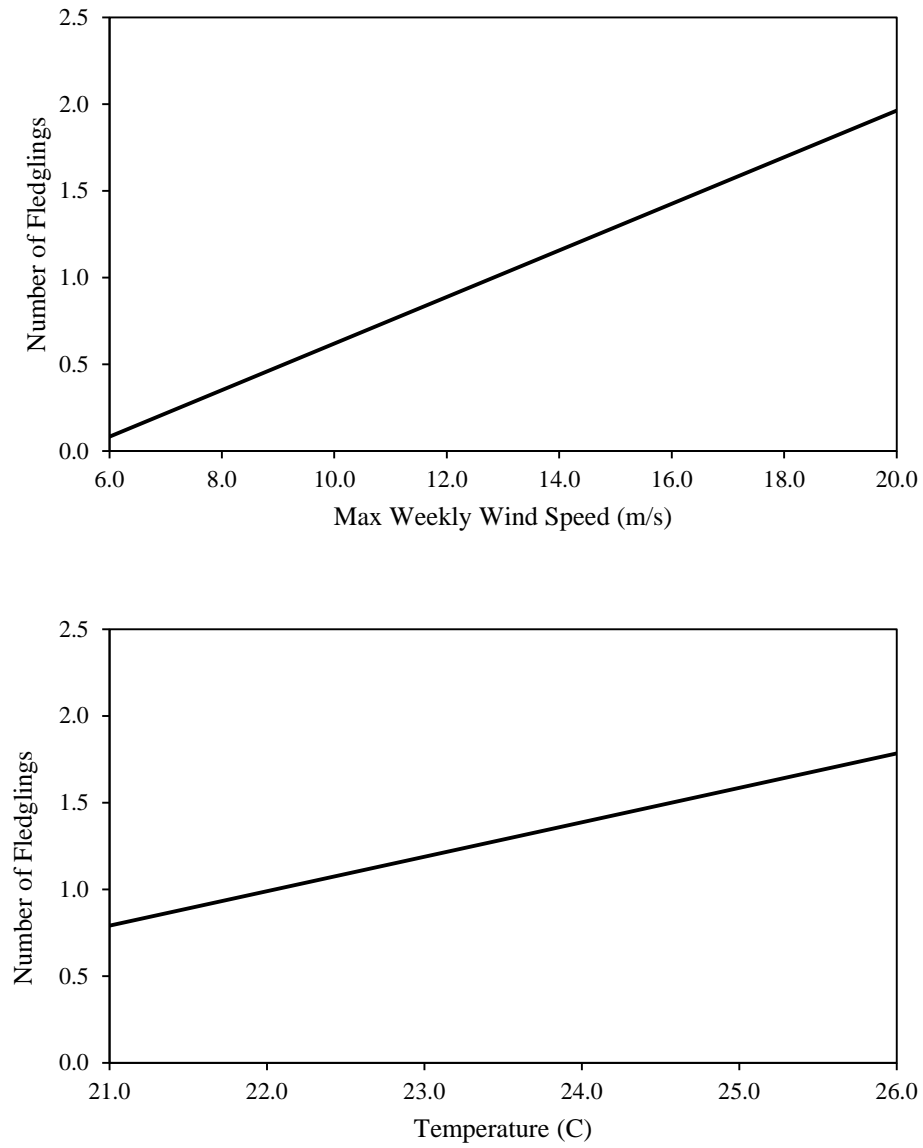
Figure 3.4. Relationship of covariates to fledgling production of Great Egret nests in 2015 and 2016.
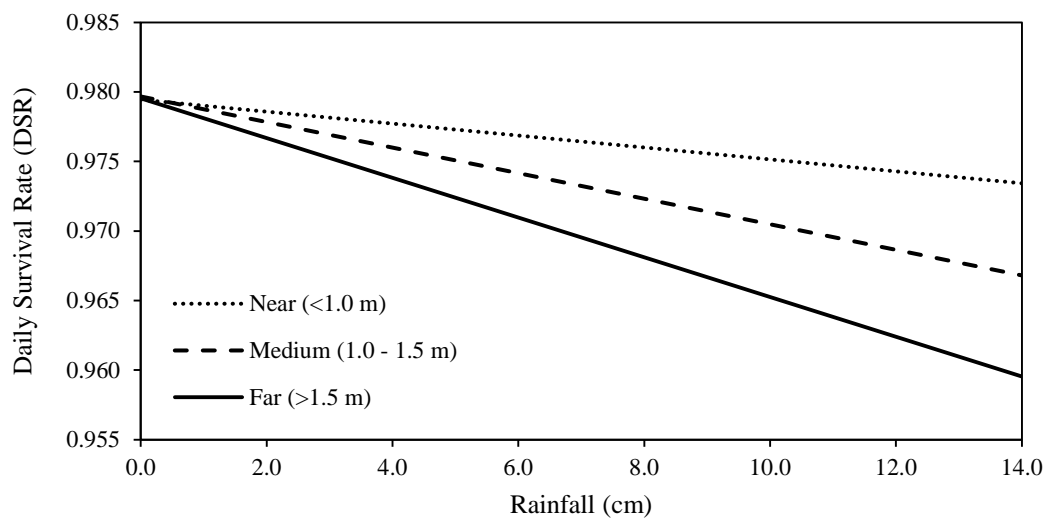
Figure 3.5. Relationship of covariates to daily survival rates of small heron nests during the incubation period in 2015 and 2016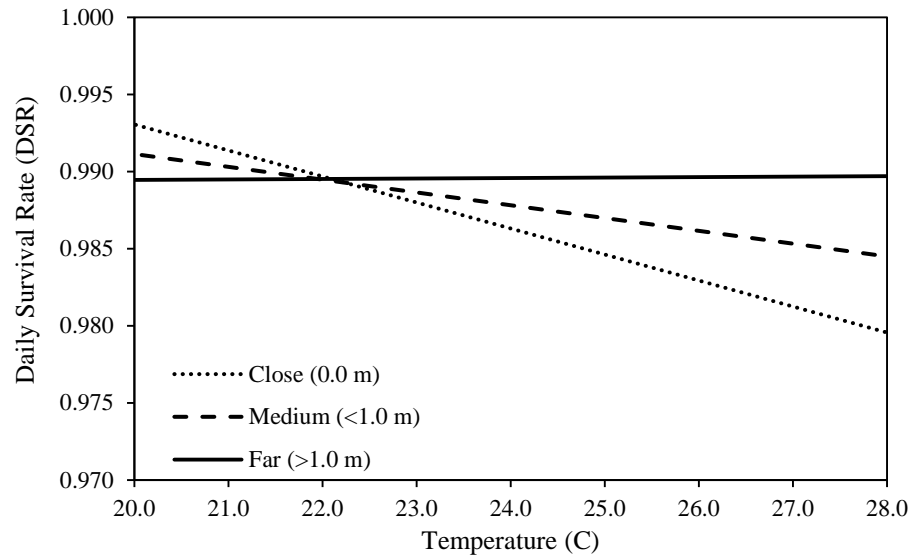. Relationship between daily survival rates of small herons during the incubation period and rainfall when nests are 0 m, <1 m, and >1 m from the canopy edge. Nests near (<1 m), medium (1.0-1.5 m), and far distances (>1.5 m) from the canopy edge are represented by dotted, dashed, and solid lines, respectively.
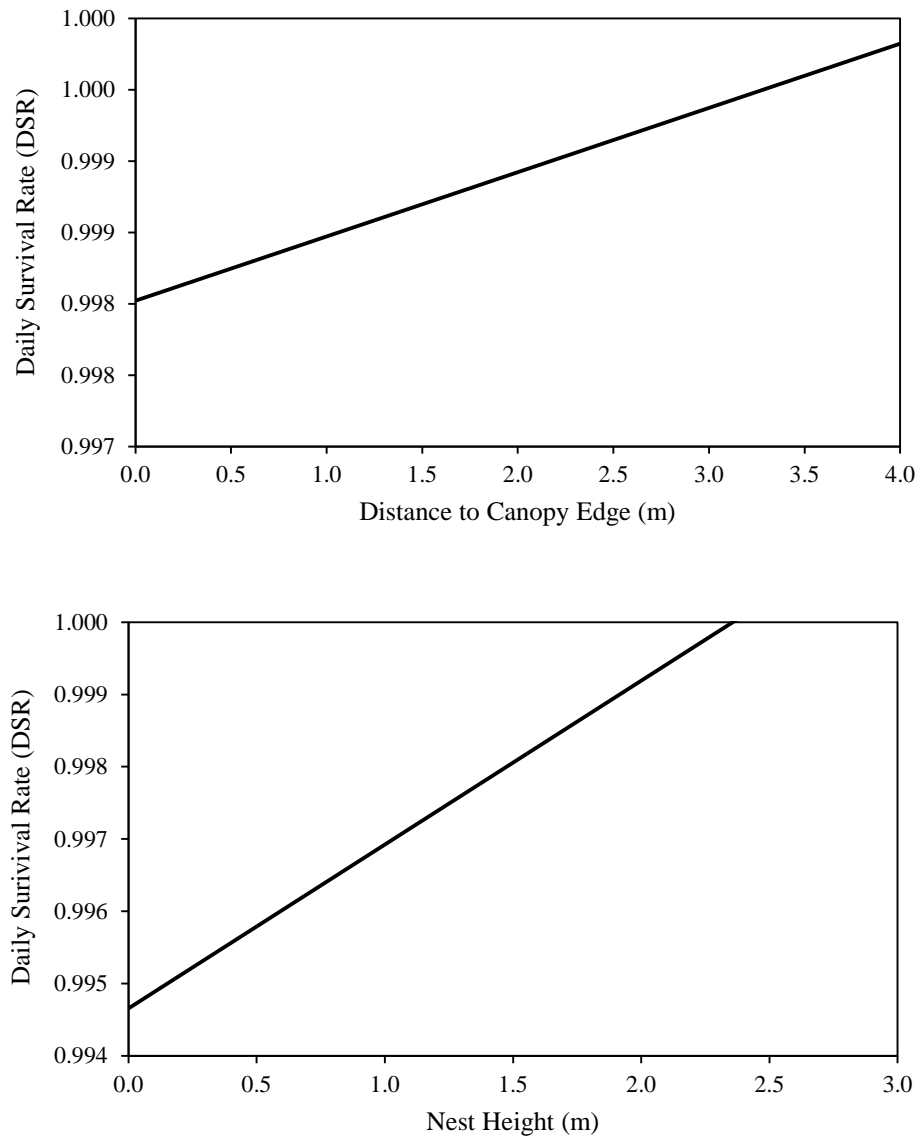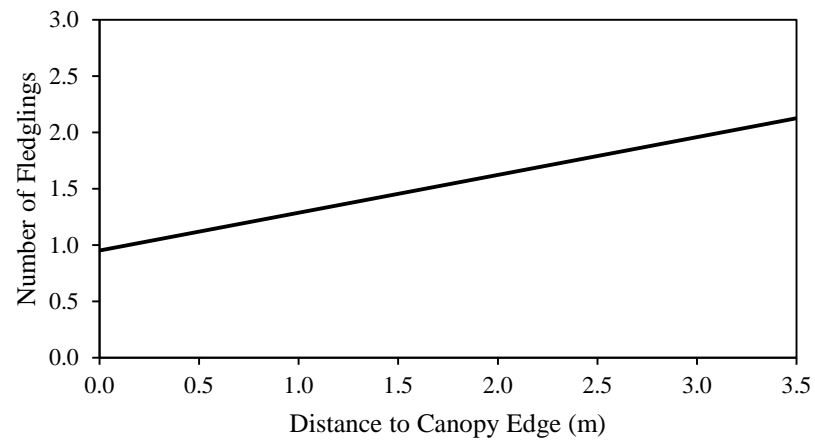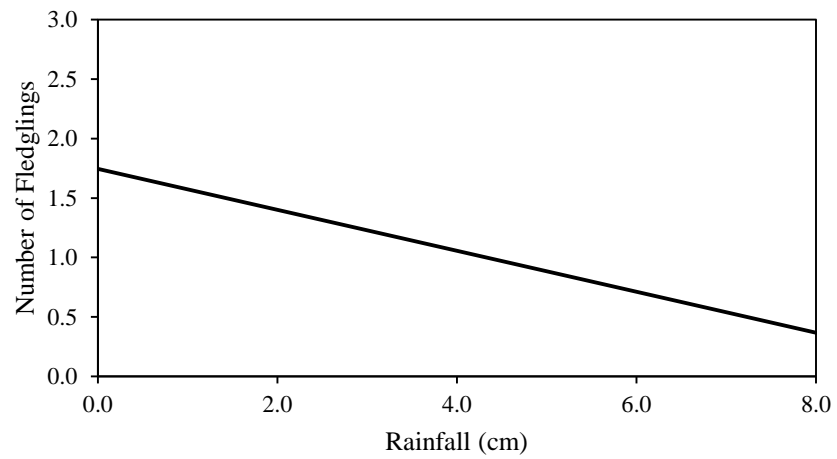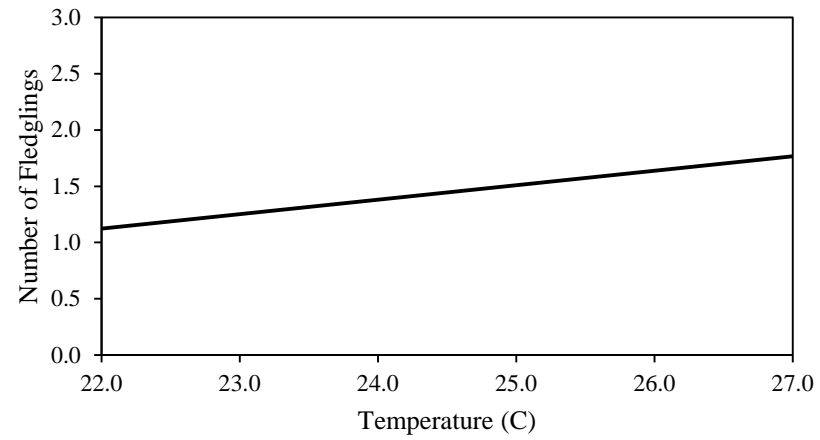
Figure 3.6. Relationship of covariates to fledgling production of small heron nests in 2015 and 2016.

CHAPTER IV. SYNTHESIS

Lake Okeechobee has been a site of extensive research and monitoring by regulatory agencies for decades. Managing water levels in Lake Okeechobee is a primary concern for resource managers because the lake serves as a principal flood-control and water-storage facility in the region (Aumen 1995).

Wading birds are useful biological indicators for the systems they inhabit (Smith and Collopy 1995). Because they are conspicuous, dynamic members of South Florida wetlands, they are often used to assess wetland integrity for the region (Frederick et al. 2009). Reproductive success of wading birds at the lake provides an evaluation parameter from which ecosystem health and water management strategies can be assessed. This is important since the construction of the Herbert Hoover Dike has had impacts on critical wildlife habitat, thus resulting in the necessity for appropriate and meticulous water management. To manage for wading bird parameter, it is necessary to understand the underpinnings of reproductive success.

Food selection and availability, examined in Chapter 2, demonstrated the ability of small herons to maintain a consistent diet through fluctuating, and extreme, environmental conditions within and across different wetland types (lacustrine vs. palustrine) (Boyle et al. 2012, Klassen et al. 2016). Consistent diets may also suggest prey composition at available foraging sites, on and off-lake, are fairly insensitive to hydrologic conditions. Changing hydrologic trends and habitat conditions may require

nesting birds to forage in shallower off-lake habitats (Zaffke, 1984, David 1994, Smith 1995, Smith et al. 1995), but they maintain a consistent diet. At Lake Okeechobee, this can be achieved through altering foraging strategies, such as engaging in aerial foraging, exploiting vegetation to forage in deeper waters, shifting to more favorable habitats within the lake, or foraging off-lake (Smith 1995, Smith 1997). The relatively high availability of prey at Lake Okeechobee is also noteworthy and contributes to the ability of wading birds to sustain nesting through different environmental conditions. Mechanisms for making prey available are similar to those observed in the Everglades, including receding water levels and the availability of deep water refugia in the landscape (Botson et al. 2016). One key mechanism that distinguishes Lake Okeechobee from the Everglades, however, is nutrient status, which contributes to relatively high secondary production. The combination of flexible foraging techniques, an array of available foraging habitat, and a highly productive system make it possible for nesting to occur even when there are slight reversals.

Nesting habitat, examined in Chapter 3, can also affect the reproduction of wading birds. Nest position with regard to distance to canopy can impact nesting survival at all nest stages for multiple species of wading birds and the effects can be different among stages and species. Being closer to the canopy can increase susceptibility to aerial predators and adverse weather conditions, while being farther from the canopy can decrease efficiency in thermoregulation. Weather conditions such as temperature and rainfall can also impact nesting success by altering foraging conditions and fish behavior (Frederick and Loftus 1993, Lantz et al. 2011). In general, model fit appeared to be weaker as the nest matured. This is expected since more factors can impact the nest once

chicks hatch and become more mobile. During the later stages, food provisioning may be more impactful on nest survival.

There was little evidence for colony type explaining survival or fledgling production for wading birds, suggesting that spoil islands can provide nesting habitat comparable to natural tree islands, at least in the short-term. Spoil islands can be particularly important during drought events since they are built along deep canals and maintain surrounding water for a longer period. Because of their larger spatial extent, natural island colonies can support a significantly higher number of nests, assuming the area surrounding the colony remains inundated. Therefore, the larger natural island colonies can produce a higher total of young, which illustrates the importance of maintaining the extant area of naturally-occurring nesting habitat. As the human population continues to increase, the degradation of natural habitats will continue to occur at a rapid rate. Man-made habitats will become increasingly important to mitigate the negative effects of human activities.

It is important to maintain the natural processes and dynamics of the system. Based on a literature review performed by Johnson et al. (2007), natural variation of lake levels fluctuating between 3.7 and 4.6 m have shown to yield optimal results for benefitting the ecosystem. Levels outside of this range can result in a multitude of negative effects on aquatic plants and, subsequently, on wildlife. Changes in abundance and distribution of individual species in response to altered hydrology may have profound effects on food web structure and function.

On a broader scale, understanding the effects of hydrologic regimes on biota at Lake Okeechobee can have practical applications not only locally, but globally as well. Large, shallow lakes are relatively common in low-lying agricultural landscapes around the world, including Lake Taihu in Asia, Lake Chad in Africa, and Lake Balaton in Europe. These ecosystems share similar problems with competing demands for water use and harbor concerns about how water levels may impact the natural resources communities depend on (Johnson et al. 2007). Findings from this study can be of immediate use to managers and could be considered when developing future management strategies. Ultimately, hydrologic regimes drive the state of the system and a better understanding of biological relationships will allow for better management of resources

APPENDIX

Table A1. Description of the Substrate Category parameter.

Substrate Category	Substrate Type	DBH (cm)
1	Herbaceous	-
2	Tree/Shrub	1-4.9
3	Tree/Shrub	5-9.9
4	Tree/Shrub	10-14.9
5	Tree/Shrub	15-19.9
6	Tree/Shrub	20 – 24.9
7	Tree/Shrub	25-29.9
8	Tree/Shrub	30+

Table A2. Variables used in candidate models predicting the nesting success and fledgling production of wading birds at Lake Okeechobee.

Predictor Variables	Description	Response Variables	Description
Colony Type	Man-made spoil island or natural tree island	Nest Fate	Success or Fail
Nest Height	Distance from the ground to the base of the nest.	Fledgling Production	Number of chicks surviving to predetermined age threshold
Substrate Category	Categories 1-8 determined by substrate type (fern/herbaceous vegetation or tree/shrub) and DBH		
Canopy	Distance from nest to canopy edge		
Rainfall	Dry season rainfall during the 1 week before survival estimate		
Wind Speed	Maximum wind speed during the 1 week before the survival estimate		
Temperature	Average weekly temperature		
Colony	Colony site (Random effect)		
Year	Nesting year (Random effect)		

LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle, in: B.N. Petrov and F. Csaki, edsl. 2nd international symposium on information theory (Akademiai Kiado, Budapest).

Aumen, N. 1995. History of human-related impacts to Lake Okeechobee, Florida (USA), related research, and lake management issues. Archiv fur Hydrobiologie Beiheft Ergebnisse der Limniologie 45: 1-16.

Alho, C. 2008. Biodiversity in the Pantanal: response to seasonal flooding regime and to environmental degradation. Brazilian Journal of Biology 68: 957-966.

Baranski, M. 2017. Lake Okeechobee wading bird foraging surveys. Pages 33-34 *in* South Florida Wading Bird Report, vol. 22 (M. I. Cook and M. Baranski, Eds.). South Florida Water Management District, West Palm Beach.

Beaver, D. L., R. G. Osborn, and T. W. Custer. 1980. Nest site and colony characteristics of wading birds in selected Atlantic coast colonies. Wilson Bulletin 92: 200-220.

Beerens, 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. The Auk 128(4):651-662.

Bennetts, R. E. and V. J. Dreitz. 1997. Possible use of wading birds as beaters by Snail
Kites, Boat-tailed Grackles, and Limpkins. Wilson Bulletin 109(1): 169-173.

Bolker, B. and R Development Core Team. 2014. bbmle: Tools for general maximum
likelihood estimation. R package version 1.0.17. http://CRAN.R-
project.org/package=bbmle.

Borgmann, K. L. and A D. Rodewald. 2004. Nest predation in an urbanizing landscape:
The role of exotic shrubs. Ecological Applications 14:1757–1765.

Botson, B. A., D. E. Gawlik, J. C. Trexler. 2016. Mechanisms that generate resources
pulses in a fluctuating wetland. PLoS ONE (11)7: e0158864.
Doi:10.1371/journal.pone.0158864.

Boyle, R. A., N. J. Dorn, and M. I. Cook. 2012. Nestling diet of three sympatrically
nesting wading bird species in the Florida Everglades. Waterbirds 35(1): 154-159.

Bryan, A. L., M. C. Coulter, and C. J. Pennycuick. 1995. Foraging strategies and
energetic costs of foraging flights by breeding wood storks. The Condor 97:133-
140.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a
practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York,
New York, USA.

Burton, N.H. K. 2006. Nest orientation and hatching success in the Tree Pipit *Anthus
trivialis*. Journal of Avian Biology 37: 312-317.

Chalfoun, A. D. and K. A. Schmidt. 2012. Adaptive breeding-habitat selection: Is it for the birds? The Auk 129(4): 589-599.

Chamberlain, D. E., and R. J. Fuller. 1999. Density-dependent habitat distribution in birds: Issues of scale, habitat definition and habitat availability. Journal of Avian Biology 30:427-436.

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.

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(1) 35-45.

Clarke, K. R. and R. N. Gorley. 2015. PRIMER v7: User Manual/Tutorial. PRIMER-E, Plymouth, 296pp

Clarke, K. R. and R. M. Warwick. 2001 Change in marine communities: an approach to statistical analysis and interpretation, second edition. PRIMER-E, Plymouth, Devon, United Kingdom.

Cochran, W. C. 1977. Sampling techniques. John Wiley and Sons, New York, New York, USA.

Collias, N. E. and E. C. Collias. 1984. Nest building and bird behavior. Princeton University Press, Princeton NJ.

Colombelli-négrel, D., & Kleindorfer, S. (2009). Nest height, nest concealment, and
    predator type predict nest predation in superb fairy-wrens (malurus cyaneus).
    Ecological Research, 24(4): 921-928.

Crawford, R. and B. Dyer. 1995. Responses by four seabird species to a fluctuation
    availability of Cape Anchovy *Engraulis capensis* off South Africa. Ibis 137: 329-
    339.

Cook, M. I., and H. K. Herring. 2007. Food availability and White Ibis reproductive
    success: An experimental study. Pages 22-25 *in* South Florida Wading Bird
    Report, vol. 12 (M. I. Cook and E. M. Call, Eds.). South Florida Water
    Management District, West Palm Beach.

Cunningham, S. J., R. O. Martin, C. L. Hojem, and P. A. R. Hockey. 2013. Temperatures
    in excess of critical thresholdes threaten nestling growth and survival in a rapidly-
    warming arid savannah: A study of common fiscals. PLOS ONE 8(9): 1-10.

Cook, M. I. and M. Baranski. 2017. Systemwide Summary. Pages 1-4 *in* South Florida
    Wading Bird Report, vol. 22 (M. I. Cook and M. Baranski, Eds.). South Florida
    Water Management District, West Palm Beach.

David, P. G. 1994. Wading bird use of Lake Okeechobee relative to fluctuating water
    levels. Wilson Bulletin 106(4):719-732.

Dawson, R. D., C. C. Lawrie, and E. L. O'Brien. 2005. The importance of microclimate
    variation in determining size, growth and survival of avian offspring:
    Experimental evidence from a cavity nesting passerine. Oecologia 144:499–507.

Dimalexis, A., M. Pyrovetsi, and S. Sgardelis. 1997. Foraging ecology of Grey Heron (Ardea cinereal), Great Egret (Ardea alba) and Little Egret (Egretta garzetta) in response to habitat at 2 Greek wetlands. Colonial Waterbirds 20(2): 261-272.

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

Erwin, R. 1980. Breeding habitat use by colonially nesting waterbirds in two mid-Atlantic US regions under different regimes of human disturbance. Biological Conservation 18:39-51.

Essian, D. A., J. C. May, and D. E. Gawlik. 2016. Wading bird colony location, size, and timing on Lake Okeechobee. U. S. Army Corps of Engineers, Florida Atlantic University, Boca Raton, FL, USA. Annual Report.

Fern, R. R., J. E. Chastant, and D. E. Gawlik. 2014. Wading bird nesting at Lake Okeechobee. Pages 28-30 *in* South Florida Wading Bird Report, vol. 20 (M. I. Cook, Ed.). South Florida Water Management District, West Palm Beach.

Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on Northern Cardinal nests: Does choice of nest site matter? Condor 96:761-768.

Frederick, P. C. and M. W. Collopy. 1988. Reproductive ecology of wading birds in relation to water conditions in the Florida Everglades. Florida Cooperative Fish and Wildlife Research Unit and the University of Florida School of Forest Resources and Conservation Technical Report 30.

Frederick, P. C. and M. W. Collopy. 1989. Nesting success of five ciconiiform species in

relation to water conditions in the Florida Everglades. Auk 106: 625-634.

Frederick, P. C., R. Bjork, G.T. Bancroft, and G.V. N. Powell. 1992. Reproductive

success of three species of herons relative to habitat in southern Florida. Colonial

Waterbirds 15(2): 192-201.

Frederick, P. C. and W. F. Loftus. 1993. Responses of marsh fishes and breeding wading

birds to low temperatures: a possible behavioral link between predator and prey.

Estuaries. 16: 198-215.

Frederick, P. C. and M. G. Spalding. 1994. Factors affecting reproductive success of

wading birds (Ciconiiformes) in the Everglades ecosystem. Everglades: the

ecosystem and its restoration: 659-691.

Frederick, P., D. E. Gawlik, J. C. Ogden, M. I. Cook, and M. Lusk. 2009. The White Ibis

and Wood Stork as indicators for restoration of the everglades ecosystem.

Ecological Indicators 9: S83–S95.

French, S., G. Johnston, and M. Moore. 2007. Immune activity suppresses reproduction

in food-limited female tree lizards *Urosaurus ornatus*. Functional Ecology 21(6):

1115-1122.

Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading

birds. Ecological Monographs 72(3):329–346.

Grant, G. S. 1982. Avian Incubation: Egg temperature, nest humidity, and behavioral

thermoregulation in a hot environment. Ornithological Monographs 30: 1-75.

Hagerthey, S. E., M. I. Cook, R. M. Kobza, and S. Newman. 2014. Aquatic faunal responses to an induced regime shift in the phosphorus impacted Everglades. Freshwater Biology 59: 1389-1405.

Hammatt, R.B.1981. Reproductive biology in a Louisiana heronry. Thesis, Louisiana State Univ., Baton Rouge.

Harrison, E., J. J. Lorenz, and J. C. Trexler. 2013. Per capita effects of non-native Mayan Cichlids (Cichlasoma urophthalus; Gunther) on native fish in the estuarine Southern Everglades. Copeia (1): 80-96.

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

Hoffman, W., G. T. Bancroft, and R. J. Sawicki. 1994. Foraging habitat of wading birds in the water conservation areas of the Everglades. In: Davis, S. M., Ogden, J. C. (Eds.), Everglades: The Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL.

Holway, D. A. 1991. Nest-site selection and the importance of nest concealment in the Black-Throated Blue Warbler. Condor 93: 575-581.

Huhta, E., J. Jokimaki, and P. Rahko. 1997. Distribution and reproductive success of the Pied Flycatcher Ficedula hypoleuca in relation to forest patch size and vegetation characteristics; the effect of scale. Ibis 140:214-222.

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.

Kazama, K., M. Sato, and K. Kosugi. 2015. Annual variation in breeding number of two gull species in response to regional stock size and local availability of Japanese sand lance on Rishiri Island, Northern Japan. Ornithological Science 15 (1): 85-94.

Kingsford, R. 1999. Aerial survey on wetlands as a measure of river and floodplain health. Freshwater Biology 41: 425-438.

Klassen, J. A., D. E. Gawlik, and P. C. Frederick. 2016. Linking wading bird prey selection to number of nests. The Journal of Wildlife Management 80(8):1450-1460.

Krebs, J. R. 1971. Territory and breeding density in the Great Tit, Parus major L. Ecology 52:2-22.

Krebs, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea Herodias*). Behaviour 51(1): 99-134.

Krebs, D. W. and J. R. Stephens. 1986. Foraging Theory. Princeton University Press, Princeton, New Jersey

Kushlan, J. 1976. Wading bird predation in a seasonally fluctuating pond. The Auk 93: 464-476.

Kushlan, J. A. and M. A. Kushlan. 1980. Everglades alligator nests: nesting sites of marsh reptiles. Copeia 1974: 930-932.

Kushlan, J.A. 1981. Sampling characteristics of enclosure fish traps. Transactions of the American Fisheries Society 110: 557-562.

Kushlan, J. A. and K. L. Bildstein. 1992. White Ibis (*Eudocimus albus*). *In* The Birds of North America, no. 570 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Lack, D. 1950. The breeding seasons of European birds. The Ibis 92: 288-316.

Lantz, S. M., D. E. Gawlik, and M. I. Cook. 2011. The effects of water depth and emergent vegetation on foraging success and habitat selection of wading birds in the Everglades. Waterbirds 34(4): 439-447.

Levin, P., R. Petrik, and J. Malone. 1997. Interactive effects of habitat selection, food supply, and predation on recruitment of an estuarine fish. Oecologia 112(1) 55-63.

Loftus, W. F. and A. M. Eklund. 1994. Long-term dynamics of an Everglades small-fish assemblage. In: Davis, S.M. and J. C. Ogden (editors), Everglades: the Ecosystem and its Restoration. St. Lucie Press, Delray Beach, FL.

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

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65(1): 101-127.

Martinez, C. 2010. Trophic niche breadth and overlap of three egret species in a neotropical mangrove swamp. Waterbirds 33: 285-292.

McCrimmon, D. A., Jr. 1978. Nest site characteristics among five species of herons on the North Carolina coast. Auk. 95(2):267-280.

McCrimmon, D. A., Jr., J. C. Ogden, and G. T. Bancroft. 2001. Great Egret (*Ardea alba*). *In* The Birds of North America, no. 570 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Minias, Piotr. 2014. Evolution of within-colony distribution patterns of birds in response to habitat structure. Behavior Ecology Sociobiology 65(5): 851-859.

Miranda, L. and J. Collazo. 1997. Food habits of 4 species of wading birds (Ardeidae) in a tropical mangrove swamp. Colonial Waterbirds 20: 413-418.

ODonoghue, M, S. Boutin, C. Krebs, and E. Hofer. 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. Oikos 80(1) 150-162.

Olah, G., G. Vigo, R. Heinsohn, and D. J. Brightsmith. 2013. Nest site selection and efficacy of artificial nests for breeding success of Scarlet Macaws *Ara macao* in lowland Peru. Journal for Nature Conservation 22(2):176-185.

Olbert, J. 2013. The breeding ecology of endangered snail kites (*Rostrhamus sociabilis plumbeus*) on a primary nesting site in central Florida, USA. Thesis. University of Florida, Gainesville, Florida.

Ostfeld, R. S. and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems, Trends in Ecology and Evolution 15: 232-237.

Parnell, J. F., R. N. Needham, R. F. Soots, J. O. Fussel, D. M. Dumond, D. A. McCrimmon, R. D. Bjork and M. A. Shields. 1986. Use of dredged-material

deposition sites by birds in coastal North Carolina, USA. Colonial Waterbirds 9(20): 210-217.

Parsons, K. C. and T. L. Master. 2000. Snowy Egret (*Egretta thula*). *In* The Birds of North America, no. 489 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Philippi, T. 2003. CERP Monitoring and Assessment Plan: Stratified Random Sampling Plan. Final Report submitted to the South Florida Water Management District, West Palm Beach, FL. Florida International University, Miami, FL.

Piper, S. D. and C. P. Catterall. (2004). Effects of edge type and nest height on predation of artificial nests within subtropical Australian eucalypt forests. Forest Ecology Management 203: 361-372.

Poizat, G. and A. Crivelli. 1997. Use of seasonally flooded marshes by fish in a Mediterranean wetland: timing and demographic consequences. Journal of Fish Biology 51: 106-119. Pyrovetsi, M. 1997. Integrated management to create new breeding habitat for Dalmatian Pelicans (Pelecanus crispus) in Greece. Environmental Management 21(5): 657-667.

Rader, R. B. and C. J. Richardson. 1994. Response of macroinvertebrates and small fish to nutrients enrichment in the northern Everglades. Wetlands 14: 134-146.

R Core Development Team 2009. R: language and environment for statistical computing. Version 2.9.0. Available at: http://www.r-project.org.

RECOVER, 2014. External Draft, 2014 System Status Report (Chapter 6). Restoration
Coordination and Verification Program, c/o United States Army Corps of
Engineers, Jacksonville District, Jacksonville, Florida, and South Florida Water
Management District, West Palm Beach, Florida.

Richardson, J. R. and T. T. Harris. 1995. Vegetation mapping and change detection in the
Lake Okeechobee marsh ecosystem. Archiv fr Hydrobiolgie (special Issues,
Advances in Limnology) 45:17-39.

Robertson, B. 2009. Nest-site selection in a postfire landscape: Do parents make tradeoffs
between microclimate and predation risk? The Auk 126(3) 500-510.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions
to Zoology 9:1-48.

Ricklefs, R. E. and F. R. Hainsworth. 1969. Temperature regulation in nestling Cactus
Wrens: The nest environment. Condor 71:32-37. Modeling nest-survival data:
Recent improvements and future directions. Pages 145-148 in Beyond Mayfield:
Measurements of nest-survival data (S. L. Jones and G. R. Geupel, eds.). Studies
in Avian Biology, no. 34.

Rotella, J. J. 2007. Modeling nest-survival data: recent improvements and future
directions. Studies in Avian Biology 34: 145-148.

Schmidt, K. A. and R. S. Ostfeld. 2003. Songbird populations in fluctuating
environments: Predator responses to pulsed resources. Ecology. Ecological
Society of America 84: 406-415.

Schreiber, R. W. and E. A. Schreiber. 1978. Colonial bird use and plant succession on dredged material islands in Florida. Technical Report D-78-14 prepared for the U.S. Army Corps of Engineers. Washington, D. C.

Selman, W. and B. E. Davis. 2015. First nesting records in southwestern Louisiana for American Oystercatchers (Haematopus palliates) and Reddish Egrets (Egretta rufescens), with implications for dredge spoil island restoration. The Wilson Journal of Ornithology 127(2):326-332.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

Simons, L. S. and T. E. Martin. 1990. Food limitation of avian reproduction: An experiment with Cactus Wren. Ecology 71(3): 869-876.

Spear, K. A., S. H. Schweitzer, R. Goodloe, and D. C. Harris. 2007. Effects of management strategies on the reproductive success of Least Terns on dredge spoil in Georgia. Southeastern Naturalist 6(1): 24-34.

Smith, J. P. 1995. Foraging flights and habitat use of nesting wading birds (Ciconiiformes) at Lake Okeechobee, Florida. Colonial Waterbirds 18(2):139-158

Smith, J. P., J. R. Richardson, and M. W. Collopy. 1995. Foraging habitat selection among wading birds (Ciconiiformes) at Lake Okeechobee, Florida, in relation to hydrology and vegetative cover. Archiv fur Hydrobiolgie Beiheft Ergebnisse der Limnologie 45: 247-285.

Smith, J. P. 1997. Nesting season food habits of 4 species of herons and egrets at Lake Okeechobee, Florida. Colonial Waterbirds 20(2): 198-220.

Smith, J. P. and M. W. Collopy. 1995. Colony turnover, nesting success and productivity, and cause of nest failure among wading birds (Ciconiiformes) at Lake Okeechobee, Florida Archiv fur Hydrobiolgie Beiheft Ergebnisse der Limnologie 45: 287-316.

Strong, A. M., G. T. Bancroft, and S. D. Jewell. 1997. Hydrological constraints on tricolored heron and snowy egret resource use. Condor 99: 894-905.

Tabib, R., A. Adamou, M. L. Ouakid, M. Gladalski, and J. Banbura (2016). Nesting height and nest-cup voloume variation in Rufous Bush Chats (Cercotrichas galactotes inhabiting Algerian oases: consequences for breeding success. Avian Biology Research 9(2): 114-119.

Taylor, I. R. and M.C. Schultz. Breeding season diets of egrets in southeast Australia: implications for future population viability. Waterbirds 31(4): 593-601.

Torres, R., P. Michelutti, J. Dominino, J. Leon, A. Mangeaud, A. Rodriguez, C. Pozzi, G. Plencovich, M. Pagot, and G. Hillman. 2010. Effects of water level on reproduction of colonial waterbirds in Laguna Mar Chiquita – Banados del Rio Dulce (Central Argentina). Ornitologia Neotropical 21: 383 – 396.

Trexler, J. C. and C. W. Goss. 2009. Aquatic fauna as indicators for Everglades restoration: Applying dynamic targets in assessments. Ecological Indicators. 9S: S108-S119.

Trimble, P. and J. Marban. 1988. Preliminary evaluation of the Lake Okeechobee regulation schedule. Technical Report 88-5. South Florida Water Management District, West Palm Beach, Florida.

Turner, A. M, J. C. Trexler, C. F. Jordan, S. J. Slack, P. Geddes, J. H Chick. 1999. Targeting ecosystem features for conservation: Standing crops in the Florida Everglades. Conservation Biology 13: 898-911.

Viñuela, J. and Sunyer, C. 1992. Nest orientation and hatching success of black kites Milvus migrans in Spain. Ibis. 134:340-345.

Wittenberger, J. F., and G. L. Hunt, Jr. 1989. The adaptive significance of coloniality in birds, p. 1-78. *In* D. S. Farner, J. R. King and K. C. Parkes [eds.], Avian biology. Vl. 8. Academic Press, New York.

Yorio. P. and P. Boersma. 1994. Causes of nest desertion during incubation in the Magellanic Penguin (*Spheniscus magellanicus*). Condor 96: 1076-1083.

Zaffke, M. 1984. Wading bird utilization of Lake Okeechobee marshes: 1977-1981. South Florida Water Management Technical Publication 84-9.

Zhang, J. and B. Sharfstein. 2012. Chapter 8: Lake Okeechobee protection program. Pages 1-71 *in* 2012 South Florida Environmental Report, vol. 1. South Florida Water Management District, West Palm Beach.