EFFECT OF DIET DIFFERENCES AND NON-NATIVE PREY CONSUMPTION ON

THE PRODUCTIVITY OF SMALL HERONS

by

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EFFECT OF DIET DIFFERENCES AND NON-NATIVE PREY CONSUMPTION ON

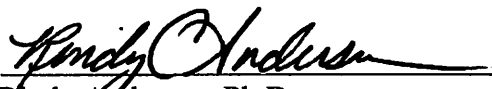# THE PRODUCTIVITY OF SMALL HERONS

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This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Dale E. Gawlik, Environmental Science Program, 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.

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ABSTRACT

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Little Blue Herons, Snowy Egrets, and Tricolored Herons that nest in the Everglades have declined sharply over the past decade, due in part to food resource limitations. Here, I examined the diet of small herons to determine how prey characteristics affected the fitness of small herons in the highly modified Florida Everglades. Analysis of these diet differences showed birds nesting in 2017, a hydrologically dryer-than average year, and a more taxonomically varied diet were associated with nest success and improved body condition of nestlings. Over half (51%) of the fish biomass Little Blue Herons consumed were non-native species, compared to 14% and 19% non-native fish biomass consumed by Snowy Egrets and Tricolored Herons, respectively. Surprisingly, <7% of fish biomass available in the Everglades were comprised of non-native fish species, suggesting that small herons, and Little Blue Herons in particular, may be using alternative foraging habitats, to supplement their dietary needs.

DEDICATION

My thesis is dedicated to my inspiring and amazing mother Maribeth, who not only gave me an affinity for learning, but also showed me by example to never shy away from the pursuit of education, no matter what the challenges.

EFFECT OF DIET DIFFERENCES AND NON-NATIVE PREY CONSUMPTION ON

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1   INTRODUCTION

1.1   ENVIRONMENTAL CHANGE

Global anthropogenic modification has forced many species to respond to human-induced rapid environmental change (HIREC; Lockwood *et al*. 2007, Fabry *et al*. 2008, Sih *et al*. 2011), which can negatively affect the success or persistence of a species (Stenseth *et al*. 2002, Walther *et al*. 2002). Habitat loss and fragmentation, exotic species, overexploitation, pollutants, and climate change have forced some organisms into novel ecosystems, not previously experienced in their evolutionary lineage (Palumbi 2001, Simberloff *et al*. 2005, Rohr *et al*. 2006). Environmental modifications such as these can result in deleterious effects for some species, while others adapt and thrive (Both *et al*. 2006, Chace and Walsh 2006, Ludwig *et al*. 2006, Wong and Candolin 2015).

Behavioral modifications are often an initial response by a species to environmental changes, in part due to the mechanisms relatively rapid pace and ability to be induced within a single generation (Candolin and Wong 2012, Wong and Candolin 2015). Behavioral changes at the individual level can also act as predictors for long-term change within the population (Candolin and Wong 2012) and can occur gradually. While several measures of behavioral responses to environmental change exists, resource selection and diet change can serve as an early response because all individuals depend on food resources to sustain a certain level of fitness (Candolin and Wong 2012), and energy reserves that might buffer against diet shifts are typically short-lived. The behavioral decision to select for non-native prey in place of, or in conjunction with native

prey will first affect the individual in terms of fitness. The outcome of this behavioral process at the individual level, will ultimately impact the population which will be affected by new food resources in one of three ways: 1) a diet shift consisting of lower nutritional content, increased toxins or greater handling time can have a detrimental effect on a population (Riley *et al*. 2007, Cattau *et al*. 2010, Plummer *et al*. 2013, Murray *et al*. 2015). 2) A diet shift of nutritionally comparable food to historic norms can help maintain species persistence (Yoda *et al*. 2012), and 3) a diet shift containing food resources of greater nutritional quality, or more spatially or temporally available than historic norms can increase population viability and persistence (Duhem *et al*. 2008).

As of yet, it is difficult to determine which species will utilize new food resources, and in turn, how a diet shift will impact the population (Candolin and Wong 2012). Variations in dietary shifts in response to environmental change can vary even among species within the same genus (Sih *et al*. 2011). Therefore, behavioral modifications may be important variables in determining why variations exist among closely related species. To examine the degree to which animals adjust their foraging habitat and behavior to accommodate rapid environmental change, I compared diet use among three species of wading birds (*Ciconiiformes*) within the genera *Egretta,* that forage sympatrically in an ecosystem heavily impacted by HIREC.

1.2   STUDY SPECIES

Wading birds of the genus *Egretta,* including Little Blue Heron (*Egretta caerulea)*, Snowy Egret (*E. thula)*, and Tricolored Heron (*E. tricolor),* collectively known as small herons, are ideal study species for resource use partitioning not only due to their close taxonomic relation, but also their physical similarities and geographic ranges. All

are apex predators and visual foragers which consume a diet of small fishes, invertebrates, and amphibians (Kushlan 1976, Kent 1986, Frohring *et al.* 1988). Tricolored Herons and Snowy Egrets are considered fish specialists, while Little Blue Herons are diet generalists, showing a greater trophic diversity in their diet (Martinez 2010, Klassen *et al.* 2016).

Morphologically alike, small herons have roughly similar body size, leg length, and bill shape (Erwin 1985, Frohring *et al.* 1988). In the Florida Everglades, small herons nest in mixed-species colonies, and frequently forage in mixed-species flocks (Kushlan 1976, Caldwell 1980, Burger 1981). Despite these similarities, each species exhibits variations in foraging strategies (Kushlan 1981, Gawlik 2002), and they exhibit differences in foraging behavior to adjust these strategies as environmental conditions change (Gawlik 2002). Such variations in foraging behavior can strongly affect individual fitness (Schmitz 1998; Blackenhorn 2000), including nest productivity and body condition.

1.3   ALTERED ECOSYSTEM PROCESSES

Small herons reside year-round in the Florida Everglades which has been heavily impacted by HIREC. Alterations to this large, sub-tropical wetland began in the 1880s and have persisted for over a century (Light and Dineen 1994, Larsen *et al*. 2011). Modifications to the Everglades include water drainage, and construction of >1500-km of canals, levees, and pump stations which have resulted in a fragmented Everglades roughly half its original size (Light and Dineen 1994). Today, approximately 70% less water flows through the Everglades as compared to historic norms, and the remaining natural ecosystem continues to be affected by surrounding agricultural and urban

developments (Perry 2004). Anthropogenic modifications to the Everglades have significantly impacted wading birds which have experienced a 61% decline in wading bird nest numbers in the southern portion of the Everglades since the 1980s (Crozier and Gawlik 2003), and a more serious decline in nest numbers in the ecosystem over the past decade (SFWMD 2016). The cause of the decline is unclear but wading birds in this ecosystem and others are often food limited (Ogden 1994, Hafner 1997; Herring *et al.* 2010).

1.3.1   Hydrologic Fluctuations

Multiple studies have shown that wading bird food acquisition is strongly correlated to hydrologic conditions in the Everglades (Loftus and Kushlan 1987, Gawlik 2002), which is dependent on natural flooding from northern headwaters traveling south into Florida Bay. Historically, these conditions provided annual wet and dry seasons (Kushlan 1989). Long periods of inundation during the wet season (June – November) allow prey biomass to increase (Loftus and Kushlan 1987, DeAngelis *et al.* 2005). During the dry season (December – May) prey take refuge in depressions in microtopography, thus increasing prey density and vulnerability (Gawlik 2002, Lantz *et al.* 2011). Wading birds coincide nest initiation with this pulse of available prey (Kahl 1964, Kushlan 1980, Loftus and Eklund 1994). However, anthropogenic modifications to the ecosystem have disrupted the abundance of available food resources (Frederick and Collopy 1989, Bancroft *et al.* 1990, Walters *et al.* 1992). Lack of food resources is considered a major factor in the decline of wading bird nesting success in the Everglades (Ogden 1994, DeAngelis *et al.* 2005), and starvation is one of the main causes of wading bird nestling mortality (Jenni 1969, Herring *et al.* 2010).

1.4 PROJECT OBJECTIVES

Other studies have compared the differences in small heron diets (Kent 1986, Smith 1997, Martinez 2010), however they were conducted prior to 2000, the year non-native fish are documented as expanding into Everglades National Park (Kline *et al.* 2014, Langston *et al.* 2010), thus fail to examine the influence of non-native fish species on the diets of small herons. Additionally, more recent studies have compared the diets of small herons with relatively low sample sizes and fail to compare all three species over space and time (see Boyle *et al.* 2012, and Klassen *et al.* 2016) which can influence prey communities, thus influence resource use partitioning. In this study, I evaluated the differences among small heron species over varying spatial and temporal scales in the highly modified Florida Everglades. In Chapter 2 I investigated the impact of diet characteristics on the overall fitness of small herons during the nesting season, by evaluating diet differences on both nest success and nestling body condition. Next, Chapter 3 investigated the presence of non-native fishes available in the Everglades landscape, and the presence of these non-native species in the diets of small herons, as well as patterns of use. Finally, in Chapter 4 I discussed the conservation and greater implications of this study.

For the entirety of this study, nestling capture, handling and bolus collection techniques followed strict protocols approved by the Florida Fish and Wildlife Conservation Commission (permit number LSSC-12-00012B) and Institutional Animal Care and Use Committee at Florida Atlantic University (permit number A12-03).

2 DIFFERENCES IN PREY CHARACTERSITICS IMPACT FITNESS OF SYMPATRIC WADING BIRDS

2.1 ABSTRACT

Wetlands have declined globally by as much as 71% during the 20th century and continue to degrade, contributing to the global loss of biodiversity driven by habitat degradation and loss. The Florida Everglades has experienced degradation and habitat loss for over a century. Because natural processes are impacted by anthropogenic activities, animals that live in natural systems near dense human populations can experience increased competition for resources. Sympatric species can mitigate the effects of competition by either diverging food resource use or differ such use temporally or spatially. Food resource use differentiation can lead to significant differences in growth, reproduction, and fitness rates among individuals. This study determined the diet composition and corresponding nesting success and nestling body condition in three species of wading birds to determine how diet characteristics affect the overall fitness of breeding small herons in the Florida Everglades. I collected 220 stomach bolus samples and determined the fate and body condition of 190 nestlings from 80 small heron nests from four Everglades wading bird colonies during the 2015-2017 nesting seasons. I found that Snowy Egret and Tricolored Heron diet consisted of 93% and 98% fish biomass, respectively. Whereas Little Blue Heron diet consisted of 43% fish, 32% crustaceans, 13% amphibians and reptiles, and 12% insect biomass, resulting a much more taxonomically diverse diet. Analysis of these diet differences showed that birds nesting in

2017 (a hydrologically dryer-than average year), and birds with more taxonomically varied diet were associated with nest success and improved body condition of nestlings.

2.2 INTRODUCTION

Wetlands are an important and valuable resource, due in part to their ecosystem services and abundant animal and plant diversity (Bobbink *et al.* 2006, Costanza *et al.* 2008). Wetlands have declined globally by as much as 71% during the 20th century and continue to degrade (Gardner *et al.* 2015), contributing to the global loss of biodiversity driven by habitat degradation and loss (Tilman *et al.* 2001, Brooks *et al.* 2002). The Florida Everglades, is the largest wetland in the United States, covering approximately 6,200 km^2 (Sutula *et al.* 2003), and has experienced degradation and habitat loss for over a century (Light and Dineen 1994, Larsen *et al.* 2011). Because natural processes are impacted by anthropogenic activities, animals that live in natural systems near dense human populations can experience increased competition for resources (Ditchkoff *et al.* 2006).

Competition may occur when species with shared feeding ecologies attempt to exploit the same limited food resource in time and space (Birch 1957, Tilman 1987, Wiens 1989). Sympatric species can mitigate the effects of competition by either diverging food resource use or differ such use temporally or spatially (MacArthur and Levins 1967, Armstrong and McGehee 1980, May and Hassell 1981, Chesson 1985, Chesson 2000). Food resource use differentiation can lead to significant differences in growth, reproduction, and fitness rates among individuals (Dewsbury 1982, Suryan *et al.* 2000, Cucherousset *et al.* 2011). Animal communities depend on natural processes, such as seasonal hydrologic fluctuations (Neckles *et al.* 1990, Alho 2008) to promote potential

competition among individuals. As these natural processes are degraded, through either natural or anthropogenic processes, mechanisms that allow for resource partitioning may be impacted.

2.2.1 Objectives

This study contained three objectives to evaluate how food resource use partitioning impacted species fitness in a highly modified environment. First, I determined if a significant difference in food resource use was present among small herons nesting in the Florida Everglades by comparing prey species use among small herons on varying temporal and spatial scales. Second, if food resource partitioning was detected, I determined which prey characteristics negatively or positively influenced two measures of nest productivity (nest success and body condition). Lastly, I determined if prey characteristics which impacted nest productivity varied among bird species or were consistent across all three small heron species.

2.3   METHODS

2.3.1   Data Collection

Food boluses (stomach regurgitation) were collected from Little Blue Heron, Snowy Egret and Tricolored Heron, in four colonies within the Everglades of Florida during the 2015, 2016 and 2017 nesting seasons (Fig. 2.1). Wading bird colonies were selected based on their historical use as colonial nest sites, diverse vegetative communities, and accessibility. Paurotis Pond (25.2811° N, 80.8016° W) is a coastal colony surrounded by brackish wetlands dominated by red mangrove (*Rhizophora mangle)* and located in the southern portion of Everglades National Park. Tamiami West colony (25.7578° N, 80.5448° W) is surrounded by freshwater marsh and is dominated

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by pond apple (*Annona glabra*) and willow (*Salix* spp.) and is located along the northern boundary of Everglades National Park. Hidden colony (25.7735° N, 80.837° W) is surrounded by forested swamp, and comprised mostly of bald cypress trees (*Taxodium distichum)* and coco plum (*Chrysobalanus icaco*) and is in the southwestern portion of Water Conservation Area 3A. The Loxahatchee slough colony (26.8686° N -80.1778° W) is surrounded by herbaceous marsh wet prairie located in the northern portion of the greater Everglades and is vegetated primarily by pine flatwoods (*Pinus spp.)* and saw palmetto (*Serenoa repens)*.

I visited active colonies and associated nests one to two times per week. Nests accessible by either climbing trees, ladders, or close enough to reach nests from the ground were chosen, with priority given to nests containing one to two-week-old nestlings. Each nest was flagged with tape and given a unique identification. Food boluses were collected from nestlings that voluntarily regurgitated as a natural response to predators (Byers 1951, Furness and Hislop 1981, Nell and Frederick 2015). When voluntary regurgitation did not occur quickly, I gently lifted the chick up and down while occasionally massaging the esophagus to induce regurgitation. Nestlings were then returned to nests and provided small fish in the nest bowl to compensate for loss of stomach contents.

To determine nestling body condition, a keel score was determined by palpating the pectoral muscle of chicks and scored as an index ranging from 1 to 5 (1: prominent keel, breast bone very sharp; 2: breast bone easily felt and sharp; 3: breast bone easily felt, but not sharp; 4- pressure needed to feel breast bone; 5- tissue greater than flush with keel, not possible to feel breast bone; Newton 1993). An overall keel score for the nest

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was determined by averaging all chicks sampled per nest over the course of a nesting season. Nests were considered successful (hereafter, apparent nest success) if a nesting attempt produced at least one chick to the age of 14 days (Hensler and Nichols 1981, Frederick and Collopy 1989), when small herons become mobile and are no longer obviously associated with a nest (Werschkul 1979, Rodgers 1987). I transported bolus samples on ice to the lab and froze until processed.

At the lab, animals in bolus samples were thawed and identified to the lowest possible taxonomic group. Standard length (fish) or total length (other animals) was measured in mm, and a wet weight was determined to the nearest 0.01 g. Length and/or weight measurements were omitted for any prey items partially digested, and recorded as such.

2.3.2   Statistical Analysis

2.3.2.1   Differences in Food Resource Use Among Small Herons

To determine differences in prey composition among small herons, bolus samples were grouped by bird species, colony, and year. Prey species that occurred only once over the duration of the study were omitted to prevent over-representation of rare species (Clarke and Gorley 2015). Prey species that contributed to 1% or less of the total biomass were categorized into higher taxonomic groups. I determined relative abundance and percent biomass for all prey species and groups of species when necessary. A one-way ANOVA was conducted to compare the effects of small heron species on the average prey length consumed.

To determine differences in prey composition among samples I used PRIMER 7 software (Clarke and Gorley 2015) to create non-metric multi-dimensional scaling

(nMDS) plots. The percent biomass of prey per sample was analyzed using a square-root

transformation, and calculated Bray-Curtis similarity matrices for each sample type.

Using the Bray-Curtis similarity matrices, I ran an ANOSIM test (analysis of similarities)

between sample types (comparison among bird species, colonies and years). An

ANOSIM is a non-parametric permutation procedure which tests for differences among

samples based on ranks of pairwise similarities in the Bray-Curtis matrix. ANOSIM test

produced an R-statistic (ranging from -1 to 1) which compares the measure of the degree

of separation of sites (Clarke and Gorley 2015) as well as a p-value. The R-statistic is

arguably more important in determining the statistical significance in an ANOSIM than

the p-value, which can be inflated by changing the number of permutations or replicates.

The R-statistic however, has more absolute interpretation as it is not affected by the

number of replicates being compared (Clarke and Gorley 2015). If a difference was

detected in the R-statistic, I then used a SIMPER (similarity percentage breakdown)

analysis to determine prey species contributions to sample dissimilarity, and a cluster

analysis to reflect samples increasing thresholds of similarity by percent biomass.

2.3.2.2   Productivity Measurements

Productivity data was not colled during the 2015 nesting season, thus bolus

samples collected during the 2016 and 2017 nesting seasons only were used to determine

if prey composition characteristics affected two productivity measurements: apparent nest

success and body condition. Bolus samples collected from each nest over the course of a

season were treated as a sample unit. I used an information theoretic approach and

Akaike's Information Criterion (AIC) (Burnham and Anderson 2002; Burnham and

Anderson 2004). I used Akaike's Information Criterion for small sample sizes (AICc) to

determine which *a priori* models were most parsimonious (Table 2.1 and 2.3). I

constructed a generalized linear mixed-model using R 3.4.1 software (Team R C 2015)

and package lme4 (Bates *et al.* 2015). Before running the models, I determined if

collinearity was present among explanatory variables. I also calculated ΔAIC_c values and

model probabilities (wi) to determine the distance between the best model and all other

models. Models with $\Delta AICs < 4$ were considered equally plausible (Burnham and

Anderson 2002). I calculated averaged parameter estimates for each model to determine

the explanatory effect of each variable on the response variable (body condition, or

apparent nest success). To examine model variability, 95% confidence intervals were

calculated for parameter estimates. A likelihood version of the correlation coefficient was

calculated for each model to examine model fit.

To examine the influence of food resource use differences on apparent nest

success and body condition, I developed the following model sets: 1) all small heron

nests (Little Blue Heron, Snowy Egret, Tricolored Heron), 2) Little Blue Heron nests

only, 3) Snowy Egret nests only, 4) Tricolored Heron nests only. Three competing

models for apparent nest success included the global model, prey model and chicks

model (Table 2.1), and a fourth competing model (year model) for body condition was

included (Table 2.3). Each nest was treated as a sampling unit. The response variable

was nest success or failure for the apparent nest success models, and average keel score

of chicks per nest (1-5) for the body condition models. The main predictor variables of

interest for both model sets were proportion of fish biomass, average prey length, and

diversity of prey taxa consumed (Table 2.2). Colony, bird species, and year were treated

as random effects. Other covariates included in the model were number of total chicks

per nest. The nest success models also included the covariate average keel score (Table 2.2), and the body condition models included the covariate year to represent different hydrologic conditions experienced during the nesting season (Table 2.4).

2.4   RESULTS

2.4.1   Differences in Food Resource Use Among Small Herons

I collected a total of 6,650 prey items from small heron chicks, in four colonies during the 2015-2017 nesting seasons (Table 2.5). Gaps in data collection are due to either birds not initiating nesting in specific colonies during certain years, or safety precautions for nestlings and field crew. Only four Snowy Egret pairs nested at Hidden in 2015, none of which produced a bolus when sampled. Little Blue Herons were not seen nesting in Tamiami West in 2015, although I did see adults near the colony. For unknown reasons, small herons did not nest in Hidden in 2016, and only two Tricolored Heron nests were observed in Hidden in 2017. The Loxahatchee slough colony was first discovered in 2017, where only one Tricolored Heron pair and no Snowy Egret nests were observed. While all small herons nested in Paurotis Pond during the 2017 season, I sampled only 3 nests because of an unusually high risk of nest predation by crows in response to observer disturbance and aggressive alligator activity.

The three most abundant species by frequency in the diet of the Little Blue Heron were grass shrimp (*Palaemonetes paludosus*), dragonfly larvae (*Odonata spp.*), and crayfish (*Procambarus spp.*), which collectively accounted for 39.5% of prey items. The most abundant prey species by frequency in Snowy Egret and Tricolored Heron diet was the Eastern mosquitofish (*Gambusia holbrooki)* which accounted for 34.9% and 36.5% of prey items, respectively (Table 2.6).

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Prey contributing to the greatest biomass in the Little Blue Heron diet were crayfish, African jewelfish (*Hemichromis letourneauxi)*, and frogs (*Anura spp.*; adult stage) contributing 23, 13, and 11%, respectively, of the total biomass. Little Blue Heron consumed 42.6% fish by weight. The most abundant prey species by mass in the diet of the Snowy Egret were sailfin molly, Eastern mosquitofish and golden topminnow which accounted for 21, 15, and 15%, respectively, of the total biomass. Snowy Egret diet contained 93.1% fish by weight. Prey species contributing most to biomass of the Tricolored Heron diet were sailfin molly (*Poecilia latipinna)* and golden topminnow (*Fundulus chrysotus)* which accounted for 18% and 18%, respectively, of the total biomass. By weight, Tricolored Heron diet contained 98.2% fish.

Of the 55 different prey species identified, 34 species represented 1% or less total prey biomass across all bird species, thus were combined into higher taxonomic groupings. This resulted in 17 prey species or categories that were used for subsequent diet comparisons. Categories were represented by eight native fish species, four non-native fish species, two crustacean, two insect, and one amphibian/reptile (herptiles) (Table 2.7, Fig. 2.2). Native and non-native fishes were grouped separately because studies have shown occurrences may vary geographically (Shafland 1996, Trexler *et al*. 2000, Kline 2014), indicating possible variations in foraging strategies among bird species.

An ANOSIM to determine if prey use differed among colonies showed a global R-statistic of 0.25 and a p-value of 0.26, demonstrating that small heron diets were slightly different among colonies. However, pairwise tests between colonies demonstrated a strong dissimilarity between Paurotis Pond and Loxahatchee (R-statistic

of 0.91), as well as between Tamiami West and Loxahatchee (R-statistic of 0.70) (Table 2.8). A one-way SIMPER showed that prey species driving the difference between Loxahatchee and the other colonies were amphibians and crayfish (collected from the Loxahatchee slough colony) and sailfin molly, African jewelfish, Eastern mosquitofish and golden topminnows (collected from Paurotis Pond and Tamiami West colonies). Because the prey identified from bolus samples collected from the Loxahatchee slough colony were so different from the other three colonies, and representative of only one year of the study (2017) and predominately one bird species (Little Blue Heron), this colony was omitted from subsequent diet comparison analysis.

Mean prey length was 2.11 ± 1.2 cm SD for Little Blue Heron, 1.99 ± 0.9 cm SD for Snowy Egret, and 2.54 ± 1.0 cm SD for Tricolored Heron. An analysis of variance showed that the effect of small heron species on the average prey length consumed was significant, $F_{(2, 186)} = 14.43$, $p = 1.49E^{-06}$ (Table 2.8).

An ANOSIM testing for differences in prey composition among years showed weak but significant differences (global $R = 0.24$, p=0.01). Pairwise tests between years showed a stronger difference in diet composition ($R = 0.42$, P=0.01; Table 2.9). A one-way analysis SIMPER showed that differences between prey consumed in 2015 verses 2016 were largely driven by a greater abundance of crayfish in 2015 contributing to 10% of the dissimilarity. Differences between prey consumed in 2015 verses 2017 were largely driven by a greater abundance of grass shrimp in 2015 contributing to 11% of the dissimilarity. Differences between prey consumed in 2016 verses 2017 were largely driven by grass shrimp contributing to 10% of the dissimilarity.

An ANOSIM testing for differences in prey composition among bird species showed moderate differences in diet composition (global R = 0.40, p=0.01). Diet differences between Snowy Egret and Tricolored Heron based on pairwise tests were only slightly different (R = 0.20), however, differences between Snowy Egret and Little Blue Heron were stronger (R= 0.45). Pairwise test between Tricolored Heron and Little Blue Heron showed a strong dissimilarity (R= 0.70; Table 2.9). A one-way analysis SIMPER showed that the difference between Snowy Egret and Little Blue Heron diets were largely driven by a greater abundance of crayfish and African jewelfish in Little Blue Heron diet, and more Eastern mosquitofish and flagfish in the Snowy Egret diet; collectively these differences in prey items contributed to 36% of the dissimilarity. While the abundance of sailfin molly, golden topminnow and flagfish in Tricolored Heron diet, versus the abundance of crayfish and African jewelfish in Little Blue Heron diet contributed to 44% of the dissimilarity.

Results from a nMDS and cluster analysis (Fig. 2.3) showed Snowy Egret and Tricolored Heron diets were 45% similar regardless of the year of nesting or colony location. Similarly, regardless of colony location, Little Blue Heron nests sampled in 2015 were 65% similar in diet, while slightly less in 2016 and 2017 Little Blue Heron nests shared a 55% similarity in diet.

2.4.2   Productivity Measurements

Two response variables were developed to determine measures of small heron productivity: a) apparent nest success (failure or success) and b) body condition (average keel score per nest). During the 2016 and 2017 nesting season 220 bolus samples, as well as apparent nest success and body condition were collected from 190 individual chicks

from 80 different nests in four Everglades colonies (Table 2.10). All prey collected from individual nests over the course of a nesting season were grouped, and each nest was treated as a sample unit. Of the 80 nests samples, 68 nests were successful, while 12 nests failed (four Little Blue Heron, one Snowy Egret, and seven Tricolored Heron). The average keel score per nest was 2.65 ±0.06 (Table 2.11).

2.4.2.1   Apparent Nest Success Models

The all small herons model (Table 2.12) treated year, colony and bird species as random effects. For individual bird species models (Table 2.13 and 2.15), year and colony were treated as random effects. Because data from only one failed Snowy Egret was collected, model development for Snowy Egret nests was not possible.

2.4.2.1.1   All Small Herons

The global model was the top model ($w_i = 0.33$; Table 2.12) for explaining apparent nest success or failure in small herons with 33% of the model weight. However, the prey model, which contributed to 28% of the total weight had a delta $AIC_c < 4$ (Burnham and Anderson 2002) suggesting this model was also plausible in explaining small heron apparent nest success. For this reason, the global model and prey model, contributing to 61% of the total weight were averaged (Table 2.13).

Model averaging showed that a higher keel score had a positive influence on apparent nest success, and because the parameter did not overlap zero, asserting confidence that keel score had a strong relationship with apparent nest success. Greater mean prey length and the number of chicks on the nest had a negative influence on apparent nest success, and although the confidence intervals did overlap zero, the overlap was very small, giving more confidence in these parameters than the others that

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overlapped zero to a larger degree. All other parameters overlapped zero indicating a weak relationship with apparent nest success (Table 2.13).

2.4.2.1.2 Little Blue Heron

The null model was the top model ($w_i = 0.74$; Table 2.14) for explaining apparent nest success or failure in Little Blue Herons, contributing to 74% of the total weight. However, the chicks model, which contributed to 16% of the total weight had a delta $AIC_c < 4$ (Burnham and Anderson 2002) suggesting this model was also plausible in explaining Little Blue Heron apparent nest success. For this reason, the null model and the chicks model, contributing to 90% of the total weight were averaged (Table 2.15).

Model averaging showed that higher average keel scores had a positive influence on apparent nest success, whereas a greater number of chicks on the nest had a negative influence on Little Blue Heron apparent nest success. Both parameters did overlap zero, however, the overlap was small, providing more confidence in these parameters than the others that overlapped zero to a larger degree (Table 2.15).

2.4.2.1.3 Tricolored Heron

The chicks model was the top model ($w_i = 0.82$; Table 2.16) for explaining apparent nest success or failure in Tricolored Herons, contributing to 82% of the total weight. However, the global model which contributed to 13% of the total weight was also plausible with a delta $AIC_c < 4$ (Burnham and Anderson 2002). For this reason, the chicks model and global model which contributed to 95% of the total weight were averaged (Table 2.17).

Model averaging showed that higher average keel scores, and a greater prey diversity index score had a positive influence on Tricolored Heron apparent nest success,

with neither parameter overlapping zero, giving confidence that these parameters had a strong relationship with apparent nest success. Greater mean prey length and number of chicks on the nest both had a negative influence on Tricolored Heron apparent nest success, and although the confidence intervals did overlap zero, the overlap was very small, giving more confidence in these parameters than the others that overlapped zero to a larger degree. All other parameters overlapped zero indicating a weak relationship with apparent nest success (Table 2.17).

2.4.2.2   Body Condition Models

Four model sets were developed including 1) all small herons, 2) Little Blue Heron, 3) Tricolored Heron, and 4) Snowy Egret.

2.4.2.2.1   All Small Herons

The year model was the top model (w_i = 0.64; Table 2.18) contributing to 64% of the total weight. However, the global model which contributed to 36% of the total weight was also plausible with a delta AIC_c < 4 (Burnham and Anderson 2002). For this reason, the year model and global model which contributed to 100% of the total weight were averaged (Table 2.19).

Model averaging showed that 2017 (a hydrologically dry year), and a greater number of chicks on the nest, were associated with a positive influence on body condition, whereas a greater percentage of fish biomass in the diet was associated with a negative influence on body condition. Because confidence intervals for year, number of chicks, and fish biomass percentage did not overlap zero, I have confidence that these parameters had a strong relationship with the average body condition of small heron nestlings. Additionally, a higher prey diversity index score had a positive influence on

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body condition and greater mean prey length had a negative influence on body condition. Although both of these parameters had confidence intervals which overlapped zero, the overlap was very small, giving more confidence in these parameters than the others that overlapped zero to a larger degree (Table 2.19).

2.4.2.2.2 Little Blue Heron

The year model was once again the top model ($w_i = 0.54$; Table 2.20) contributing to 54% of the total weight. However, the global model and prey model which contributed toward 25% and 14%, respectively, were also plausible with a delta $AIC_c < 4$ (Burnham and Anderson 2002). For this reason, the year model, global model, and prey model which contributed to 93% of the total weight were averaged (Table 2.21).

Once again, the year 2017 (a hydrologically dry year) and the percentage of fish biomass in the diet were important for affecting body condition. Model averaging showed that the year 2017 was associated with a positive influence on body condition, and a greater percentage of fish biomass in the diet was associated with a negative influence on body condition. Neither parameter overlapped zero, giving us confidence that these parameters had a strong relationship with the average body condition of Little Blue Heron nestlings. Unlike the small heron model, Little Blue Heron model results showed a greater mean prey length had a positive influence on body condition and a greater number of chicks, and higher prey diversity index score had a negative influence on body condition. These three parameters had confidence intervals which overlapped zero, however, the overlap was very small, giving more confidence in these parameters than the others that overlapped zero to a larger degree (Table 2.21).

2.4.2.2.3 Snowy Egret

The year model was once again the top model (w_i = 0.57; Table 2.22) contributing to 57% of the total weight, while the null model contained 35% of the total weight with a delta AIC_c < 4 (Burnham and Anderson 2002). For this reason, the year model, and null model which contributed to 92% of the total weight were averaged (Table 2.23).

Once again, the year 2017 (a hydrologically dry year) was associated with good body condition. Model averaging showed that 2017 had a positive influence on body condition and did not overlap zero, giving confidence that this parameter had a strong relationship with the average body condition of Snowy Egret nestlings (Table 2.23).

2.4.2.2.4 Tricolored Heron

The year model was once again the top model (w_i = 0.97; Table 2.24) contributing to 97% of the total weight. Because all other models had a delta AIC_c > 4 (Burnham and Anderson 2002) the year model only was used for parameter analysis (Table 2.25).

Once again, the year 2017 (a hydrologically dry year) was an important factor for affecting body condition. Model averaging showed that 2017 was associated with good body condition and did not overlap zero, giving confidence that this parameter had a strong relationship with the average body condition of Tricolored Heron nestlings (Table 2.25).

2.5   DISCUSSION

The diet of Little Blue Herons compared to Snowy Egrets and Tricolored Herons differed consistently across varying spatial and temporal scales (three years, and four nesting colonies). Differences were significant in both prey species composition and

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prey size. Little Blue Herons consumed a greater breadth of prey taxa than did other small herons. Although fish were a prominent component in Little Blue Heron diet (43% biomass), the species consumed less than half the amount of fish biomass than did the Snowy Egret and Tricolored Heron, which consumed 93% and 98% fish biomass, respectively. These results support the characterization of the Little Blue Heron as diet generalist and the Snowy Egret and Tricolored Heron as fish specialists (Jenni 1969, Kushlan 1981, Klassen *et al.* 2016).

Little Blue Herons which demonstrated a more diversified diet than Snowy Egrets and Tricolored Herons, may be able to exploit a greater diversity of nesting sites due to a maximum foraging radius of 30-km (Strong *et al.* 1997). Results suggest Little Blue Herons may be able to nest with greater success than Snowy Egrets and Tricolored Herons in colonies surrounded by foraging habitat with less concentrated and vulnerable fish communities. Instead, Little Blue Herons can switch prey types as needed, using a greater diversity of prey taxa available based on environmental conditions or competition from sympatric species. This greater dietary breadth may be why Little Blue Herons nearly exclusively nested at Loxahatchee Slough colony, where the colony was comprised of 50 Little Blue Heron nests, and only one Tricolored Heron nest. From this colony, stomach boluses from Little Blue Heron nestlings contained <2% fish biomass. In addition, the majority (88% total fish biomass) of the fish consumed by Little Blue Herons came from brown hoplo (*Hoplosternum littorale*), an exotic catfish found in low-oxygen waters and ditches (FFWCC 2017). Compared to Tricolored Heron stomach boluses which contained 94% fish biomass. This difference in diet among the small herons is an example of how a diet generalist such as the Little Blue Herons can exploit a

greater diversity of habitats than diet specialists such as Snowy Egrets and Tricolored Herons.

When determining how different levels of productivity were influenced by prey characteristics, a few patterns fell out as consistent among model sets (Table 2.26). The apparent nest success model set showed that improved body conditions positively influenced nest success. For this reason, it was valuable to look further into what may be influencing the body condition of small heron nestlings. This was investigated in the body condition model set which produced two parameters of importance (Table 2.26). The first parameter that fell out as consistent in the body condition model set was year, which represented hydrologic differences on a coarse scale. The 2016 nesting season experienced strong El Niño conditions which produced the wettest dry season in 58 years (SFWMD 2017), likely increasing aquatic fauna biomass so that it was available during the 2017 nesting season (DeAngelis *et al.* 1997, Chick *et al.* 2004, Ruetz *et al.* 2005). While the 2017 nesting season experienced a weak La Niña episode leading to drier than average conditions (National Weather Service 2017). Differences in hydrologic conditions may impact small heron diet in two additional ways. First, water levels >19 cm, the maximum foraging depth of small herons (Powell 1987, Bancroft *et al.* 1990, Gawlik 2002), can prohibit these short-legged waders from accessing foraging areas, resulting in greater spatial constraints during a wetter than average dry season. Secondly, hydrologic differences can alter prey communities available to small herons (Loftus and Kushlan 1987, Trexler *et al.* 2002, DeAngelis *et al.* 2005). When water levels fail to recede to suitable foraging depths, prey are less concentrated and vulnerable for capture by small herons (Gawlik 2002, Lantz *et al.* 2011). Results from this study examining the

productivity of small herons are consistent with the characterization of 2016 as one of the worst wading bird breeding seasons over the past decade, with more than a 73% increase in nesting activity in 2017 (SFWMD 2018). Additionally, results are consistent with previous studies emphasizing the connection between small heron diet and hydrology (Boyle *et al.* 2012).

The second parameter that fell out as consistent in the body condition model set was the percentage of fish biomass consumed. Our results suggest that small herons with a smaller proportion of fish in their diet were able to exploit a greater variety of prey and habitat types as needed, thus having chicks with improved body conditions. This prey switching ability enabled birds to continue to meet the greater dietary demands experienced during the nesting season, even when suboptimal foraging conditions for fish capture were present. This in turn may have resulted in better fed chicks throughout the nesting season, thus a positive influence on the average body condition of chicks.

2.6   CONCLUSION

The diet differences between Little Blue Herons compared to Tricolored Herons and Snowy Egrets may intensify as landscape modifications continue in the Florida Everglades. Previous studies have shown the specialist-generalist gradient in bird communities become more apparent with habitat degradation (Julliard *et al.* 2006). Moreover, Snowy Egrets and Tricolored Herons may be particularly sensitive to continued urban development on wetlands, as specialists are believed to have an increased risk of extinction (McKinney 1997) due to their more specific dietary needs illustrated in this study. Drastic landscape changes impacting habitat availability have been shown to have a greater impact on specialists than generalists (Vazquez and

Simberloff 2002). Such sensitivities of dietary and habitat specialists have been

documented in coral reefs (Munday 2004), insects (Hughes *et al.* 2000), reptiles

(Foufopoulos and Ives 1999), birds (Julliard *et al.* 2004), and mammals (Harcourt *et al.*

2002). Uncertainties surrounding the drivers of the decline in small heron nest numbers

should be further investigated as these sensitive species represent valuable indicators of

wetland habitat quality.

Table 2. 1 A priori models predicting apparent nest success of small herons in the Florida Everglades 2016-2017.

A priori models	Description
Global[1]	Y = fish prey biomass + mean prey length + prey diversity index + keel score + number of chicks
1) **Prey**[1]	Y = fish prey biomass + mean prey length + prey diversity index
2) **Chicks**[1]	Y = keel score + number of chicks
3) **Null**	Y= bird species + colony

Y= Nest success or failure (0 or 1)

[1] Bird species, year, and colony added as random variables to all models

Table 2. 2 Model parameters for factors influencing apparent nest success of small herons in the Florida Everglades 2016-2017.

Explanatory variable	Description
Fish prey biomass	Percent biomass of fish present in bolus sample
Mean prey length	Mean length of all prey in bolus sample (STD in fish, Total length in all other animals)
Prey diversity index	Proportion of prey categories included in bolus sample (0-1) Categories include: crustaceans insects small fish spp. (native marsh fish) large fish/ spp. (native sunfish) non-native fishes amphibians & reptiles
Keel score	Keel of chick (1-5) 1- prominent keel, breast bone very sharp; 2- breast bone easily felt and sharp; 3- breast bone easily felt, but not sharp; 4- pressure needed to feel breast bone; 5- tissue greater than flush with keel, not possible to feel breast bone
Number of chicks	Total number of chicks found in associated nest during season

Table 2. 3 A priori models predicting body condition of small herons in the Florida Everglades 2016-2017.

A priori models	Description
1) **Global**[1]	Y = fish prey biomass + mean prey length + prey diversity index + number of chicks + year
2) **Prey**[1]	Y = fish prey biomass + mean prey length + prey diversity index
3) **Chicks**[1]	Y = number of chicks
4) **Year**[1]	Y = year
5) **Null**	Y= bird species + colony

Y= average keel score of chicks per nest (1-5)

[1] Bird species and colony added as random variables to all models

Table 2. 4 Model parameters for factors influencing body condition of small herons in the Florida Everglades 2016-2017.

Explanatory variable	Description
Fish prey biomass	Percent biomass of fish present in bolus sample
Mean prey length	Mean length of all prey in bolus sample (STD in fish, Total length in all other animals)
Prey diversity index	Proportion of prey categories included in bolus sample (0-1) Categories include: crustaceans insects small fish spp. (native marsh fish) large fish spp. (native sunfish) non-native fishes amphibians & reptiles
Year	Year of nesting 2016 (wet year) 2017 (dry year)
Number of chicks	Total number of chicks found in associated nest during season

Table 2. 5 Number of prey items and bolus samples () collected during the 2015, 2016 and 2017 nesting seasons from Little Blue Heron, Snowy Egret, and Tricolored Heron from 4 Everglades wading bird colonies. (*) indicates that birds did not nest in respective colony that year.

	Little Blue Heron	Snowy Egret	Tricolored Heron	Total
2015				
Hidden	152 (37)	0	398 (35)	550 (72)
Paurotis Pond	245 (21)	229 (20)	93 (25)	567 (66)
Tamiami West	0	651 (24)	312 (28)	963 (52)
Total 2015	**397 (58)**	**880 (44)**	**803 (88)**	**2080 (190)**
2016				
Hidden	0*	0*	0*	0
Paurotis Pond	330 (17)	447 (13)	386 (40)	1163 (70)
Tamiami West	122 (10)	101 (8)	317 (18)	540 (36)
Total 2016	**452 (27)**	**548 (21)**	**703 (58)**	**1703 (106)**
2017				
Hidden	0*	0*	20 (1)	20 (1)
Loxahatchee	633 (45)	0*	9 (1)	642 (46)
Paurotis Pond	64 (3)	0	6 (2)	70 (5)
Tamiami West	588 (9)	642 (18)	905 (33)	2135 (60)
Total 2017	**1285 (57)**	**642 (18)**	**940 (37)**	**2867 (112)**
Total	**2134 (142)**	**2070 (83)**	**2446 (183)**	6650 (408)

Table 2. 6 Percent biomass and (relative abundance) of prey species within small heron bolus samples, south Florida wading bird colonies 2015-2017. (*) Indicates non-native species.

Prey species	TRHE	SNEG	LBHE
Fish species			
African jewelfish (*Hemichromis letourneauxi*)*	12 (4)	4 (1)	13 (4)
Bluefin killifish (*Lucania goodie*)	3 (9)	3 (10)	2 (7)
Blue tilapia (*Oreochromis aureus*)*	<1 (<1)		
Bluegill *(Lepomis macrochirus)*		3 (<1)	
Bluespotted sunfish (*Enneacanthus gloriosus*)	1 (<1)	<1 (<1)	
Brook silverside (*Labadesthes sicculus*)	<1 (<1)		<1 (<1)
Brown hoplo *(Hoplosternum littorale)* *			1 (1)
Diamond killitfish (*Adinia Xenica*)		<1 (<1)	
Dollar sunfish (*Lepomis marginatus*)	<1 (<1)	1 (<1)	
Eastern mosquitofish (*Gambusia holbrooki*)	11 (32)	15 (29)	3 (8)
Everglades pygmy sunfish (*Elassoma evergladei*)	<1 (<1)	1 (3)	<1 (1)
Flagfish (*Jordanellae floridae*)	11 (10)	9 (8)	1 (1)
Golden shiner *(Notemigonus crysoleucas)*			3 (1)
Golden topminnow (*Fundulus chrysotus*)	18 (12)	15 (5)	2 (2)
Goldspotted killifish (*Floridichthys carpio*)	<1 (<1)	1 (<1)	<1 (<1)
Jaguar cichlid (*Parachromis managuensis*)*			<1 (<1)
Largemouth bass (*Micropterus salmoides*)	1 (<1)		
Least killifish (*Heterandria Formosa*)	1 (5)	2 (10)	<1 (5)

Marsh killifish (*Fundulus confluentus*)	7 (4)	4 (2)	2 (1)
Mayan cichlid (*Cichlasoma urophthalmus*) *	1 (<1)	2 (<1)	<1 (<1)
Orinoco sailfin catfish (*Pterygoplichthys*		<1 (<1)	
multiradiatus) *	3 (1)	3 (<1)	<1 (<1)
Pike killifish (*Belonesox belizanus*) *	<1 (<1)	<1 (<1)	
Rainwater killifish (*Lucania parva*)	1 (<1)	1 (<1)	
Redear sunfish (*Lepomis microlophus*)	18 (12)	21 (7)	2 (2)
Sailfin molly (*Poecilia latipinna*)	<1 (<1)		1 (1)
Sheepshead minnow (*Cypriodon variegatus*	1 (<1)	1 (<1)	
hubbsi)	1 (<1)	<1 (<1)	<1 (<1)
Spotted sunfish (*Lepomis punctatus*)	<1 (<1)		
Spotted tilapia (*Tilapia mariae*) *	<1 (<1)		<1 (<1)
Swamp darter (*Etheostoma fusiforme*)	1 (<1)	2 (<1)	2 (<1)
Unknown pickerel (*Esox spp.*)	1 (<1)	1 (<1)	1 (<1)
Unknown sunfish (*Lepomis spp.*)			
Warmouth (*Lepomis gulosus*)			
	<1 (<1)	<1 (<1)	<1 (<1)
Invertebrate species			<1 (<1)
Alligator flea (*Agasicles hygrophila*)			
Bee (*Anthophila spp.*)			
Beetle (*Coleoptera spp*)	<1 (<1)	<1 (<1)	<1 (<1)
Caterpillar (*Lepidoptera spp.*)		<1 (<1)	
Crayfish (*Procambarus spp.*)	<1 (<1)	<1 (<1)	23 (10)
Dragonfly (adult; *Odonata spp.*)	1 (2)	<1 (<1)	<1 (<1)
Dragonfly (larvae; *Odonata spp.*)	<1 (<1)	1 (2)	7 (13)
Fly (larvae; *Diptera spp*).	<1 (<1)	<1 (<1)	1 (5)
Giant water bug (*Belostomatidae spp.*)	<1 (<1)	<1 (<1)	1 (2)
Grass shrimp (*Palaemonetes paludosus*)	1 (3)	3 (15)	3 (16)
Grasshopper (*Othoptera spp.*)			<1 (<1)
Mosquito (*Culicidae spp.*)		<1 (2)	<1 (<1)
Predacious diving beetle (*Dytiscidae spp.*)	<1 (<1)	<1 (<1)	<1 (<1)
Snail (*Helicidae spp.*)			<1 (<1)
Spider (*Aranese spp.*)	<1 (<1)	<1 (<1)	1 (3)
Unknown insect (*Insecta spp.*)		<1 (<1)	<1 (<1)
Water scavenger beetle (*Hydrophilidae spp.*)	<1 (<1)	<1 (<1)	<1 (<1)
Amphibian & Reptile species			
Anole (*Anolis spp.*)			1 (<1)
Frog (adult; *Anura spp.*)	<1 (<1)	2 (<1)	11 (4)
Frog (tadpole; *Anura spp.*)	<1 (<1)		7 (9)
Siren (*Sirenidae spp.*)			<1 (<1)
Snake (*Serpentes spp.*)			1 (<1)
Unknown amphibian (*Amphibia spp.*)			<1 (<1)
n	2439	2071	2135

Table 2. 7 Major prey categories of small herons shown by percent biomass and (relative abundance) during the 2015-2017 nesting season in the Florida Everglades. (*Amphibians and reptiles includes: anole, frog (adult and tadpole), snake and unknown amphibian. Other insects include: alligator flea, beetle, dragonfly (adult), fly (larvae), giant water bug, grasshopper, mosquito, predacious diving beetle, snail, spider, water scavenger beetle, and unknown insect. Other non-native fish includes: brown hoplo, spotted tilapia. Other small marsh fish includes: brook silverside, diamond killifish, Everglades pygmy sunfish, golden shiner, goldspotted killifish, least killifish, rainwater killifish, and sheepshead minnow. Sunfish and largemouth bass includes: bluegill, bluespotted sunfish, dollar sunfish, largemouth bass, redear sunfish, spotted sunfish, unknown sunfish, and warmouth*).* (*) Indicates non-native species.

Prey Species	Tricolored Heron	Snowy Egret	Little Blue Heron
African jewelfish *	9.5 (5.8)	4.5 (3.4)	13.9 (5.7)
Amphibians and reptiles	1.5 (1.4)	0.0 (0.1)	16.5 (8.3)
Bluefin killifish	2.5 (6.0)	3.5 (7.0)	4.0 (5.2)
Crayfish	0.0 (0.2)	0.3 (0.1)	26.6 (10.8)
Dragonfly (larval stage)	0.1 (0.2)	1.9 (1.7)	9.5 (10.2)
Eastern mosquitofish	26.6 (34.9)	18.3 (36.5)	3.0 (11.1)
Flagfish	16.0 (8.7)	11.9 (8.4)	1.2 (1.2)
Golden topminnow	9.3 (7.6)	10.6 (5.0)	6.1 (4.6)
Grass shrimp	0.5 (2.4)	4.5 (11.7)	6.4 (17.0)
Mayan cichlid *	0.8 (0.5)	2.9 (0.2)	0.0 (0.1)
Marsh killifish	4.2 (3.1)	6.6 (2.4)	1.5 (1.6)
Other insects	0.2 (3.8)	1.6 (3.7)	3.4 (13.2)
Other non-native fish*	0.9 (0.3)	0.4 (0.0)	0.3 (0.5)
Other small marsh fish	2.9 (4.9)	6.8 (10.6)	4.6 (7.5)
Pike killifish*	1.9 (1.1)	2.3 (0.4)	0.3 (0.2)
Sailfin molly	16.6 (17.3)	11.6 (8.1)	1.7 (2.4)
Sunfish & bass	6.7 (1.6)	12.5 (0.7)	0.9 (0.3)

Table 2. 8 One-way ANOVA testing for differences in mean prey length among Little Blue Heron, Snowy Egret, and Tricolored Heron nesting in four Everglades colonies 2015-2017.

	Sum of Squares	df	Mean Square	F	p-value
Between groups	2683.903	2	1341.951	14.43039	1.49E^{-06}
Within groups	17297.03	186	92.9948		
Total	19980.93	188			

Table 2. 9 Pairwise ANOSIM to test for differences between colonies, data included prey collected from Hidden, Paurotis Pond, and Tamiami West 2015-2017. (+) Indicates data does not include bolus samples collected from Loxahatchee.

Pair-wise Groups	R -statistic	P-value
Hidden-Paurotis	0.006	0.417
Hidden-Tamiami	-0.099	0.689
Hidden-Loxahatchee	-0.250	0.667
Paurotis-Tamiami	0.116	0.100
Paurotis-Loxahatchee	0.909	0.028
Tamiami-Loxahatchee	0.698	0.022
2015-2016 [+]	-0.004	0.446
2015-2017 [+]	0.246	0.097
2016-2017 [+]	0.417	0.014
Snowy Egret – Tricolored Heron [+]	0.203	0.450
Snow Egret – Little Blue Heron [+]	0.448	0.020
Tricolored Heron – Little Blue Heron [+]	0.669	0.020

Table 2.10 Total number of nest observed as apparent success or failure during the 2016 and 2017 nesting seasons from Little Blue Heron, Snowy Egret, and Tricolored Heron from three Everglades wading bird colonies. Number of failed nests are shown to the right ( ) of total nest numbers. (*) indicates birds did not nest in respective colony that year.

	Little Blue Heron	Snowy Egret	Tricolored Heron	Total
2016				
Paurotis Pond	4 (0)	3 (0)	13 (2)	20 (2)
Tamiami West	4 (0)	4 (1)	6 (3)	14 (4)
Total 2016	**8 (0)**	**7 (1)**	**19 (5)**	**34 (6)**
2017				
Loxahatchee	16 (4)	*	1 (1)	17 (5)
Paurotis Pond	1 (0)	*	2 (0)	3 (0)
Tamiami West	4 (0)	8 (0)	13 (0)	25 (0)
Hidden	*	*	1 (1)	1 (1)
Total 2017	**21 (4)**	**8 (0)**	**17 (2)**	**46 (6)**
Total	**29 (4)**	**15 (1)**	**36 (7)**	**80 (12)**

Table 2. 11 Parameter values in model development from 80 small heron nests during the 2016 and 2017 nesting seasons. Values are further broken down into bird species specific nests for greater comparison among Little Blue Heron, Snowy Egret, and Tricolored Heron from four Everglades wading bird colonies.

	Variable	Mean	SE	Range
Small Herons n = 80	Average keel score per nest (1-5)	2.65	±0.06	1.00 – 3.67
	Mean prey length (cm)	2.59	±0.90	0.41 – 4.58
	Average fish biomass %	70.0	±0.05	0.0 – 100.0
	Prey diversity index (0-1)	0.33	±0.02	0.166 – 0.667
	Number of chicks	2.85	±0.10	1 – 5
Little Blue Herons n = 29	Average keel score per nest (1-5)	2.82	±0.09	2.00 – 3.50
	Mean prey length (cm)	16.06	±1.20	0.41 – 3.04
	Average fish biomass %	28.5	±0.08	0.0 – 100.0
	Prey diversity index (0-1)	0.34	±0.03	0.166 – 0.667
	Number of chicks	2.97	±0.20	1 – 5
Snowy Egrets n = 15	Average keel score per nest (1-5)	2.76	±0.10	2.00 – 3.00
	Mean prey length (cm)	1.97	±1.98	0.77 – 3.80
	Average fish biomass %	89.7	±0.04	50.0 – 100.0
	Prey diversity index (0-1)	0.34	±0.03	0.166 – 0.50
	Number of chicks	2.87	±0.17	2 – 4
Tricolored Herons n = 36	Average keel score per nest (1-5)	2.46	±0.10	1.00 – 3.67
	Mean prey length (cm)	2.46	±1.26	1.25 – 4.58
	Average fish biomass %	95.4	±0.02	40.0 – 100.0
	Prey diversity index (0-1)	0.33	±0.03	0.166 – 0.667
	Number of chicks	2.75	±0.13	1 – 4

Table 2. 12 Results of generalized mixed models for determining apparent nest success or failure in small herons nesting in 2016 and 2017 from four Everglades colonies. Models are described with -2 log likelihood (-2Loglike), number of parameters (k), AIC_c values, differences in AIC_c values between the best model and each candidate model (ΔAIC_c), AIC_c weights (w_i).

Model	-2Loglike	k	AIC_c	ΔAIC_c	w_i
Global model	94.54	9	113.55	0	0.33
Prey	99.26	7	113.88	0.33	0.28
Chicks	101.54	6	114	0.45	0.27
Null	107.48	4	115.7	2.15	0.11

Table 2. 13 Model averaged parameter estimates (β), 95% confidence limits (LCL, UCL), predicting percentage of apparent nest success in small herons during the 2016 and 2017 nesting seasons in four Everglades colonies. *** indicates parameter did not overlap zero, * indicates parameter barely overlapped zero.

Apparent Nest Success Model: All small herons				
Parameter	β	LCL	UCL	
Prey diversity Index	4.187786	-0.8356058	9.2111778	
Average keel score	1.560477	0.0521218	3.0688322	***
Intercept	0.791441	-9.0205973	10.603479	
Mean prey length	-0.007842	-0.0609874	0.0453034	*
Number of chicks	-0.247927	-0.929372	0.433518	*
Fish prey biomass	-5.724034	-13.410276	1.9622079	

Table 2. 14 Results of generalized mixed models for determining apparent nest success or failure in Little Blue Herons nesting in 2016 and 2017 from three Everglades colonies. Models are described with -2 log likelihood (-2Loglike), number of parameters (k), AIC_c values, differences in AIC_c values between the best model and each candidate model (ΔAIC_c), AIC_c weights (w_i).

Model	-2Loglike	k	AIC_c	ΔAIC_c	w_i
Null	47.92	3	54.25	0	0.74
Chicks	46.48	5	57.33	3.08	0.16
Prey	45.4	6	58.59	4.34	0.08
Global model	43.04	8	61.15	6.9	0.02

Table 2. 15 Model averaged parameter estimates (β), 95% confidence limits (LCL, UCL), predicting percentage of apparent nest success or failure in Little Blue Herons during the 2016 and 2017 nesting seasons in three Everglades colonies. *** indicates parameter did not overlap zero, * indicates parameter barely overlapped zero.

Apparent Nest Success Model: Little Blue Heron nests				
Parameter	β	LCL	UCL	
Intercept	8.95683	-6.7731892	24.686849	
Average keel score	0.2919	-1.8454212	2.4292212	*
Number of Chicks	-0.47782	-1.38432	0.42868	*

Table 2. 16 Results of generalized mixed models for determining apparent nest success or failure in Tricolored Herons nesting in 2016 and 2017 from four Everglades colonies. Models are described with -2 log likelihood (-2Loglike), number of parameters (k), AIC_c values, differences in AIC_c values between the best model and each candidate model (ΔAIC_c), AIC_c weights (w_i).

Model	-2Loglike	k	AIC_c	ΔAIC_c	w_i
Chicks	39.66	5	50.45	0	0.82
Global model	36.22	8	54.19	3.74	0.13
Null	50.74	3	57.05	6.6	0.03
Prey	44.8	6	57.91	7.46	0.02

Table 2. 17 Model averaged parameter estimates (β), 95% confidence limits (LCL, UCL), predicting percentage of apparent nest success or failure in Tricolored Herons during the 2016 and 2017 nesting seasons in four Everglades colonies. *** indicates parameter did not overlap zero, * indicates parameter barely overlapped zero.

Apparent Nest Success Model: Tricolored Heron nests				
Parameter	β	LCL	UCL	
Prey diversity index	7.40914	3.0594884	11.758792	***
Average keel score	5.13847	0.5673384	9.7096016	***
Mean prey length	-0.02009	-0.432278	0.392098	*
Number of chicks	-0.81735	-2.4108692	0.7761692	*
Fish prey biomass	-4.21614	-37.47589	29.04361	
Intercept	-14.37623	-36.948452	8.1959924	

Table 2. 18 Results of generalized mixed models for determining body condition in small herons nesting in 2016 and 2017 from four Everglades colonies. Models are described with -2 log likelihood (-2Loglike), number of parameters (k), AIC_c values, differences in AIC_c values between the best model and each candidate model (ΔAIC_c), AIC_c weights (w_i).

Model	-2Loglike	k	AIC_c	ΔAIC_c	w_i
Year	78.64	5	89.46	0.00	0.64
Global	70.08	9	90.64	1.19	0.36
Prey	90.12	7	105.67	16.22	0.00
Null	98.98	4	107.51	18.05	0.00
Chicks	97.46	5	108.28	18.82	0.00

Table 2. 19 Model averaged parameter estimates (β), 95% confidence limits (LCL, UCL), predicting the body condition of small herons during the 2016 and 2017 nesting seasons in four Everglades colonies. *** indicates parameter did not overlap zero, * indicates parameter barely overlapped zero.

Body Condition Model: All small herons				
Parameter	β	LCL	UCL	
intercept	2.366985	1.9352421	2.7987279	
Year 2017	0.518195	0.3083672	0.7280228	***
Number of chicks	0.45236	0.353527	0.551193	***
Prey diversity index	0.010282	-0.607655	0.628219	*
Mean prey length	-0.004999	-0.0167766	0.0067786	*
Fish biomass percentage	-0.34911	-0.6524259	-0.0457941	***

Table 2. 20 Results of generalized mixed models for determining body condition in Little Blue Herons nesting in 2016 and 2017 from three Everglades colonies. Models are described with -2 log likelihood (-2Loglike), number of parameters (k), AIC_c values, differences in AIC_c values between the best model and each candidate model (ΔAIC_c), AIC_c weights (w_i).

Model	-2Loglike	k	AIC_c	ΔAIC_c	w_i
Year	22.92	4	32.6	0	0.54
Global	10.94	8	34.14	1.55	0.25
Prey	19.52	6	35.34	2.74	0.14
Null	30.34	3	37.30	4.7	0.05
Chicks	30.18	4	39.85	7.25	0.01

Table 2. 21 Model averaged parameter estimates (β), 95% confidence limits (LCL, UCL), predicting the body condition of Little Blue Herons during the 2016 and 2017 nesting seasons in three Everglades colonies. *** indicates parameter did not overlap zero, * indicates parameter barely overlapped zero.

Body Condition Model: Little Blue Heron nests				
Parameter	β	LCL	UCL	
intercept	2.550199	1.8634581	3.2369399	
Year 2017	0.626497	0.2774328	0.9755612	***
Mean prey length	0.003803	-0.015209	0.022815	*
Number of chicks	-0.047245	-0.180229	0.085739	*
Prey diversity index	-0.161546	-1.4121475	1.0890555	*
Fish biomass percentage	-0.664577	-1.1278289	-0.2013251	***

Table 2. 22 Results of generalized mixed models for determining body condition in Snowy Egrets nesting in 2016 and 2017 from two Everglades colonies. Models are described with -2 log likelihood (-2Loglike), number of parameters (k), AIC_c values, differences in AIC_c values between the best model and each candidate model (ΔAIC_c), AIC_c weights (w_i).

Model	-2Loglike	k	AIC_c	ΔAIC_c	w_i
Year	9.2	4	21.19	0.00	0.57
Null	13.98	3	22.17	0.98	0.35
Chicks	13.42	4	25.41	4.22	0.07
Prey	8.86	6	31.35	10.16	0.00
Global	6.88	8	46.88	25.69	0.00

Table 2. 23 Model averaged parameter estimates (β), 95% confidence limits (LCL, UCL), predicting the body condition of Snowy Egrets during the 2016 and 2017 nesting seasons in two Everglades colonies. *** indicates parameter did not overlap zero, * indicates parameter barely overlapped zero.

Body Condition Model: Snowy Egret nests				
Parameter	β	LCL	UCL	
intercept	2.5021	2.106572	2.897628	
Year 2017	0.4345	0.101104	0.767896	***

Table 2. 24 Results of generalized mixed models for determining body condition in Tricolored Herons nesting in 2016 and 2017 from four Everglades colonies. Models are described with -2 log likelihood (-2Loglike), number of parameters (k), AIC_c values, differences in AIC_c values between the best model and each candidate model (ΔAIC_c), AIC_c weights (w_i).

Model	-2Loglike	k	AIC_c	ΔAIC_c	w_i
Year	41.22	4	50.51	0.00	0.97
Global	36.26	8	57.59	7.08	0.03
Null	55.96	3	62.71	12.2	0.00
Chicks	54.66	4	63.96	13.45	0.00
Prey	51.68	6	66.58	16.07	0.00

Table 2. 25 Model averaged parameter estimates (β), 95% confidence limits (LCL, UCL), predicting the body condition of Tricolored Herons during the 2016 and 2017 nesting seasons in four Everglades colonies. *** indicates parameter did not overlap zero, * indicates parameter barely overlapped zero.

Body Condition Model: Tricolored Heron nests				
Parameter	β	LCL	UCL	
intercept	2.118975	1.6798762	2.5580738	
Year 2017	0.691499	0.3885869	0.9944111	***

Table 2. 26 Summary of apparent nest success and body condition model sets including top models used in model averaging and total weight (w_i) contribution. Parameters with confidence intervals which did not overlap zero are included as parameters of importance, as well as the parameters positive (+) or negative (-) influence on the response variable.

Model Set	Top models	Total w_i	Parameters of importance	Influence
Apparent nest success				
All small herons	Global Prey	61%	Average keel score	+
Little Blue Herons	Null Chicks	90%	none	n/a
Tricolored Herons	Chicks Global	95%	Average keel score Prey diversity index	+ +
Body condition				
All small herons	Year Global	100%	Year 2017 Fish biomass percentage Number of chicks	+ - +
Little Blue Herons	Year Global Prey	93%	Year 2017 Fish biomass percentage	+ -
Snowy Egrets	Year Null	92%	Year 2017	+
Tricolored Herons	Year	97%	Year 2017	+
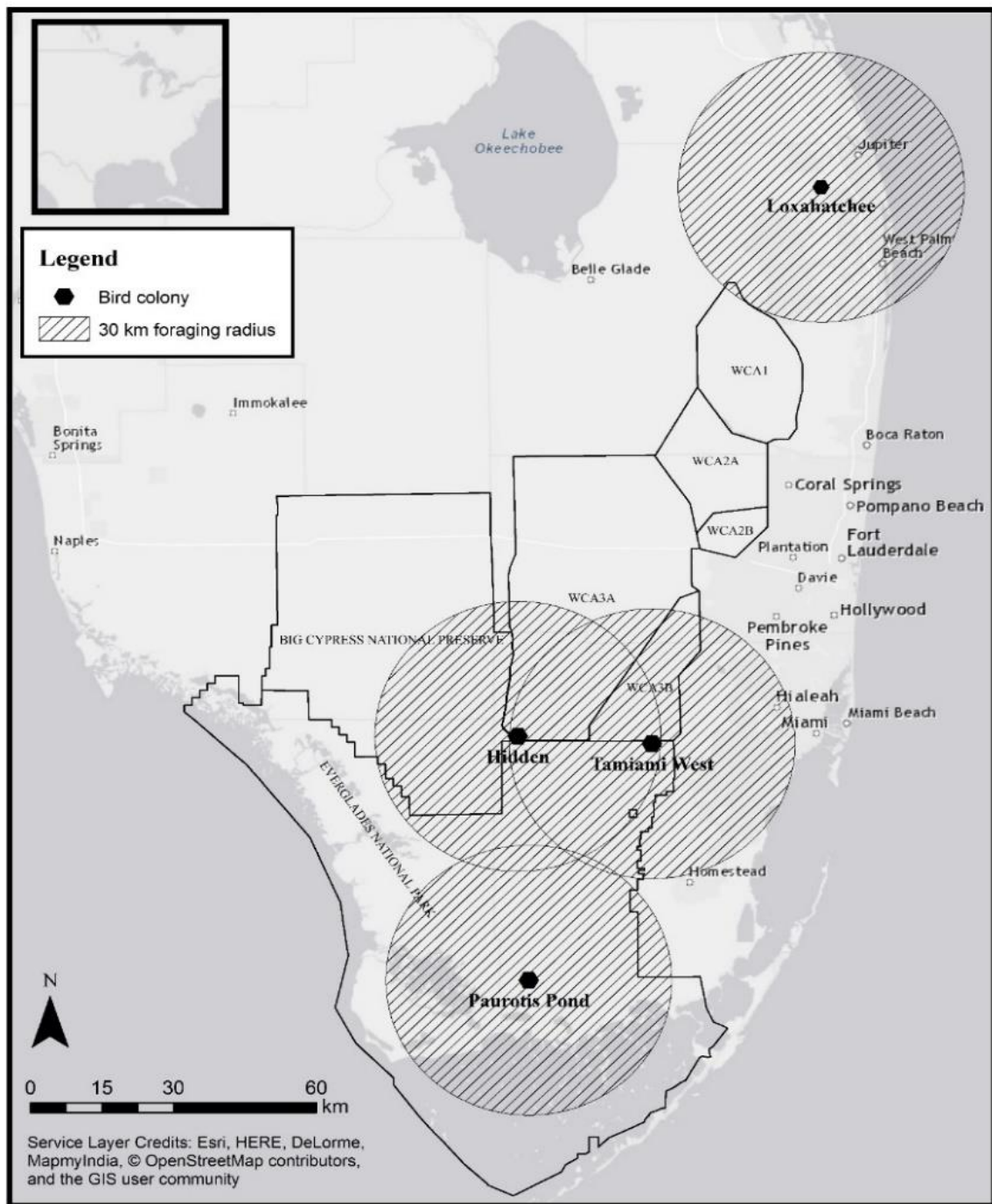
Figure 2.1 Wading bird colony locations and 30 km maximum small heron foraging radius, Florida Everglades, 2015-2017.
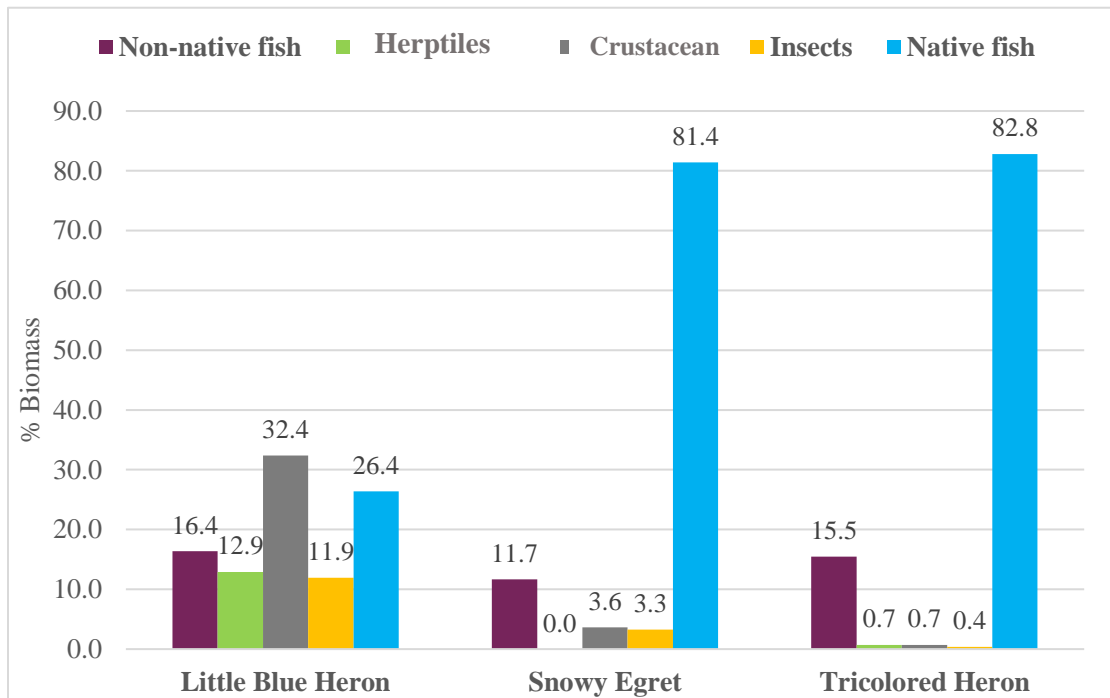
Figure 2.2 Percent biomass of five main taxonomic prey categories consumed by small herons during the 2015-2017 nesting season in four greater Everglades colonies.
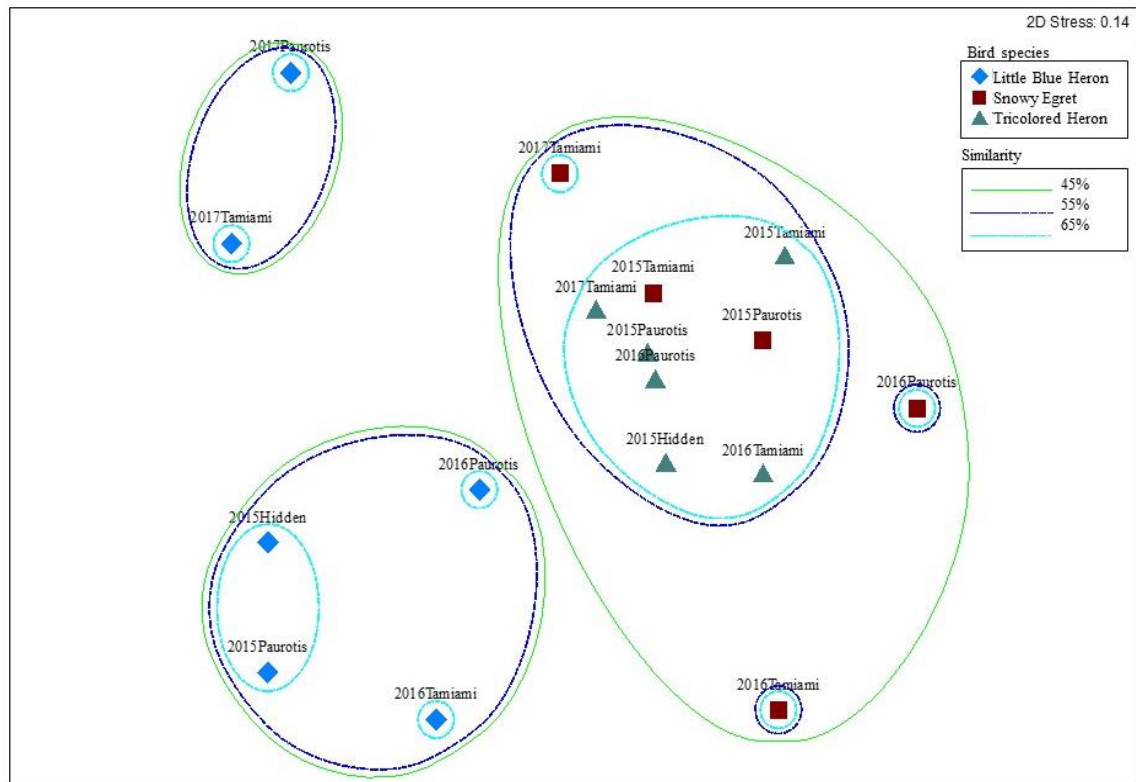
Figure 2.3 nMDS plot with 0.14 stress level displaying diet similarity among small heron bolus samples collected from three Everglades colonies (Tamiami West, Paurotis Pond, and Hidden) during the 2015-2017 nesting seasons. Similarity clusters among groups is identified at similarity levels of 45%, 55%, and 65%.

3   NON-NATIVE PREY CONSUMPTION BY NATIVE AVIAN PREDATORS IN

THE FLORIDA EVERGLADES

3.1   ABSTRACT

The introduction and persistence of non-native species are well documented as the

greatest threat to biodiversity, second only to habitat loss. Although a large body of

literature explores the impacts of predator-prey interactions, the majority focus on how

native prey adapt to non-native predators, while the impacts of non-native prey on native

predators is less frequently studied. Evaluating these relationships is critical as non-native

species have the potential to change prey communities as well as to alter the behavior and

fitness levels of native predators. In this chapter I examine factors driving the

consumption of non-native prey by native predators in the Florida Everglades. The

establishment of non-native fishes in Florida dates to the 1950s. Today, more than 50

species of non-native fishes have been introduced into south Florida waterways, over two

dozen of which are considered established, reproducing populations. Non-native fishes,

although present in the Everglades are primarily concentrated in urban canals, which

provide warm, deep-water refuges for these tropical and sub-tropical species. When

foraging conditions in the Everglades are suboptimal due to either anthropogenic

modifications or naturally occurring rain events, it is unclear if some species of wading

birds seek alternative foraging habitats such as canals. Unlike the Everglades, canals are

not dependent on seasonal flooding, therefore, may be exploited by wading birds during

times of poor prey production or availability in the natural marsh. By shifting from a diet

of predominately native fishes found in the natural marsh to non-native fishes found primarily in urban canals, wading birds may be able to supplement their dietary needs adequately to meet greater dietary demands experienced during the nesting season.

I collected 362 food boluses (stomach regurgitation) from Little Blue Heron, Snowy Egret and Tricolored Heron, in three mixed species colonies within the Everglades of Florida during the 2015, 2016 and 2017 nesting seasons. I found that over half (51%) of the fish biomass consumed by Little Blue Herons were non-native species, compared to 14% and 19% non-native fish biomass consumed by Snowy Egret and Tricolored Heron, respectively. Surprisingly, <7% of fish biomass available in the Everglades was comprised of non-native fish species, suggesting that small herons, and Little Blue Herons, in particular, may be using alternative foraging habitats to supplement their dietary needs during the nesting season. Additionally, in 2016 (a wet year), 4.5% of fish biomass collected in throw-traps were non-native, while 26.2% of fish biomass consumed by small herons were non-native. In 2017 (a dry year), 6.6% of fish biomass collected in throw-traps were non-native, while 7.8% of fish biomass consumed by small herons were non-native, suggesting that during suboptimal foraging conditions such as those present in 2016, small herons may be using alternative foraging habitats to a greater degree.

These results illustrate that Little Blue Herons, a native predator to the Everglades, is now reliant, to a large degree on non-native prey. These results may be an indication that Little Blue Herons are foraging in urban water bodies such as canals which provide a more stable environment than the fluctuating natural marsh. Future research should focus on determining if small herons foraging in the natural marsh are

showing a preference for non-native fish such as African jewelfish, or if they are foraging more frequently in urban waterbodies, thus using non-native prey more readily simply because of their greater abundance.

3.2   INTRODUCTION

Non-native species, defined as species introduced into areas outside of their historic range (Warren 2007), are key drivers of human-induced rapid environmental change (HIREC; Fabry *et al.* 2008, Sih *et al.* 2011). The introduction and persistence of non-native species are well documented as the greatest threat to biodiversity, second only to habitat loss (Light and Dineen 1997, Lowe *et al.* 2001). Studies have demonstrated that non-native species can alter the dynamics of populations, communities, and ecosystems (Sergio *et al.* 2006), including predator-prey relationships (Lima 2002, Johnson and Agrawal 2003). Although a large body of literature explores the impacts of predator-prey interactions, the majority focus on how native prey adapt to non-native predators (McIntosh and Townsend 1994), while the impacts of non-native prey on native predators is less frequently studied (King *et al.* 2006, Carlsson *et al.* 2009, Cattau *et al.* 2016). Evaluating these relationships is critical as non-native species have the potential to change prey communities as well as to alter the behavior and fitness levels of native predators (Carlsson *et al.* 2009). Here I examine factors driving the consumption of non-native prey by native predators in the Florida Everglades.

3.2.1   A Modified Ecosystem

The establishment of non-native species in Florida is due in part to the Florida Everglades having been heavily impacted by HIREC. In addition to significant landscape alterations, humans have facilitated the introduction and dispersal of aquatic, non-native

fish species through intentional stocking, aquarium releases, and canal construction (Rahel and Olden 2008, Roberts and Rahel 2008, Parkos and Trexler 2014).

The establishment of non-native fishes in Florida dates back to the 1950s (Kline *et al.* 2014). Today, more than 50 species of non-native fishes have been introduced into south Florida waterways (Shafland 1996, Trexler *et al.* 2000, Kline 2014), over two dozen of which are considered established, reproducing populations (Kline *et al.* 2014). Non-native fishes, although present in the Everglades are primarily concentrated in urban canals (Shafland 1996, Trexler *et al.* 2000, Kline 2014), which provide warm, deep-water refuges for these tropical and sub-tropical species (Loftus 1988, Trexler *et al.* 2000, Kline 2014). African jewelfish (*Hemichromis letourneuxi)*, Mayan cichlid (*Cichlasoma urophthalmus)* and pike killifish (*Belonesox belizanus)* are the most widespread and abundant non-native fishes throughout Everglades National Park (Kline *et al* 2014).

3.2.2   Hydrologic Fluctuations

The timing of the dry down in the Everglades is used as an environmental cue for wading birds to initiate nesting (Kushlan 1976). Environmental conditions that alter this hydrologic pattern can cause wading birds to delay nesting or not form nesting colonies at all (Fleming *et al.* 1994). Heavy rainfall events during the dry season, known as reversals, result in the sudden reversal of receding water levels and may cause an immediate loss of suitable wading bird foraging habitat, particularly for short-legged foragers such as small herons (Fleming *et al.* 1994). Maximum suitable foraging water depth for Tricolored Heron, Little Blue Heron and Snowy Egret is 19 cm (Powell 1987, Bancroft *et al.* 1990, Gawlik 2002), the average leg length of each small heron (Powel 1987). Because rising water levels allow previously vulnerable (concentrated) prey to disperse, the occurrence

of extreme water-level reversals after nest initiation can result in nest abandonment for several nests, or an entire colony (Frederick and Collopy 1989, Bancroft *et al.* 2002).

When foraging conditions in the Everglades are suboptimal due to either anthropogenic modifications or naturally occurring rain events, it is unclear if some species of wading birds seek alternative foraging habitats such as canals. Unlike the Everglades, canals are not dependent on seasonal flooding, therefore, may be exploited by wading birds during times of poor prey production or availability in the natural marsh. By shifting from a diet of predominately native fishes found in the natural marsh to non-native fishes found primarily in urban canals (Shafland 1996, Trexler *et al.* 2000, Kline 2014), wading birds may be able to supplement their dietary needs adequately to meet greater dietary demands experienced during the nesting season.

3.2.3   Objectives

To better understand what may be driving these dietary shifts I 1) quantified the abundance of native and non-native fish species available to and used by small herons nesting in the Everglades; and 2) tested the effect of hydrologic fluctuations and non-native fish use by small herons during the nesting season.

3.3   METHODS

3.3.1   Fish-prey Use

I collected food boluses (stomach regurgitation) from Little Blue Herons, Snowy Egrets and Tricolored Herons, in three mixed species colonies within the Everglades of Florida during the 2015, 2016 and 2017 nesting seasons (Fig. 3.1). Food boluses provide prey consumption data from breeding pairs of adult wading birds. Chicks recently fed by their parents readily regurgitate in the presence of predators including humans (Byers

1951, Furness and Hislop 1981, Nell and Frederick 2015). The stomach contents regurgitated by nestlings are typically whole intact specimens that can be easily identified to the species level. For prey items that are partially digested, most remain identifiable by unique markings or physical attributes. However, occasionally prey items are beyond recognition, at least to the species level. In these instances, prey items are determined to the lowest taxonomic level possible.

Wading bird colonies were selected based on their historical use as colonial nest sites, diverse vegetative communities, and accessibility. Paurotis Pond, surrounded by coastal brackish wetlands is dominated by red mangrove (*Rhizophora mangle)*, and located in the southern portion of Everglades National Park. Tamiami West, an interior colony surrounded by freshwater marsh is dominated by Pond apple (*Annona glabra*) and willow (*Salix* spp.) and is located along the northern boundary of Everglades National park. Hidden, an interior colony surrounded by freshwater marsh and cypress forests is dominated by bald cypress trees (*Taxodium distichum)* and coco plum (*Chrysobalanus icaco*) and located in the southwestern portion of Water Conservation Area 3A, just outside the boundary of Big Cypress National Preserve.

I visited each colony and associated nests 1-2 times per week during the nesting season (April – June), the duration of each visit was < 2 hours with frequent movement between nests to reduce disturbance. Nests were chosen at random throughout each colony with priority given to nest containing 1-2-week-old nestlings. Each nest was flagged with tape and a unique identification. I collected food boluses from nestlings that voluntarily regurgitated as a natural response to predators (Byers 1951, Furness and Hislop 1981, Nell and Frederick 2015). When voluntary regurgitation did not occur, I

gently lifted the chick up and down while occasionally massaging the esophagus to induce regurgitation. Nestlings were then returned to nests and provided small fish in the nest bowl to compensate for loss of stomach contents. I transported bolus samples on ice to the lab and froze until processed.

Animals in bolus samples were thawed and identified to the lowest possible taxonomic group. Standard length (fish) or total length (other animals) was be measured in mm, and weight determined to the nearest 0.01 g. Due to of varying levels of digestion, length and/or weight measurements were omitted for any prey items partially digested, and recorded as such.

3.3.2   Fish-prey Availability

To determine the percentage of prey available in the natural marsh, I sampled aquatic fauna in the Everglades during the 2016 and 2017 dry seasons as part of a long-term study monitoring aquatic fauna throughout the Everglades as part of the Everglades restoration (Botson *et al.* 2016). The broadest sampling unit, landscape unit (LSU) (Fig. 3.1), was determined by vegetative characteristics and hydroperiod (mean number of days per year an area is inundated with water). Each LSU contains at least seven randomly placed 500 x 500-m primary samling units (PSU) which remain consistant from year-to-year. Within each PSU two locations (sites) are randomly generated, which vary each year to adequatly sample the entire PSU. Using aerial surveys, I identified the location of suitable wading bird foraging habitat within each site prior to sampling. Suitable habitat is defined as an area with sparse to moderate vegetation, and a water depth less than 30 cm (Lantz *et al.* 2011). A maximum of two throw-trap samples ≥10 m apart were collected at random locations within the designated suitable foraging habitat at

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each site. I removed vegetation within the throw-trap prior to using a bar seine to collect aquatic fauna. All animals <15 cm in total length were collected and transferred into marked jars containing tricain methane-sulfonate (MS-222), a euthanasia agent. Animals ≥15 cm were identified, photographed, measured and released. I considered the throw-trap cleared after 5 consecutive sweeps of the bar seine produced no fauna. I transported jars on ice to a field lab, then rinsed and covered prey in a color-fixative (Prefer) for 3-4 days. I then transfered prey into a 70% ethanol solution for preservation. Prey identification followed the same protocol as outlined for food bolus collection.

3.3.3 Hydrologic Fluctuation Measurements

To determine mean water depth and rainfall in the Everglades, I used Everglades Depth Estimation Network (EDEN). EDEN is an integrated network of water-level gauges that generates a daily estimate of water depths and rainfall on a 400 x 400-m grid across the freshwater portion of the Everglades (Telis 2006). On each date of bolus collection I determined the mean water depth (cm) within a 30-km range of each colony, the maximum foraging distance for small herons (Strong *et al.* 1997). Similarly, I used total average rainfall accumulation (cm) within a 30-km radius within 2 days of bolus collection.

3.3.4 Statistical Analysis

To determine if prey availability differed from prey use, I used PRIMER 7 software (Clarke and Gorley 2015) to create non-metric multi-dimensional scaling (nMDS) plots. I combined bolus samples collected from the same nest on each colony visit, and combined prey collected from throw-traps within the same PSUs each year. I excluded non-fish prey items from the analysis, thus I only included daily nest samples

which contained some proportion of fish in the bolus sample. Additionally, I excluded prey species in bolus samples that accounted for <1% of total fish biomass to prevent over-representation of rare species (Clark and Gorley 2015). To determine similarity between fish species consumption by small herons and availability in the natural marsh, I square-root transformed biomass data for fish biomass percentages within boluses and throw-traps, and calculated Bray-Curtis similarity matrices for each sample type (nest per visit and PSU per year). Using the Bray-Curtis similarity matrices, I ran an ANOSIM test (analysis of similarities) between sample types. An ANOSIM is a non-parametric permutation procedure which tests for differences among samples based on ranks of pairwise similarities in the Bray-Curtis matrix. ANOSIM test produced an R-statistic (ranging from -1 to 1) which compares the measure of the degree of separation of sites (Clarke and Gorley 2015).

To determine if non-native fish consumption was affected by hydrologic variables I created competing predictive models to explain how hydrologic patterns influence the use of non-native fish in the diets of small herons and used them in an information theory framework (Burnham and Anderson 2002; Burnham and Anderson 2004). I developed five *a priori* candidate models for non-native fish use (Table 3.1). The first hypothesis, the global model, includes all explanatory variables. The second hypothesis, the hydrologic model states that non-native fish use is most influenced by increasing water depth and rainfall, which in part determines the vulnerability of fish to wading bird capture (Gawlik 2002; Pierce and Gawlik 2010). The third hypothesis, the bird model, states that non-native fish use is most influenced by the species of bird predating on the fish, which may be due to behavioral traits or morphological adaptations

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inherent to different bird species (Herrera 1978; Kent 1986; Robinson and Holmes 1982; Remsen *et al.* 1993; Beerens *et al.* 2011). The fourth hypothesis, the spatial model states that non-native fish use is most influenced by the colony from which small herons nest. Differing colony locations may contribute to spatial constraints or differences in available prey communities (Trexler *et al.* 2000; Kline *et al.* 2014). Because non-native fish use is likely not influenced by any discrete hypothesis, the fourth hypothesis bird + hydrologic model, is a combination of the hydrologic model and bird model. Lastly, I created a null model to evaluate the performance of other models in the candidate set.

I used the information theoretic approach and Akaike's Information Criterion for small sample sizes (AICc) to determine which a priori models were most parsimonious (Burnham and Anderson 2004). I also calculated ΔAIC_c values and model probabilities (wi) to determine the distance between the best model and all other models. I calculated averaged parameter estimates for each model to determine the explanatory effect of each variable on non-native fish biomass. To examine model variability, 95% confidence intervals were calculated for parameter estimates. A likelihood version of the correlation coefficient was calculated for each model to examine model fit.

I constructed a generalized linear mixed-model using R 3.4.1 software (Team R C 2015) and package lme4 (Bates *et al.* 2015) to test for effects of hyrologic flucuations on the use of non-native fish by small herons. The continuous response variable was the daily percentage of non-native fish biomass per nest. Main predictor variables of interest were average water depth within 30-km radius of colony on the date of bolus collection, and the amount of rainfall within a 30-km radius of colony within 2 days of bolus collection. Other covariates included bird species and colony. I treated year as a random

effect (Table 3.2). Before running the models I confirmed that multicollinearity was not present between variables.

3.4   RESULTS

3.4.1   Fish-prey Use

I collected a total of 362 small heron bolus samples containing fish from 157 different nests among 3 Everglades colonies. For unknown reasons, small herons did not initiate nesting at Hidden in 2016 and 2017, a pattern consistent with other Everglades' colonies as, most wading bird species had lower nest numbers in 2016 (SFWMD 2016). In 2017 limited accessibility due to crow nest predation and aggressive alligator activity in Paurotis Pond limited data collection to only 3 nests (Table 3.3).

I identified 4,585 prey items to 32 different fish species in bolus samples, including 7 non-native species (Table 3.4). The most numerous fish species found in Tricolored Heron and Snowy Egret boluses were Eastern mosquitofish (*Gambusia holbrooki*) which accounted for 33.7% and 37.5%, respectively. The most numerous fish species found in Little Blue Heron boluses were Eastern mosquitofish and bluefin killifish (*Lucania goodie*) with accounted for 45.7%. The majority of fish prey biomass for Tricolored Herons included golden topminnow (*Fundulus chrysotus)*, and sailfin molly (*Poecilia latipinna)*, which accounted for 38.2%. The majority of fish prey biomass for Snowy Egrets included sailfin molly, golden topminnow, and Eastern mosquitofish which accounted for 56.7%. The majority of fish prey biomass for Little Blue Herons came from African jewelfish (*Hemichromis letourneauxi)* which accounted for 39.1%. Mean prey length was 2.27 ± 1.02 cm for Little Blue Herons, 2.11 ± 0.88 cm for Snowy Egrets, and 2.57 ± 0.98 cm for Tricolored Herons.

Non-native fishes in bolus samples accounted for 39.6% total biomass in Little Blue Heron, 10.6% in Snowy Egret, and 18.11% in Tricolored Heron diets (Fig. 3.2a). Non-native fish biomass collected from Hidden, Paurotis Pond, and Tamiami West accounted for 18.8%, 31.8% and 7.73% total fish biomass, respectively (Fig. 3.2b). Non-native fish biomass consisted of 20.3% total fish biomass in 2015, 26.22% in 2016, and 7.8% in the 2017 nesting season (Fig. 3.2c).

3.4.2   Fish-prey Availability

During the 2016 and 2017 dry seasons I collected 4,552 prey items from 283 throw-traps to 33 different fish species, including 7 non-native species (Table 3.4). The most numerous fish species found in 2016 throw-traps were Eastern mosquitofish and least killifish (*Heterandria Formosa*) which accounted for 61.4% of fish abundance. The most numerous fish species found in 2017 throw-traps were bluefin killifish and Eastern mosquitofish which accounted for 63.5% of fish abundance. The majority of fish prey biomass in 2016 included sailfin molly and Eastern mosquitofish which accounted for 41.6% of the total fish biomass. The majority of fish prey biomass in 2017 throw-traps included bluefin killifish, bluespotted sunfish (*Enneacanthus gloriosus)*, and Eastern mosquitofish which accounted for 48.36% of the total fish biomass. Mean prey length was 1.59 ± 0.76 cm in 2016 throw-traps, 2.11 ± 0.88 cm, and 1.78 ± 0.67 cm in 2017 throw-traps.

3.4.3   Prey Use verses Availability

No throw-trap prey data were collected during the 2015 dry season; therefore, to account for variations in available prey among years, I did not use boluses from the 84 nests sampled in 2015 as part of the comparison.

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During the 2016 and 2017 seasons, I found 23 (72%) of the fish species occurred in both bolus samples and throw-trap samples, including 6 non-native species. In 2016 (a wet year), 4.5% of fish biomass collected in throw-traps were non-native, while 26.2% of fish biomass consumed by small herons were non-native. In 2017 (a dry year), 6.6% of fish biomass collected in throw-traps were non-native, while 7.8% of fish biomass consumed by small herons were non-native (Fig. 3.3).

I used a multivariate analysis to determine the similarity in prey use (found in bolus samples) compared to prey availability (found in throw-trap samples). I included only throw-trap samples collected from PSUs within 30 km of the corresponding colony, the maximum foraging radius for small herons (Strong *et al.* 1997) (13 PSUs in 2016, 30 PSUs in 2017). To accurately compare years of throw-trapping data, I used Primary Sampling Unit (PSU) which is the finest level of sampling that remains constant every year, thus each throw-trap data point represents prey collected from 4 throw-traps. An ANOSIM showed there was slight difference between available fish species composition in the Everglades and fish used by small herons (global R= 0.254; Fig 3.4a). A one-way analysis SIMPER (similarity percentage) showed that the non-native African jewelfish was the top species contributing to the dissimilarity between Little Blue Heron bolus and throw-trap samples (17.3%), while they contributed to 9.5% in Tricolored Heron and 5.1% in Snowy Egret diets (Fig 3.4b).

An ANOSIM comparing prey use and availability in 2016 and 2017 showed a slight difference between prey availability and use (global R = 0.19 and 0.17, respectively). A SIMPER showed that in 2016 the prey species driving the difference between use and availability were Eastern mosquitofish (16.79%), Sailfin molly

(13.74%) and African jewelfish (10.59%). In 2017 the top contributors to the difference were Bluefin killifish (12.89%), Golden topminnow (12.23%) and African jewelfish (9.24%) (Table 3.5).

A SIMPER was used to determine which fish prey species drove the dissimilarity between fish prey use and availability during 2016 and 2017 for each species of small heron (Table 3.5). Sailfin molly was the top contributor to Tricolored heron dissimilarity between fish prey use and availability in both 2016 and 2017, contributing to 15.2% and 13.2%, respectively. Eastern mosquitofish was the top contributor to Snowy Egret dissimilarity in 2016, contributing 20.95%, while Bluespotted sunfish and Bluefin killifish contributed to the greatest dissimilarity (11.97%, 11.25% respectively) for Snowy Egrets in 2017. In 2016, the greatest driver of fish prey dissimilarity in Little Blue Heron use was African jewelfish, which contributed 19.46%. In 2017, Bluefin killifish and African jewelfish were the top contributors to dissimilarity in Little Blue Heron fish prey use, contributing 17.66% and 17.65%, respectively.

3.4.4   Hydrologic Fluctuations

The Everglades experienced hydrologically dissimilar conditions among years for the duration of the study in terms of water depth, recession rates, and reversal events, which resulted in an average year (2015), a wet year (2016), and a dry year (2017) (Fig. 3.5). Water depth and recession rates in 2015 were optimal for wading bird foraging until heavy rain in late April caused a reversal event. The 2016 dry season experienced strong El Niño conditions which produced the wettest dry season in 58 years (SFWMD 2017), while the 2017 dry season experienced a weak La Niña episode leading to drier than average conditions (National Weather Service 2017).

Paurotis Pond had the lowest water levels over all years sampled, while Tamiami

West had the highest, averaging 160% higher water levels than Paurotis Pond across all

years sampled, and 71% higher water levels than Hidden in 2015 (the only year small

herons nested at Hidden) (Fig. 3.5). Water levels at Paurotis Pond remained below 19 cm,

the maximum foraging depth for small herons (Powell 1987, Bancroft *et al.* 1990, Gawlik

2002), and experienced an increase of 8.4 cm in mean water depth over a 24-hour period

during the 2015 reversal in late April. Water levels at Tamiami West remained below 19

cm for the entire 2015 data collection period. Water levels also remained below the 19-

cm mark for the 2017 dry season until early June when water levels suddenly rose by

16.7 cm over a 48-hour period. Water levels in 2016 averaged 106% above 19 cm leg

level and remained at substantially higher levels for the duration of the data collection

period. Water levels at Hidden remained below the 19-cm depth cut off and were

punctuated by a 5.5 cm increase over a 24-hour period during the 2015 reversal in late

April (Fig. 3.5).

During the 2015-2017 nesting seasons, 227 bolus collection dates from 157

different nests on 51 different days were used for model development. The global model

was the top model ($w_i = 0.57$, $R^2 = 0.14$; Table 3.6) for explaining the percentage of non-

native fish consumption of small herons. The second-best model was the bird species

model, containing the variable bird species ($w_i = 0.43$, $R^2 = 0.10$; Table 3.6). Together

these models accounted for 100% of the Akaike weight.

Non-native fish biomass in small heron diets was highest for Little Blue Herons

and was positively influenced by birds utilizing Paurotis Pond as a nesting site. The

percent biomass of non-native fish was also positively associated with increased water

depth. Parameter estimates for all other variables (including the primary predictor variable rainfall) overlap zero substantially, suggesting they have little effect on non-native fish biomass consumption (Table 3.7).

3.5   DISCUSSION

3.5.1   Hydrologic Fluctuations

Results indicate that increased water depth was positively associated with the consumption of non-native fish, which further illustrates the influence of hydrologic conditions association with wading bird food resource acquisition. Additionally, on a coarser scale, variations in non-native prey consumption varied between 2016 (a very wet year) and 2017 (a very dry year). An unexpected finding was the similarity in the availability of non-native fish in 2016 and 2017 (5% and 7% non-native fish biomass, respectively) in the natural marsh, with greatly different patterns of consumption (26% and 8% non-native fish biomass, respectively). One possible explanation for this pattern is the difference in the amount of foraging habitat available to small herons in the natural marsh due to hydrologic conditions. Record breaking high water levels in 2016 led to only 2,709 km^2 of available landscape to birds as suitable foraging habitat; 24% below a 12-yr average (Gawlik *et al.* unpubl. report 2017). Due to the suboptimal foraging habitat available in the natural marsh during the 2016 nesting season, small herons may have turned to areas outside of their traditional foraging locations such as canals or mangrove creeks to supplement their dietary needs.

3.5.2   Bird Species

Prior to the construction of canals, refuges from seasonal drying were previously uncommon in the Everglades (Kline *et al.* 2014). Canals offer a stable habitat for aquatic

fauna, providing permanent, warm, deep-water refugia. Due to the tropical origin of most introduced fish species, they are susceptible to low-temperature stress (Loftus 1988; Trexler *et al.* 2000; Kline *et al.* 2014) and likely seek thermal refuge in deep-bodied canals. During the construction of canals, the limestone bedrock was penetrated, and many south Florida canals continue to receive warm water from the aquifer which penetrates through the porous limestone bedrock, maintaining temperatures above 17 ℃ (Shafland 1996, Trexler *et al.* 2000). Multiple studies have shown that introduced, non-native fish dominate the canals (Shafland 1996, Trexler *et al.* 2000).

Interspecific variations of foraging methods may explain differences in the level of exploitation of canals among small herons. Foraging behavior is considered a mechanism of resource partitioning, which may result in the capture of different prey, even among taxonomically and morphologically similar species such as small herons (Jenni 1969, Kent 1986). In a study examining five possible foraging behaviors, Little Blue Herons were observed utilizing the 'walking slowly' behavior 100% of the time, while Snowy Egrets and Tricolored Herons were observed utilizing up to five foraging methods including 'disturb-and-chase', and 'foot stirring' (Kent 1986). Little Blue Herons prefer foraging along the edges of habitat while searching under and around obstacles and vegetation for prey, while Snowy Egrets and Tricolored Herons prefer to forage in open expanses of shallow water with little to no vegetation (Lodge 2010). This method makes Little Blue Herons ideal foragers along canals which are composed primarily of long stretches of vegetated edges, whereas the less vegetated centers preferred by Tricolored Herons and Snowy Egrets, are generally deeper than the 19-cm leg length of these short-legged waders.

Low percentages (<7% biomass) of non-native fishes available in the Everglades, coupled with a large proportion (~ 40% biomass) of non-native fishes in Little Blue Heron diet suggest that Little Blue Herons may be utilizing alternative foraging habitats more frequently than other small heron species. Previous studies support these findings that non-native fish comprise a low percentage of the fish biomass in the Everglades (Shafland 1996, Trexler *et al.* 2000, Kline 2014), and that Little Blue Heron diet contained a higher percentage of exotic fish species than did that of the Tricolored Heron or Snowy Egret (Klassen *et al.* 2016). These results illustrate that Little Blue Herons, a native predator to the Everglades, is now reliant, to a large degree on non-native prey. These results may be an indication that Little Blue Herons are foraging in urban water bodies such as canals which provide a more stable environment than the fluctuating natural marsh.

3.5.3   Temporal Variation

Results indicate the majority of non-native fish were consumed from small herons nesting at Paurotis Pond which contained 32% non-native fish biomass. This finding is surprising considering Paurotis Pond encompasses less urban habitat than Tamiami West (Fig. 3.1), in which small herons consumed the least amount of non-native fish biomass (8%). This suggests that although the majority of non-native fish are found in canals (Shafland 1996, Trexler *et al.* 2000, Kline 2014), small herons may be accessing these non-native fishes elsewhere.

African jewelfish, which accounted for > 95% of the non-native fish biomass in bolus and throw-trap samples, were first detected in the northeastern portion of Everglades National Park in 2000 (Kline *et al.* 2014), and since have expanded rapidly to

the southwestern areas of the mangrove creeks at a rate of 4 km/year (Rehage *et al.*,

unpubl. data). Kline *et al.* 2014 found non-natives fishes comprised 8% of the total catch

in mangrove creeks. Paurotis Pond, a coastal colony surrounded by brackish wetland

encompasses these mangrove creeks within the 30-km small heron foraging radius (Fig.

1) and is a habitat unique to this colony among those involved in this study.

3.5.4 Conclusions

These results clearly demonstrate that Little Blue Herons (a diet generalist)

consumed non-native fishes, primarily African jewelfish, to a greater degree than

Tricolored Herons and Snowy Egrets (fish specialists), and by all small heron species

nesting in coastal Paurotis Pond, which experiences warmer water temperatures and

higher saline levels than other colonies in the study. Additionally, African jewelfish were

more readily consumed in 2016, an extremely wet year as compared to an average (2015)

or dry year (2017). What is unclear however, is the habitat type (natural or urban) from

which small herons capture non-native prey. Future research should focus on determining

if small herons foraging in the natural marsh are showing a preference for non-native fish

such as African jewelfish, or if they are foraging more frequently in urban waterbodies,

thus using non-native prey more readily simply because of their greater abundance.

3.5.5 Implications

African jewelfish are considered one of the most abundant and widespread non-

native fishes in Everglades National Park, and one of the most successful non-native

exploiters of both the Florida canal system and the natural marsh (Kline *et al.* 2014). First

observed in Florida in the 1960s, African jewelfish have recently and rapidly expanded

its range to include Everglades National Park in 2000 (Kline *et al.* 2014, Langston *et al.*

2010). This aggressive, fresh-water cichlid is a diet generalist that can feed opportunistically on native fish populations (Kline *et al.* 2014), dominant in the diets of Snowy Egret and Tricolored Herons.

The success of African jewelfish is due in part to its great physiological flexibility in terms of environmental variables (Schofield *et al.* 2010). Morphological, behavioral, and anatomical adaptations have allowed African jewelfish to live in otherwise harsh conditions such as hypoxic conditions experienced in the marsh and high salinity levels experienced in mangrove creeks (Chippari-Gomes *et al.* 2005). Studies have shown African jewelfish to be highly adaptive to hypoxic conditions experienced during the dry-down in the Everglades (Schofield *et al.* 2007, Chippari-Gomes *et al.* 2005), as well as withstand salinity levels 15 ppt above those experienced in estuarine and marine waterways of south Florida (Langston *et al.* 2010). A low-thermal tolerance (loss of equilibrium < 11.2º C or 52.2º F, and death < 7.9º C or 46.2º F) appears to be the main environmental stressor limiting the expansion of African jewelfish to the north (Schofield *et al.* 2010). Based on these findings it is not surprising that the relative abundance of African jewelfish is greatest in the canal system and the southern portion of the Everglades, including Paurotis Pond, which experiences warmer winter temperatures (Trexler *et al.* 2002).

Hyper-successful invasions of non-native species into an ecosystem, such as the African jewelfish into south Florida are known to alter native species abundance and composition at upper and lower trophic levels (Carlsson *et al.* 2009). Non-native fishes can alter marsh fish community dynamics through predation on native species as well as compete for resources, thus altering wading bird foraging behavior (Dineen and

Robertson 2010). Our results show native fish species including sailfin mollies, golden topminnow, Eastern mosquitofish, and bluefin killifish made up the bulk of the diet, both in frequency and biomass, for Snowy Egrets and Tricolored Herons. The continued success of non-native species such as the African jewelfish can potentially reduce native prey populations and the predators which rely on them. One such example is the New Zealand mud snail (*Potamopyrgus antipodarum*) that became so successful in Yellowstone National Park, Wyoming, that after 7 years of its introduction native invertebrates comprised only 3% of the total biomass (Hall *et al.* 2003). If the range and abundance of non-native fishes continue to expand, and native fish communities begin to diminish, the prey-switching ability of small herons will become increasingly important. If African jewelfish push out native fish communities through either competition or predation, these non-native fish may increasingly become a pivotal part of small heron's diet. A possible reliance on this thermal-intolerant species may be further problematic when Florida experiences a winter cold-snap below 11.2°C, which could deplete the African jewelfish population, potentially leaving small herons with a significantly diminished food supply.

If African jewelfish push out native fish communities through either competition or predation, these non-native fish may increasingly become a pivotal part of small heron's diet. A predator shown to feed on non-native species such as Little Blue Herons, may have a fitness advantage over predators that do not, thus a pre-switching ability in the face of HIREC can affect the growth and body condition of the predator (Carlsson *et al.* 2009). Other accounts of a native predators switching to non-native prey, include the non-native zebra mussel which has become a primary food source from many native

North American turtles, birds, and fish (Bulte and Blouin-Demers 2008, Petrie and

Knapton 1999, Magoulick and Lewis 2002, Molloy *et al.* 1994), and the invasive round

goby (*Neogobius melanostomus*) which has become important prey to breeding Double-

crested Cormorants (*Phalacrocorax auritus*) at Lake Ontario (Somers *et al.* 2003). In

south Florida, ready consumption of an invasive apple snail (*Pomacea maculata*) may

permit the recovery the endangered Everglade Snail Kite (*Rostrhamus sociabilis*), which

has otherwise been limited as a dietary specialist (Cattau *et al.* 2016).

Understanding the relationship between non-native prey and native predators is

more important than ever as non-native species invasions are an increasing threat to

biodiversity, and ecosystem functions (Holway *et al.* 2002, Carlsson *et al.* 2009).

Determining how non-native prey compete with other lower-trophic level species, as well

as determining what allows certain native predators to adapt, will allow us to better

understand why some species adapt and thrive, while others decline in the face of HIREC

(Both *et al.* 2006, Chace and Walsh 2006, Ludwig *et al.* 2006, Wong and Candolin

2015).

Table 3. 1 *A priori* models predicting the presence of non-native fish biomass in small heron bolus samples based on hydrologic parameters.

Hypothesis	Model
Global[1]	Y = WaterDepth + Rainfall + BirdSpp + Colony
Hydrological[1]	Y = WaterDepth + Rainfall
Bird Species[1]	Y = BirdSpp
Spatial[1]	Y = Colony
Bird Species + Hydrological[1]	Y = BirdSpp + WaterDepth + Rainfall
Null	Y = Year

Y= Percentage of non-native fish biomass (0-100)
[1] Year added as random variable to all models

Table 3. 2 Model parameters for factors influencing the presence of non-native fish in small heron bolus samples.

Fixed Effects	*Description*
Water Depth	Average daily water depth (cm) within a 30-km radius of colony
Rainfall	Total rainfall (cm) within a 30-km radius of colony within 2 days of bolus collection
BirdSpp	Bird species from which bolus was collected
Little Blue Heron	
Snowy Egret	
Tricolored Heron	
Colony	Nesting colony from which bolus was collected
Hidden	
Paurotis Pond	
Tamiami West	
Random Effect	
Year	Year when bolus was collected
2015	
2016	
2017	
Response variable	
Non-native Fish	Daily percentage of non-native fish biomass per nest

Table 3. 3 Number of nests sampled during the 2015, 2016 and 2017 nesting seasons from Little Blue Heron, Snowy Egret, and Tricolored Heron from 3 Everglades wading bird colonies.

	Little Blue Heron	Snowy Egret	Tricolored Heron	Total
2015				
Hidden	10	0	15	25
Paurotis Pond	5	12	16	33
Tamiami West	0	14	13	24
Total 2015	**15**	**26**	**44**	**82**
2016				
Paurotis Pond	5	9	16	30
Tamiami West	3	4	7	14
Total 2016	**8**	**13**	**23**	**44**
2017				
Paurotis Pond	1	0	2	3
Tamiami West	4	8	13	25
Total 2017	**5**	**8**	**15**	**28**
	28	**47**	**82**	**157**

Table 3. 4 Frequency of fish species within throw-traps during the 2016 and 2017 dry season, and small heron bolus samples collected during the 2015, 2016 and 2017 nesting season, Everglades, FL. Non-native fish species denoted with (*).

Common Name	Species Name	Throw-traps	Tricolored Heron	Snowy Egret	Little Blue Heron
*African jewelfish	*Hemichromis letourneauxi*	30	91	26	89
*Black acara	*Cichlisoma bimaculatum*	1	0	0	0
*Blue tilapia	*Oreochromis aureus*	4	1	0	0
Bluefin killifish	*Lucania goodie*	1184	229	198	163
Bluegill	*Lepomis macrochirus*	2	7	7	0
Bluespotted sunfish	*Enneacanthus gloriosus*	113	6	1	0
Brook silverside	*Labadesthes sicculus*	0	2	0	9
Diamond killifish	*Adinia Xenica*	0	0	4	0
Dollar sunfish	*Lepomis marginatus*	7	1	1	0
Eastern mosquitofish	*Gambusia holbrooki*	1353	761	604	165
Everglades pygmy sunfish	*Elassoma evergladei*	249	6	63	28
Flagfish	*Jordanellae floridae*	168	249	163	12

Common name	Scientific name				
Golden shiner	*Notemigonus crysoleucas*	0	0	0	11
Golden topminnow	*Fundulus chrysotus*	195	292	107	48
Goldspotted killifish	*Floridichthys carpio*	0	3	16	1
*Jaguar cichlid	*Parachromis managuensis*	4	0	0	1
Largemouth bass	*Micropterus salmoides*	2	5	0	0
Least killifish	*Heterandria Formosa*	879	122	211	103
Marsh killifish	*Fundulus confluentus*	69	95	38	25
*Mayan cichlid	*Cichlasoma urophthalmus*	3	10	4	1
*Orinoco sailfin catfish	*Pterygoplichthys multiradiatus*	0	0	1	0
*Pike killifish	*Belonesox belizanus*	7	25	5	1
Rainwater killifish	*Lucania parva*	0	13	1	0
Redear sunfish	*Lepomis microlophus*	9	1	2	0
Redfin pickerel	*Esox americanus*	1	0	0	0
Sailfin molly	*Poecilia latipinna*	211	303	146	43
Sheepshead minnow	*Cypriodon variegatus hubbsi*	7	8	0	10
Spotted sunfish	*Lepomis punctatus*	13	5	1	0
*Spotted tilapia	*Tilapia mariae*	1	6	1	1
Swamp darter	*Etheostoma fusiforme*	0	1	0	0
Tadpole madtom	*Nocturus gyrinus*	4	0	0	0
Taillight shiner	*Notropis maculatus*	6	0	0	0
Unknown killifish	*Cyprinodontidae spp.*	5	0	0	0
Unknown pickerel	*Esox spp.*	0	2	0	1
Unknown shiner	*Luxilus spp.*	0	0	0	2
Unknown sunfish	*Lepomis spp.*	9	13	8	3
Warmouth	*Lepomis gulosus*	3	1	1	1
Total		4552	2258	1609	718

Table 3. 5 Fish prey species dissimilarity between prey use (bolus samples) and prey availability (throw-trap samples) separated by bird species and year (2016 and 2017) from two Everglades wading bird colonies (Paurotis Pond and Tamiami West). Top three fish species driving dissimilarity between use and availability are displayed by percent contribution (% Cont.) and cumulative percent contribution (Cum. %). The data type from which the % contribution of dissimilarity for each fish species is found (bolus samples or throw-trap samples) is indicated by Use/Avail. (*) indicates fish prey use and availability were only collected from Tamiami West.

Year	Bird	Fish prey species	Use/Avail	% Cont.	Cum. %
2016					
	TRHE	Sailfin Molly	Use	15.19	15.19
		Eastern mosquitofish	Avail	14.78	29.97
		African jewelfish	Use	9.89	39.87
	SNEG	Eastern mosquitofish	Use	20.95	20.95
		Sailfin molly	Use	15.41	36.36
		Marsh killifish	Use	15.32	51.68
	LBHE	African jewelfish	Use	19.46	19.46
		Eastern mosquitofish	Avail	16.38	35.84
		Bluefin killifish	Avail	9.55	45.39
2017					
	TRHE	Sailfin Molly	Use	13.20	13.20
		Golden topminnow	Use	12.77	25.96
		Bluefin killifish	Avail	11.41	37.37
	SNEG*	Bluespotted sunfish	Avail	11.97	11.97
		Bluefin killifish	Avail	11.25	23.22
		Golden topminnow	Use	9.92	33.14
	LBHE	Bluefin killifish	Avail	17.66	17.66
		African jewelfish	Use	17.65	35.31
		Golden topminnow	Avail	13.69	48.99

Table 3. 6 Results of generalized mixed models for percentage of non-native fish biomass in small heron diet during the 2015-2017 nesting seasons in 3 Everglades colonies. Models are described with -2 log likelihood (-2Loglike), number of parameters (k), AIC_c values, differences in AIC_c values between the best model and each candidate model (ΔAIC_c), AIC_c weights (w_i), and the likelihood coefficient of determination (R^2). Models include the following terms: Global (Y = WaterDepth + Rainfall + BirdSpp + Colony); Hydrological (Y = WaterDepth + Rainfall), Bird Species (Y = BirdSpp), Spatial (Y = Colony), Bird Species + Hydrological (Y = Bird + WaterDepth + Rainfall), Null (Y=Year). Y= Percentage of non-native fish biomass (0-100). Year was added as random variable to all models.

Model	**-2Loglike**	**k**	**AIC_c**	**ΔAIC_c**	**w_i**	**R^2**
Global	2182.2	9	2201.02	0	0.57	0.14
Bird species	2191.34	5	2201.61	0.59	0.43	0.10
Spatial	2199.92	7	2214.44	13.42	0	0.07
Bird species + Hydro	2205.76	5	2216.03	15.01	0	0.04
Hydrological	2209.18	5	2219.46	18.44	0	0.03
Null	2216.10	3	2222.2	21.18	0	0

Table 3. 7 Model averaged parameter estimates (β), 95% confidence limits (LCL, UCL), predicting percentage of non-native fish biomass in small heron diet during the 2015-2017 nesting seasons in 3 Everglades colonies. Significant factors marked by (***) indicate the parameter estimate associated with the predictor variable does not overlap zero, (*) indicate the parameter estimate associated with the predictor variable overlaps zero slightly.

Parameter	β	LCL	UCL
Intercept	7.4354	-7.16229	22.03309
Rainfall	-0.6891	-7.00167	5.623472
Water Depth	0.1438	-0.39677	0.684368 *
Bird Species			
Tricolored Heron	5.4354	-4.08883	14.95963
Little Blue Heron	17.8585	5.63104	30.08596 ***
Snowy Egret	0		
Colony			
Paurotis Pond	15.0413	3.083144	26.99946 ***
Tamiami West	-7.1285	-20.4988	6.241836
Hidden	0		
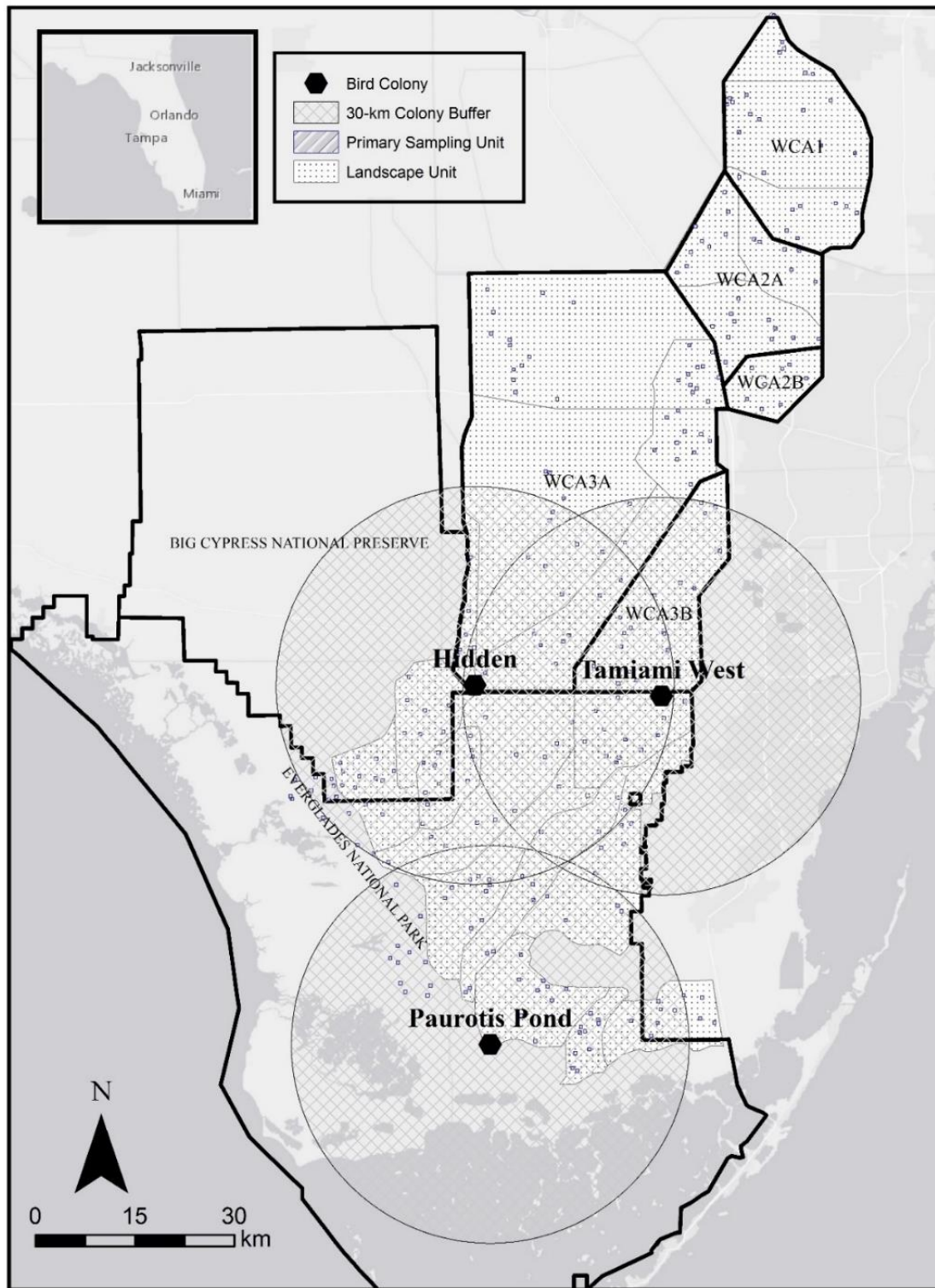
Figure 3.1 Map of small heron colonies with 30-km maximum foraging radius, and throw-trap data collection sites, landscape units (LSU) and primary sampling units (PSU).
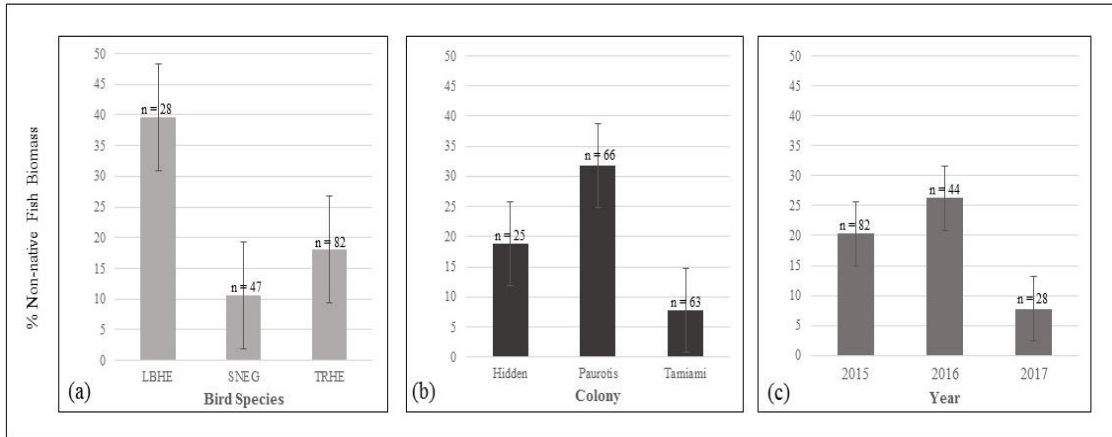
Figure 3.2 Average percent biomass of non-native fish among bird species, colonies, and years sampled.
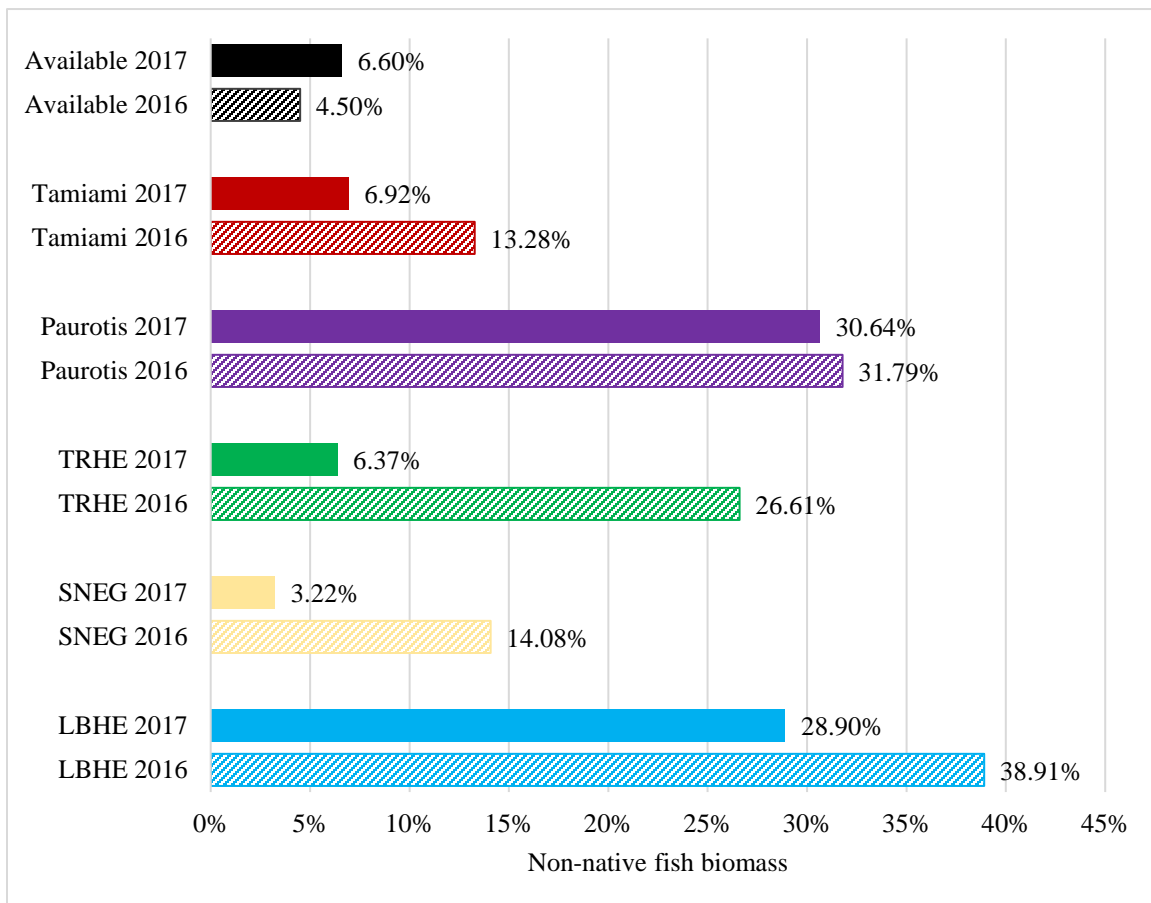
Figure 3.3 Percent biomass of non-native fish available in Everglades and consumed by small herons (broken down by colony, and bird species) in a wet year (2016) vs. a dry year (2017).

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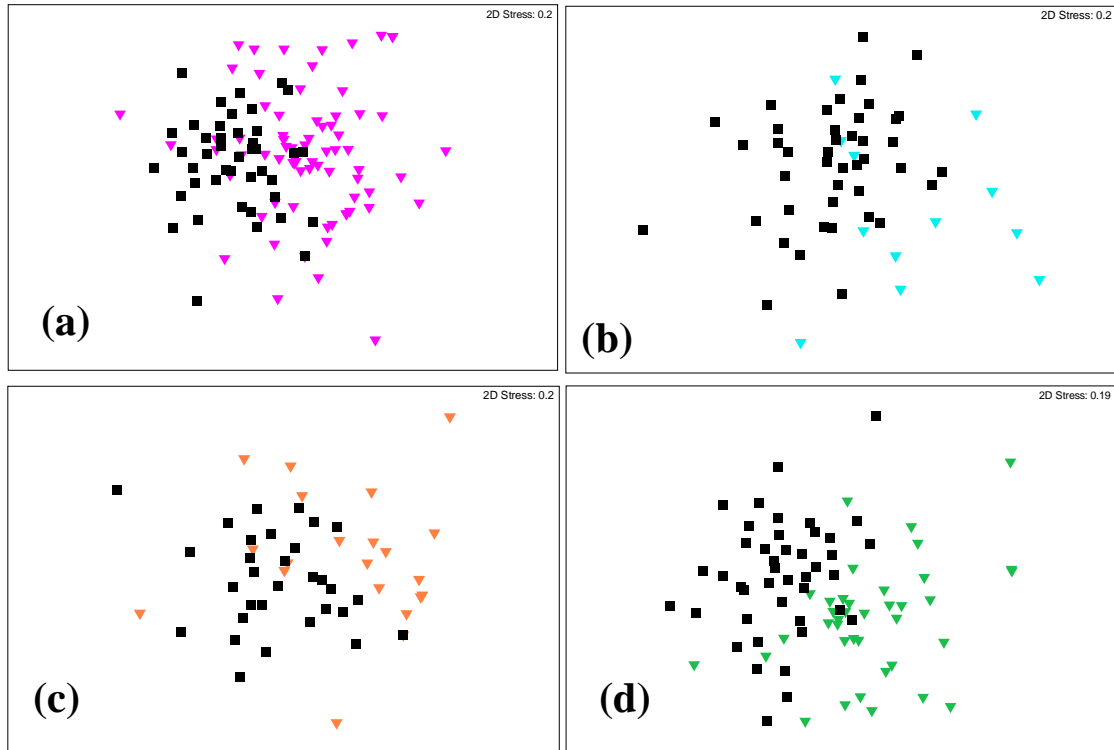
Figure 3.4 nMDS plot of total fish biomass percentage collected in small heron bolus samples (colored triangles) versus throw-trap samples (black squares). Each bolus point represents a single nest over the course of a nesting season. Each throw-trap point represents 4 throw-traps in a PSU per year. (a) All small heron nests, (b) Little Blue Heron nests only, (c) Snowy Egret nests only, and throw-trap samples from within 30-km range of Tamiami West only, (d) Tricolored Heron nests only.
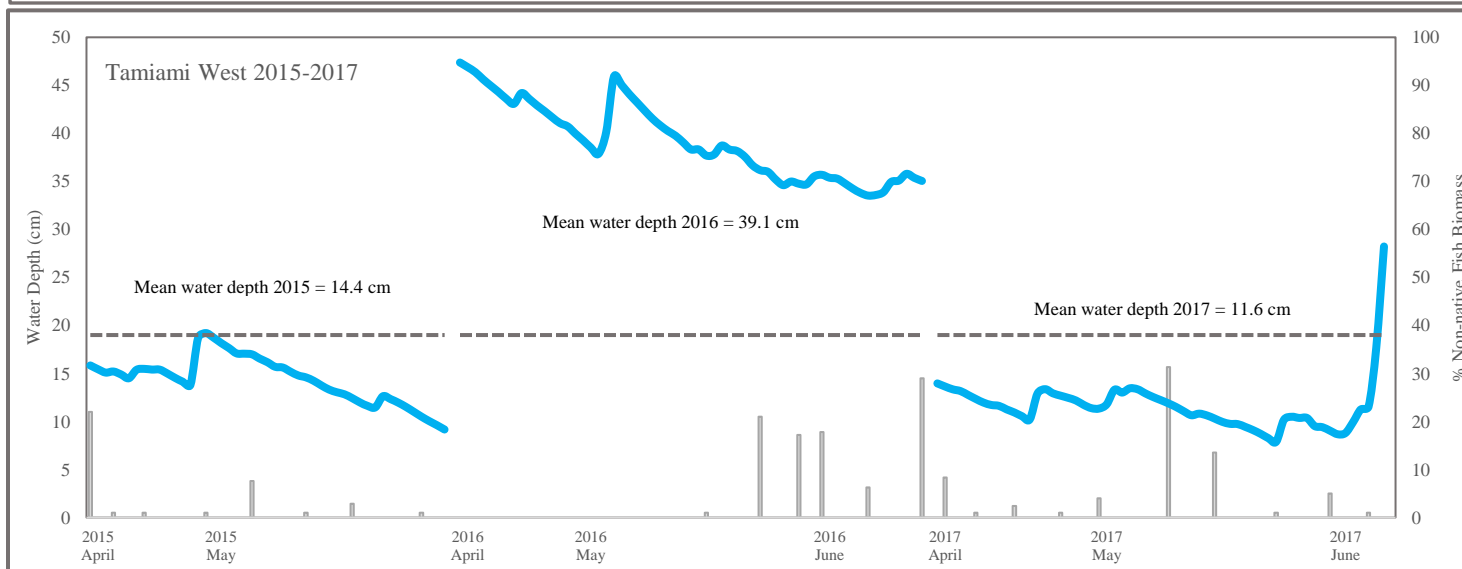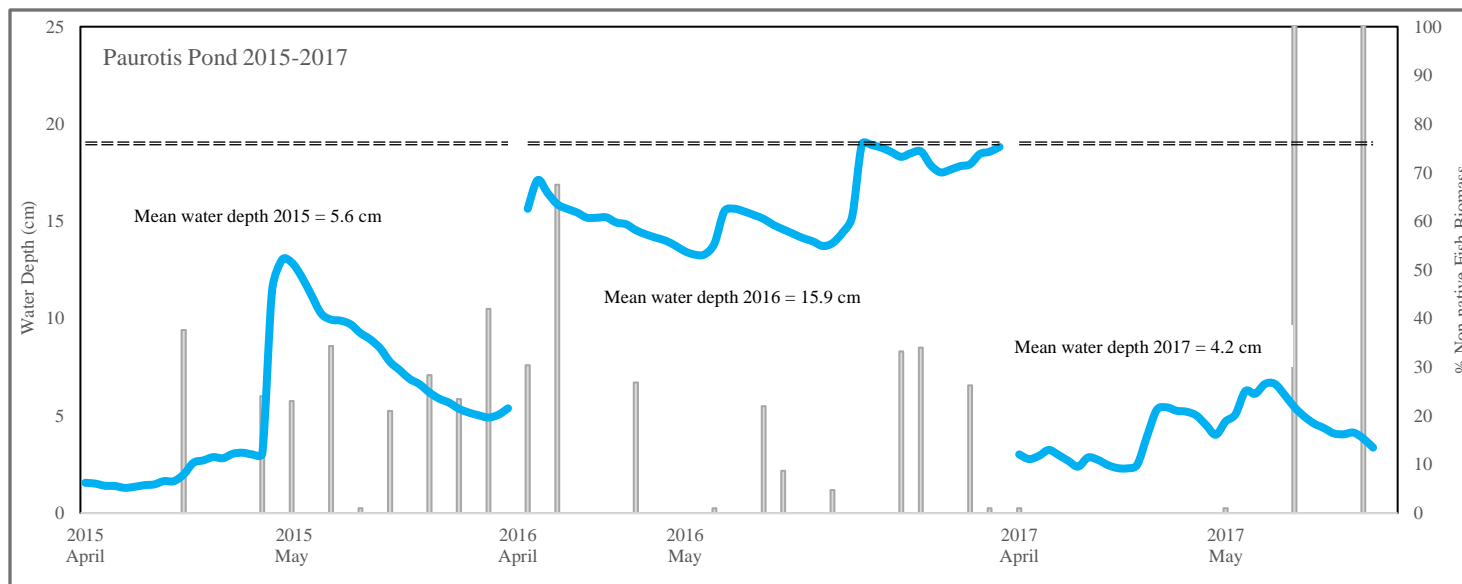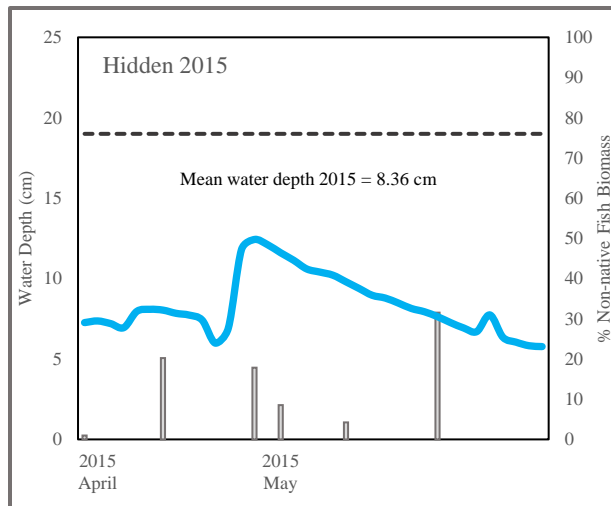
Figure 3.5 Daily average water depth and mean non-native fish biomass in small heron diets from 3 Everglades wading bird colonies during the 2015-2017 nesting seasons. Blue line represents the average daily water depth (cm) with in 30-km radius of each colony during periods of data collection. Grey bars represent the average percent of non-native fish biomass among all nests on date of each visit. One was added to each day of data collection to account for effort on days which resulting in no contribution from non-native fishes. Dashed line shows the small heron maximum foraging depth at 19 cm.

4   CONCLUSION

Studying small herons in the Florida Everglades provided a unique opportunity to examine how closely related predators that experience the same environmental conditions greatly affected by HIREC respond to such variation. The time-period of this study (2015-2017) was ideal, as it provided an array of varying hydrologic conditions including an average year, an above average wet year and an above average dry year. Such taxonomic similarities, and environmental variability allowed me to determine which prey characteristics influenced the overall fitness of small herons, and which environmental patterns influenced the use of the ever-increasing non-native fish community in the Everglades.

The diets of Snowy Egret and Tricolored Heron were comprised of mostly fish biomass (>90%), while the diet of Little Blue Heron included a wider array of prey taxa. My study was consistent with most single species studies that showed Snowy Egret and Tricolored Heron are fish specialists, while Little Blue Heron are diet generalists. My investigation into how variations in diet affected the overall fitness of small herons showed that a diet containing a variety of prey taxa and less of a reliance on fish, was positively associated with good body condition of small heron chicks. Additionally, I found that in a hydrologically dryer-than-average nesting season (2017) small herons produced chicks with a higher body condition and overall nest success than during the other years.

To further examine the influence of non-native fishes now established in south Florida, my study found that non-native fish constitute over half the biomass of fish consumed by Little Blue Heron. Additionally, and that <7% of the fish available to small herons within a 30-km radius of each colony were non-native, suggesting that Little Blue Herons may be utilizing foraging areas other than the fresh water marsh portion of the Everglades, including mangrove creeks, or urban canals. Increased water depth during the nesting season and an overall hydrologically wet year was associated with the consumption of non-native fish. Additionally, spatial scale played an important part in non-native fish consumption, as small herons nesting at the Paurotis Pond colony, which was closest the mangrove creeks, was associated with a higher consumption of non-native fishes.

This study illustrated the important relationship between hydrologic conditions and small heron prey. Additionally, it suggests that water management regimes could impact the overall fitness of small herons by affecting their diets. Also, this study provided the strongest evidence to date that non-native fish, primarily African jewelfish, constitute a considerable proportion of Little Blue Heron diet. If African jewelfish push out native fish communities through either competition or predation, these non-native fish may increasingly become a pivotal part of small heron's diet. A predator shown to feed on non-native species such as Little Blue Herons, may have a fitness advantage over predators that do not.

Understanding the relationship between non-native prey and native predators is more important than ever as non-native species invasions are an increasing threat to biodiversity, and ecosystem functions (Holway *et al.* 2002, Carlsson *et al.* 2009).

Determining how non-native prey compete with other lower-trophic level species, as well as determining what allows certain native predators to adapt, will allow us to better understand why some species adapt and thrive, while others decline in the face of HIREC (Both *et al.* 2006, Chace and Walsh 2006, Ludwig *et al.* 2006, Wong and Candolin 2015).

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