DIETARY NICHE RELATIONSHIPS OF WHITE IBIS, TRICOLORED HERON AND

SNOWY EGRET NESTLINGS IN THE NORTHERN EVERGLADES

by

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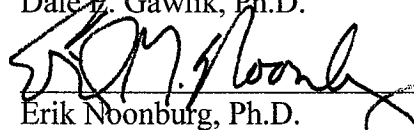
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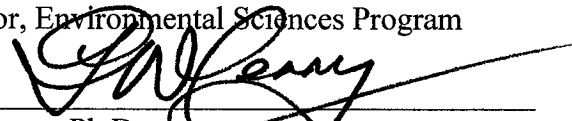
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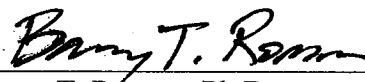Thesis Advisor

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ABSTRACT

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Food availability is the primary factor affecting the reproductive success in many species of birds. Diet composition can indicate diet quality, habitat use and niche requirements for breeding birds and may be variable across short and long-term time scales. Identifying primary prey types of nesting wading birds is important for the hydrologic restoration of wetlands. I collected nestling boluses during the 2008 and 2009 nesting seasons from three species of wading birds that nest in the northern Everglades: White Ibis, Tricolored Herons and Snowy Egrets. White Ibis bolus composition was dominated by crayfish in both years, but exhibited some variation with landscape water depth in 2009; fish use was greatest when the wetland landscape was relatively dry. In contrast, the prey of Tricolored Herons and Snowy Egrets were primarily fish and their respective diets did not differ from one another in either fish species composition or size structure.

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CHAPTER 1 – GENERAL INTRODUCTION

Introduction

Food limitation is considered a primary limiting factor for the variation in
breeding success of many bird species (Martin 1987, Butler 1994, Granbom and Smith
2006) and diet composition can indicate diet quality, habitat use and niche requirements
for breeding birds (Willard 1977, Smith 1997, Martínez 2004, Eeva et al. 2005). Diet
composition can vary within and between years and among species and it is important to
conduct diet studies that are temporally comprehensive (Smith 1997, Naef-Daenzer et al.
2000). In the Everglades, the working hypothesis (Gawlik 2002) is that hydrologic
variation drives prey availability and prey production which in turn affects reproductive
success. Previous research indicates that the time spent foraging in a particular patch by
wading birds is a function of both prey density and water depth (Gawlik 2002).

One goal of hydrologic restoration of the Everglades is the rejuvenation of
wetland prey production and an increase in the availability of prey for wading birds
(Ogden et al. 2003). However, the Everglades wetlands support numerous small fishes,
crayfishes (*Procambarus fallax and P. alleni*), grass shrimp (*Palaemonetes spp.)* and
other small aquatic animals (Turner et al. 1999). The importance of different prey types
for different wading birds is only partially resolved (Trexler and Goss 2009) and
restoration efforts may affect different species in different ways depending on how
restoration efforts affects their primary prey.

The White Ibis is one of the flagship species of the Everglades restoration efforts (Frederick et al. 2009). Previous studies have shown that White Ibis have a broad diet and feed on fish, crayfish, aquatic insects, terrestrial insects and garbage (Kushlan 1979, Heath et al. 2009, Dorn et al. *in review*). Kushlan (1979) conceptualized the relationship between landscape water depth and the types of prey eaten by ibis. Kushlan (1979) suggested that ibis feed on crayfish when surrounding water depths are relatively high and fish densities are low and only switch to using fish when water levels drop and fish become highly concentrated in isolated pools (Figure 1). Tricolored Herons and Snowy Egrets are two co-occurring wading bird species in the Everglades. Tricolored Herons and Snowy Egrets are ecologically similar species and previous research indicates that their diet mainly consists of fish (Frederick 1997, Smith 1997, Parsons and Master 2000). A similarity in diet composition may be an indication of competition.

An accurate assessment of diet composition is dependent upon the techniques used to collect diets and analyze the prey. Pellets (indigestible material) and prey remains underestimate diet composition (Seefelt and Gillinghan 2006, Figueroa and Stappung 2003). Reporting intact/whole prey only is a method often used in diet studies (Kushlan 1979, Findholt and Anderson 1995, Smith 1997) but may poorly reflect prey abundance, composition and biomass. Figueroa and Stappung (2003) used pellets and prey remains (partially digested animal remains) to quantify the prey of Great Egrets (*Ardea alba*) in Chile and found higher prey diversity in pellets than in prey remains. Passive observations of birds feeding in the marsh will likely produce inaccurate results due to identification error by the observer and poor resolution of prey sizes. Prey items

consumed by White Ibis are relatively small and easy to misidentify (Cezilly and Wallace 1988).

A study using all measurable prey remains in boluses or stomachs should provide a more accurate description of diet composition and prey biomass (Dorn et al. 2008, Dorn et al. *in review*). Seefelt and Gillingham (2006) found that bolus collection provides the best estimate of prey composition and biomass without having to sacrifice any birds. Findholt and Anderson (1995) used both boluses and stomach contents of American White Pelican chicks (*Pelecanus erythrorhynchos*) in Wyoming and found no difference in prey composition between the two methods. In this thesis I quantified boluses by reconstructing prey sizes from remaining prey parts in the boluses.

In chapter 2, I quantified and compared diet variation of White Ibis in Loxahatchee National Wildlife Refuge over 2 years. Specifically, I compared the diets of White Ibis between and within nesting seasons. Diets were collected during the 2008 and 2009 nesting seasons from 3 colonies in Loxahatchee; 2 smaller colonies in 2008 and 1 large colony in 2009. Multivariate analyses were used to compare diet composition between years and across collections within years. Specifically, I looked for a shift in prey composition consistent with Kushlan's (1979) depth-dependent diet observations. I also used univariate analyses to look for differences in biomass (total biomass, aquatic biomass and terrestrial biomass) and caloric content between years. I performed correlation analyses to explore potential relationships between hydrologic variation (water depth, recession rate) and bolus size or energy content. In chapter 3, I compared the prey use of White Ibis and co-occurring Tricolored Herons and Snowy Egrets. I contrasted the diet composition of the three species and then used additional fine scale

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categories to contrast heron and egret prey use. I was less interested in the temporal

variations in prey use in chapter 3 and rather focused on the inter-specific differences in

diet composition.
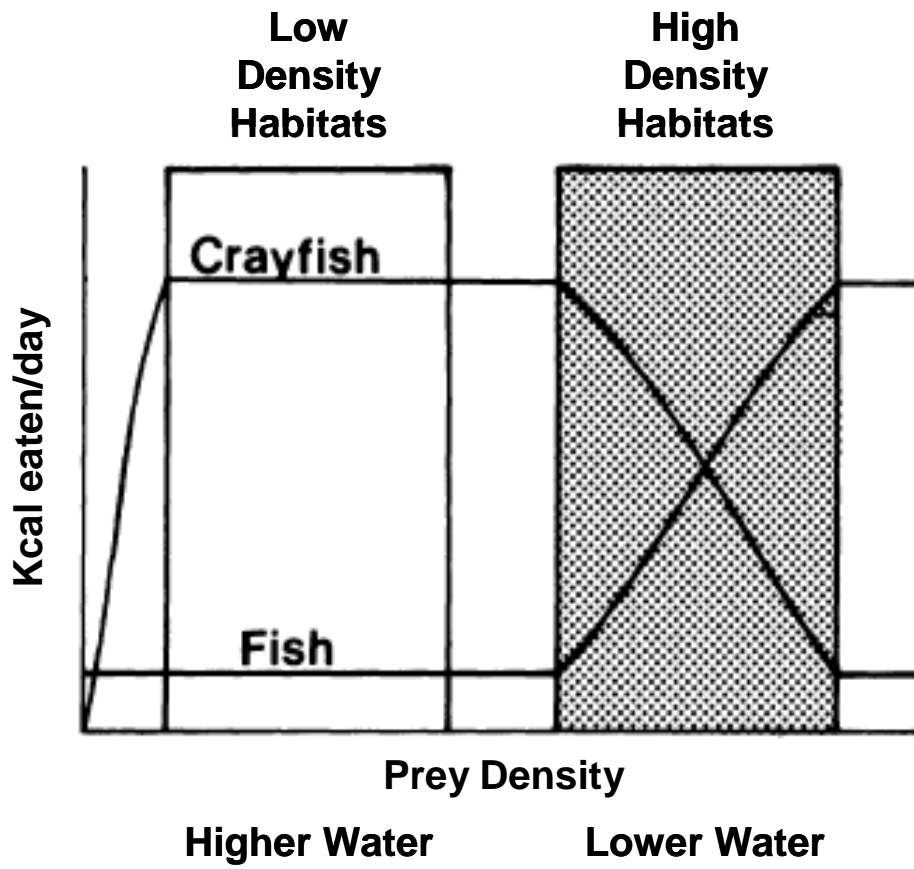
Figure 1. Conceptual diagram from Kushlan (1979) describing the potential relationship between water depth and the types of prey eaten by White Ibis. The x-axis was modified from the original figure.

CHAPTER 2 - WHITE IBIS NESTLING DIETS IN THE EVERGLADES: ASSESSING
THE RELATIONSHIP BETWEEN DIET COMPOSITION AND HYDROLOGY

Abstract

One of the goals of ecological restoration in the Everglades is the enhancement of wading bird colonies through changes in hydrologic management. However, the diets of nesting White Ibis, the dominant nesting wader, remain poorly researched. The main objective of this study was to quantify and compare White Ibis diets in Arthur R. Marshall Loxahatchee National Wildlife Refuge, the northern Everglades, during the 2008 and 2009 nesting seasons. Water levels in the northern Everglades were relatively higher and stable in 2008 and the total nesting numbers were lower than in the excellent nesting season of 2009 when landscape water depths receded to a greater degree.

87 boluses were collected in 2008 and 145 in 2009 from the largest nesting colonies in Loxahatchee. I took 4 collections in 2008 at Loxahatchee West and Colony 73 (2 collections each) and in 2009 4 collections were taken at New Colony 4. All prey and prey parts were identified and their sizes (g dry mass) were estimated in order to quantify the biomasses of each prey type.

The mean total biomass per bolus did not differ between years. Crayfish were the dominant prey type in both years and were present in 58-88% of the boluses in any given collection. These results indicate that crayfish are a heavily used prey type over all of the observed water conditions in Loxahatchee. In spite of annual differences in hydrologic

conditions, nesting numbers, and spatial location of colonies in Loxahatchee, crayfish

consistently contributed 55-65% of the total energy fed to the average chick at each of the

three colonies. Fish accounted for 0-36% of all prey biomass across the collections in

2008 and 0.8-27% in 2009. Terrestrial prey and garbage use was highest when the depths

of the surrounding wetlands were relatively high.

Prey composition did not vary between any collections in 2008, but differed

significantly between early and late collections in 2009. In 2009 the biomasses of both

small-bodied fishes and sunfish increased and crayfish biomass decreased in the last

collection when the surrounding wetlands were shallower and less total wetland habitat

was available for foraging. Our results indicate that crayfish are a dominant component

of White Ibis diets in Loxahatchee during relatively poor and excellent nesting seasons

and that fish are only used by a large number of the nesting ibis if/when the wetland

landscape water levels are relatively low. The similarity in prey use coupled with

differences in nesting effort suggests that ibis nesting effort may be largely determined by

environmental conditions (i.e., appropriate prey densities and landscape water depths

earlier in the dry season) prior to nest initiation.

Introduction

Food limitation is considered a primary limiting factor for variation in breeding

success of many bird species (Martin 1987, Butler 1994, Granbom and Smith 2006). The

composition of boluses fed to chicks can indicate diet quality, habitat use, and niche

requirements for breeding birds (Willard 1977, Smith 1997, Martínez 2004, Eeva et al.

2005). Environmental variation can affect the prey productivity, prey composition and

prey availability for foraging adult birds (Gawlik 2002, Hebert et al. 2008). Environmental management and restoration efforts require identification of environmental conditions leading to success of particular sentinel species, and for bird populations this often means identifying conditions that produce plentiful high quality diets for their young. However, there is considerable spatial and temporal variation in diet and nesting success for many avian species (Naef-Daenzer et al. 2000) so identifying important prey types and the related environmental conditions requires studies of diet variation in space and/or time. If those conditions can be identified then new research into prey production/availability as well as environmental management can proceed accordingly (Frederick and Spalding 1994, Ma et al. 2010).

Since the 1930s, the number of wading bird nests in the Everglades has decreased by ~70% (Crozier and Gawlik 2003). White Ibis (*Eudocimus albus*) nests have declined by about 87%, Wood Storks (*Mycteria americana*) by 78%, and Tricolored Heron (*Egretta tricolor*) and Snowy Egrets (*Egretta thula*) by 66%. Much of this loss seems to be a result of decreased prey availability (Frederick and Spalding 1994, Gawlik 2002). While prey production across the South Florida landscape has certainly been affected by the 50% reduction in the size of the wetland (Davis and Ogden 1994, Rader 1999), highly altered hydrologic regimes also affect prey production (Loftus and Eklund 1994, Ruetz et al. 2005) and the availability of the prey to nesting birds (Gawlik 2002).

One goal of hydro-restoration of the Everglades is the rejuvenation of wetland prey production and an increase in the availability of the prey for wading birds (Ogden et al. 2003). However the Everglades supports numerous small fishes, crayfishes (*Procambarus fallax and P. alleni*), grass shrimp (*Palaemonetes spp.)* and other small

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aquatic animals (Turner et al. 1999), and the importance of different prey types for different wading birds is only partially resolved (Trexler and Goss 2009). This challenge is complicated because prey species have different energetic or nutritional value (Kushlan 1986) and the production and availability of different prey types may depend on hydrology in various ways (e.g., Kushlan 1979, Gawlik 2002, Ruetz et al. 2005, Dorn and Trexler 2007). For example, the populations of Everglades crayfish (*Procambarus alleni*) are favored by moderate hydroperiods and drying events (Dorn and Trexler 2007) while total fish density and abundance of large-bodied fishes increase with long periods of inundation (Trexler et al. 2002, Ruetz et al. 2005). Kushlan (1979) further indicated that fish, crayfish and other prey animals reach their highest concentrated biomasses at different water depths in a drying marsh.

In order to restore the ecosystem processes that encourage prey production for nesting wading birds, researchers need to identify the prey assemblages necessary for fueling their nesting colonies. The White Ibis is one of the flagship species of the Everglades restoration efforts (Frederick et al. 2009). It is a highly nomadic species; it ranges along the coastal areas of the southeast United States, the Caribbean, and the Gulf Coast of Texas and Mexico south to Belize. The majority of White Ibis in Florida nest in the Everglades wetlands and some nest along the coast (Heath et al. 2009). In most years it is the most abundant nesting wading bird species in the Everglades (Kushlan et al. 1986). Historically, White Ibis contributed to the majority of the nesting effort in mixed-species nesting colonies (Kushlan et al. 1986, Crozier and Gawlik 2003, Frederick et al. 2009) with nests numbering in the tens of thousands.

White Ibis are generalist, probing foragers and have a broad diet (Kushlan 1979, Heath et al. 2009, Dorn et al. *in review*). Although the adults are often seen foraging close to the nesting colony (<15 km), they are able to fly >35 km to obtain prey (Smith 1995). In wetlands, ibis forage in water up to 25 cm deep (Beerens 2008, Heath et al. 2009) but typical depths are 5-10 cm. They use two principle techniques for capturing prey: bill sweeping is used when fish concentrations are high whereas tactile probing is used to extract crayfish, fiddler crabs (*Uca spp.*) and other aquatic invertebrates from the sediments (Heath et al. 2009). Probing is also used in urban habitats while foraging for terrestrial prey and ibis have the capability of switching between aquatic and terrestrial habitats in the Everglades (Dorn et al. *in review*); however the profitability of terrestrial diets is not well known. White Ibis nesting in the Everglades normally starts in late spring (e.g., March), but may be delayed due to unfavorable water levels/feeding conditions. Altricial chicks are born after an average incubation period of 21 days and are fed by both parents starting at two days old. Ibis chicks are fed regurgitated food (hereafter boluses) up to nine times daily from two to fifteen days old. By four to five weeks old chicks are able to fly short distances to and from the colony site and are able to forage in the surrounding marsh (Heath et al. 2009).

Hydrologic patterns affect fish production (Ruetz et al. 2005) and prey availability (Gawlik 2002). Therefore foraging success, bolus size, bolus composition, and nesting success of the White Ibis are expected to be correlated with recent hydrology (Kushlan 1979, Bildstein et al. 1990, Gawlik 2002, Herring et al. 2010). Stable deep water levels throughout the nesting season prevent the concentration of fish in pools and may keep crayfish from becoming available as well. Steady recession rates and lower water depths

that increase prey availability have been related to high nesting success of wading birds in the Everglades (Russell et al. 2002). Kushlan (1979) suggested that ibis may feed on crayfish when landscape water depths are relatively high (i.e., more of the landscape is flooded) and that fish are only accessible when the system is relatively dry (i.e., depth-dependent diets). Recent diet analyses (Dorn et al. *in review*) give some additional support to depth-dependent diets; however the sample sizes of bolus collections were rather small from dates early during the nesting season when landscape water depths were relatively high.

Steady recession each year during the dry season will sequentially expose wetland habitats with longer and longer hydroperiods (i.e. lower elevation sites) for foraging by wading birds. The movement of the foraging birds down gradient with lower landscape water depths may explain diet shifts if the longer hydroperiod areas lower on the landscape produce and/or concentrate more fish. The population density of crayfish may be distributed equally across the landscape or declining in abundance in lower elevation/longer hydroperiod habitats (Dorn and Volin 2009) but the regularity of this prey shift and the mechanism responsible are still unclear (Dorn et al. *in review*). While White Ibis can forage on fish, crayfish, and other aquatic and terrestrial prey (Dorn et al. 2008, Heath et al. 2009), we do not know which prey types are primarily or consistently responsible for supporting the colonies in good versus bad nesting years.

I compared diets of nestling White Ibis collected from the Northern Everglades, Arthur R. Marshall Loxahatchee National Wildlife Refuge (hereafter "Loxahatchee") within and between years in a relatively poor nesting year (2008) and a very good nesting year (2009). In order to assess the relationship between bolus composition and changes

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in hydrology, I evaluated prey composition, associated hydrologic variables, and bolus energy content. Specifically, my objectives were to (1) analyze the prey composition of nestling White Ibis from 2008 and 2009 looking for variations in diet consistent with a significant switch from crayfish to fish use (Dorn et al. *in review*), (2) test for an association between the total energy content of a bolus and bolus composition (Kushlan 1986), (3) analyze bolus biomass and energy content between years to look for overall differences in diet that may have been caused by water level variation (stable high water levels vs. low receding water levels), (4) investigate potential associations between hydrologic variation (landscape water depth, recent recession) and mean bolus size and energy content and (5) quantify the energetic contribution of each prey type for each colony in 2008 and 2009 using the temporal variation in percent contributions of different prey (% kcal).

Methods

Area of Study

Loxahatchee is located in Palm Beach County, Florida. The refuge is a 57,324-ha area of remnant Everglades wetland in the northern reaches of the Everglades ecosystem (Fig. 1). Loxahatchee is a peat-based wetland with seasonally fluctuating water levels, but is separated from other water conservation areas by a series of canals and levees (Brandt et al. 2000). The number of wading bird nests in Loxahatchee has steadily increased in the last 5 years, varying between 5,000 and 15,000 (Frederick and Simon 2008). The two nesting years examined in this study were independently judged to be poor and very good respectively, based on nesting numbers and hydrologic patterns in

Loxahatchee. 2008 had high stable water with reversals and ~6,000 White Ibis nests, and 2009 had steady water recession, moderate-low water depths and ~9,300 ibis nests (Frederick and Simon 2008, 2009). Landscape water depths were higher at the initiation of the 2008 nesting season and water depth further increased after the initial sampling date in 2008 while 2009 experienced steady recession rates and a lower initial landscape water depth (Fig. 2). Nesting started earlier in 2009 than in 2008 (Fig. 2) and the majority of 2009 nests had already fledged before the onset of the rainy season and the attendant increase in water depth.

Diet Collection and Analysis

I collected 232 boluses from White Ibis chicks in 2008 (n = 87) and 2009 (n = 145). In 2008 boluses were collected from Loxahatchee West (hereafter "Lox West") and from Colony 73 (locations in Fig. 1). In 2009 boluses were collected from one large nesting colony, New Colony 4 (hereafter "NC 4", Fig. 1). No White Ibis nested at NC 4 in 2008 or at Colony 73 in 2009 and only 1,000 White Ibis nested at Lox West in 2009. Bolus collection dates, colony designations and the total number of boluses collected during the 2008 and 2009 nesting seasons are shown in Table 1. Boluses were collected between 0800 and 1200 hours and total time spent on the colony did not exceed one hour in order to limit stress to both the chicks and adults.

Approximately 90% of boluses were collected from the ground after voluntary regurgitation by the chicks. Tracheal massage to induce regurgitation was used on chicks that appeared to hold a bolus in their crop. Approximately 20 nestlings were handled in 2008 in order to obtain a bolus; no nestlings were handled in 2009. All boluses were

placed in plastic Ziploc® or Whirl-pak® bags and placed on ice for transport back to the lab. In the lab the boluses were preserved in 80% ethanol until sorted.

In the lab I rinsed each bolus in a mesh net (0.63 µm), and sorted the prey remains under a magnifying lamp. Boluses were searched twice and all identifiable prey items or parts found were collected, counted and placed in labeled glass scintillation vials. For most prey items, excluding garbage and large terrestrial vertebrates, I used length-length and length-mass regressions to calculate dry mass. Other prey items were dried at 55°C to a constant mass and weighed to determine dry mass. Detailed methods for biomass determination and regression parameters can be found in Appendix 1. Caloric content for common prey items was determined and compared to Kushlan (1986). Both aquatic and terrestrial prey types were analyzed and detailed methods and prey caloric content values can be found in Appendix 2.

Hydrologic Conditions and Foraging Habitat around the Colonies

I estimated water depths and available habitat around the colonies for the different sampling dates in 2008 and 2009 (Fig. 2). Hydrologic conditions around the colonies were calculated using the Everglades Depth Estimation Network (EDEN) and the xy Locator Tool (v1.4). EDEN is an integrated network that uses both ground elevation and water surface data to produce real-time water level estimates for the entire fresh water portion of the Everglades ecosystem (400x400 m cell resolution). Using the EDEN grid and a GIS (ESRI ArcMap® V 9.2) I selected the cells within a 15-km radius around each of the 3 nesting colonies. Previous studies (Smith 1995, Beerens 2008) indicated that the average foraging distances of nesting White Ibis were less than 15 km from the nesting

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colony so wetland conditions within a 15-km radius should reflect conditions experienced in more than 50% of the foraging trips. The xy Locator Tool was used to determine the depth of each cell on each collection date. The mean water depth of all cells within a 15-km radius was calculated. The estimate of mean depth was based solely on the foraging flight distances that ibis are capable of.

Different landscape water depths indicate that different parts of the wetland are available for foraging (Beerens 2008) and I assumed that foraging ibis were moving across the landscape throughout the nesting season if the landscape depths were receding. While I am unsure of exactly where on the landscape the birds were foraging, telemetry studies in 2006 and 2007 by Beerens (2008) indicated that White Ibis foraging in Loxahatchee targeted depths between -16.0 and 15.5 cm (according to the EDEN water depth model). Using this finding I assumed that available foraging habitat could be estimated as the number of locations (cells) around the colony with appropriate water depths within a particular distance based on typical flight distances. Using this assumption, I calculated available wetland habitat (km^2) for each colony on each collection date from the cells with a depth range of -16.0 to 15.5 cm. I also calculated the per capita amount of available habitat by dividing the available area (km^2) by the peak size of the colony (maximum number of nests).

The EDEN water gauge, WCA1ME located in central Loxahatchee was used to calculate recession rate during the 7 days prior to a collection. Recession rate was calculated by subtracting the water depth on a collection date from the water depth 7 days prior to the collection divided by 7 (Beerens 2008); positive values indicate that the water is receding. Because ibis can change landscape foraging tactics quickly (Smith 1995,

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Dorn et al. *in review*) recent changes in recession from positive to negative (rises in water depth caused by rain or management) might affect prey use.

Statistical Methods

Prey items were lumped into 8 distinct categorie s or prey functional groups; crayfish (all identifiable individuals were *Procambarus fallax*), sunfish (*Lepomis* and *Enneacanthus* spp.), small-bodied fishes (*Gambusia holbrooki, Jordanella floridae, Poecilia latippina*, and killifishes), grass shrimp, aquatic insects, terrestrial insects, garbage (mostly rotten chicken and dog food) and other vertebrate prey. These groupings are consistent with another analysis of diet data from the Everglades (Dorn et al. *in review*) and are based on habitat type (terrestrial vs. aquatic foraging), adult prey size, and taxonomy (i.e., life history and functional relationships with water depths; Kushlan 1979).

Diets were analyzed with multivariate and univariate methods to test for significant within- and between-year variation and a shift in diet composition or size/caloric value at the lowest landscape water depths. For multivariate tests and analyses of diet energetic content boluses were treated as independent observations of diet. Frequency of occurrence of prey and average proportional contributions of each prey type to the diets on each collection date were used to help interpret the multivariate results.

To analyze biomass composition across collections I used graphical and statistical multivariate techniques outlined by Clarke and Warwick (2001, PRIMER v6). A traditional multivariate analysis of the data (e.g., MANOVA) was impractical because of

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the large number of zero values. Although the inter-annual differences are more challenging to interpret, the potential foraging areas in the wetlands did overlap to a large degree (1451-2296 km^2 overlap). To help compare years and address potential causes of diet variation I included both inter- and intra-annual statistical comparisons in the results and the discussion.

Biomass of each prey type in each bolus was square root transformed before calculation of the Bray-Curtis resemblance matrix. Square root transformation was used in order to down-weight the influence of overly heavy and/or exceptionally important prey items (i.e., vertebrates and crayfish), and to detect subtle differences in prey composition. Using the resemblance matrix, diet similarity was visually inspected with 2-Dimensional and 3-D MDS (non-metric multi-dimensional scaling) plots. The ANOSIM test was used to determine if there were differences in diet composition between collections. SIMPER analyses were run on the original transformed dataset to determine which prey types were most responsible for the similarity within and dissimilarity between collections.

The association between diet composition and caloric content was analyzed two ways. First I used the BEST (Bio-Env) procedure to look for an association between diet composition and total caloric content of each bolus. Bio-Env is used to find the best match between multivariate among-sample patterns and associated environmental variables. The Bio-Env procedure was only performed on the 2009 diet data because the ANOSIM test did not find any compositional differences between collections in 2008. Diet composition can differ in many ways and I wanted to determine whether fish diets (diets with at least 1 fish) in 2009 were more energetically profitable than those diets

lacking fish. For this analysis I categorized the 2009 diets according to the presence (n = 47) or absence (n = 98) of fish and analyzed their total caloric content directly. I used a nonparametric Wilcoxon test (Sokal and Rohlf 1995) because residuals could not be normalized.

Inter and intra-annual differences in total biomass, total aquatic biomass, total terrestrial biomass and total caloric content were analyzed with ANOVA (SAS® V 9.2 PROC GLM; SAS Institute). Annual variation was analyzed using the mean and median total biomass, aquatic biomass, terrestrial biomass and caloric content for each collection as independent measures of diet size or quality. I analyzed inter-annual variation by comparing the 2008 and 2009 collections using each bolus as a replicate to determine whether there was any variation in diet size between collections. For one of the dominant prey types (crayfish) I compared the sizes of crayfish (mm carapace length, CL) in the diets between years and the availability of crayfish in Loxahatchee prior to the nesting season. The mean size of crayfish in the diets was analyzed with ANOVA (SAS® V 9.2 PROC GLM; SAS Institute). Pre-nesting season crayfish densities at 4 throw trap sites in Loxahatchee was calculated for both years with five traps taken from random points at each site in January. Crayfish densities in the sloughs were analyzed with a paired t-test (SAS® V 9.2 PROC GLM; SAS Institute, Dorn et al. 2005). Analyses were run on log-transformed data.

After establishing that there were statistically significant (α = 0.05) differences between collections in bolus size and energy content I proceeded to look for correlations between hydrologic conditions and bolus size using the 8 collection means from 2008 and 2009. I wanted to know whether bolus size or use of particular habitat types varied

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linearly in Loxahatchee colonies with hydrologic variation around the colonies. The

hydrologic variables analyzed were recent recession rate (net change in water depth

during the previous 7 days), mean water depth surrounding the colony and amount of

available habitat surrounding the colony. The bolus characteristics in each of the

correlations included mean total biomass, mean aquatic biomass, mean terrestrial biomass

and mean caloric content; correlations on raw data were run in SAS (SAS® V 9.2 PROC

CORR; SAS Institute).

In order to quantify the energy intake of each colony in 2008 and 2009 I

calculated the average proportional contributions of each prey type on each collection

date. Proportions were calculated from the total calories per prey type per bolus. I then

calculated the mean contribution for each prey type for each year-colony combination

using the collection date mean caloric content.

Results

Wetland conditions During Provisioning

The nesting White Ibis experienced variable habitat and water depth conditions in

2008 and 2009 (Table 1). The total amount of available foraging habitat around a colony

was lowest at the highest water depths in 2008 ('08b and '08d, Table 1). Water depths

reached the lowest point in this study at the end of 2009 ('09d, Table 1), but the amount

of available ideal foraging habitat remained relatively high. In 2009 longer hydroperiod

wetland sites were available for foraging. Indeed, no new wetland habitats were

becoming available at the end of the 2009 nesting season; all unavailable wetland cells

within 15 km of the colony were too dry for foraging meaning that the lowest elevation

sites on the wetland landscape were all available for foraging. The average 7-day

recession rates for the colonies in 2008 were both negative (-0.62 and -0.21 cm/day)

indicating net water level rise during the provisioning period. The average 7-day

recession rate for 2009 was 0.33 cm/day indicating a steady decrease in landscape water

depth.

Diet Composition

In total I found 803 prey items in 2008 and 1,958 items in 2009 excluding garbage

items like chicken, dog food, and unknown tissue that are difficult to count. The percent

occurrence of the different prey types in each collection is summarized in Table 2. 58-

88% of all boluses across all dates contained at least one crayfish. The only other prey

type to exceed 50% occurrence on any collection was the small-fish prey type at the end

of 2009 (67%).   Vertebrates, sunfish, small-bodied fishes, and shrimp prey were missing

from 2 or more of the 8 collections (Table 2). Crayfish biomass dominated the diets,

making up >53% of the average biomass in each collection in both years (Table 3).

When small-bodied fishes and sunfish were combined their mean proportional biomass

varied from 0-36% in 2008 and 0.8-27% in 2009 (Table 3).

Crayfish use remained high throughout the sampling period (Table 2), but the

percent contribution to within collection similarity was lowest when mean water depth

surrounding the colony was lowest (Table 4). There were significant compositional

differences in ibis diets when all collections were compared (global $P = 0.009$). Diet

composition from collections in 2008 was not different from one another (*P*-values >

0.1), but there were several differences in diet composition between collections in 2009

(statistically significant comparisons in Table 5). In general the use of both small-bodied fishes and sunfish increased as the mean water depth surrounding the colony and the available habitat decreased (e.g., '09a and '09c vs. '09d, Table 5). The MDS plot for collection '09a and '09d can be seen in Fig. 3, and illustrates the crayfish dominated diets of collection '09a versus the mixed fish and crayfish diets of collection '09d. Although the diet composition of collections '09b and '09d were not statistically different the P-value was small ($P = 0.07$), and prey composition differences were consistent with the other comparisons of earlier collections at higher landscape water depths versus the last collection at the lowest landscape water depth ('09d, see Table 5).

Inter-annual pairwise comparisons of 2008 and 2009 collections showed significant compositional differences (P-values < 0.05) between 8 of 16 pairs of collections (Table 5). In general, the use of small-bodied fishes and sunfish increased from the 2008 collections versus the last collection in 2009 ('09d) (Table 5). Other compositional differences were primarily explained by use of the terrestrial foods (insects and garbage), which were generally higher in 2008 (Table 5). In the significant contrasts between years, aquatic prey types (not including crayfish) were generally less abundant in the 2008 boluses.

I found a significant correlation between diet composition dissimilarity and caloric content ($r = 0.317$, $P = 0.01$, Bio-Env). Inspection of the MDS plots revealed that the boluses with the highest caloric content were generally the boluses with higher biomasses of small-bodied fishes. When boluses were categorized by fish presence boluses with fish were not different from boluses that did not contain fish (Wilcoxon: $P = 0.16$, medians: fish = 6.11 kcal, no fish = 4.61 kcal).

Bolus biomass and energy content

None of the biomass (total, aquatic, terrestrial) or caloric content values differed between years when collection means were treated as independent observations ($F_{(1,6)}$ values ≥ 0.06, *P*-values > 0.23). However there was significant collection-level variation in some of these variables when all collections were compared using boluses as replicates (total biomass: $F_{(7,224)} = 3.42$, $P = 0.002$; aquatic biomass: $F_{(7,224)} = 2.29$, $P = 0.03$; terrestrial biomass: $F_{(7,224)} = 2.97$, $P = 0.005$; and total caloric content: $F_{(7,224)} = 3.33$, $P = 0.002$) suggesting that environmental conditions (e.g., mean water depth) might have produced differences in bolus size or energetic content on some dates.

When years were compared directly, the 2008 diets contained larger crayfish than the 2009 diets ($F_{(1,6)} = 8.32$, $P < 0.001$). In 2008 and 2009, the mean crayfish size per bolus (CL) was 21.5 mm (SE $\pm$ 0.49) and 17.6 mm (SE $\pm$ 0.38) respectively. The pre-nesting season crayfish availability was not different between years ($t_{(4)} = -1.58$, $P = 0.19$). Crayfish density ranged from 5.4 to 15.4 crayfish/m^2 in 2008 and 5.0 to 18.4 crayfish/m^2 in 2009.

Mean aquatic biomass per bolus was positively correlated with recession rate ($r = 0.809$, $P = 0.02$, n = 8; Table 6, Fig. 4), but there were no other significant correlations between diet size or energetic content and environmental variables (Table 6).

Energetic Contributions

Biomass specific energy content (kcal/g dry mass) of the prey varied substantially (Appendix 2) with crayfish having relatively lower values (mean kcal/g $\pm$ SE; 3.02 $\pm$ 0.29) and several species of fishes and sunfish having means from 4.30 to 4.95 kcal/g.

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Suriname cockroaches had the highest mean value (5.27 kcal/g ± 0.21; see Appendix 2

for means and SEs of all common prey). When biomass was converted to energy (kcal)

and averaged across collections for each colony, the energy from crayfish accounted for a

consistent 55-65% of the total energy per bolus in each of the three colonies (Table 7).

Aquatic and terrestrial insects contributed proportionally more to the caloric content of a

bolus in colonies during 2008 than in 2009. Shrimp contributed little to the total energy

intake across all colonies; their maximum contribution was only 1% of the kcal/bolus at

NC 4 in 2009. At NC 4 in 2009 the sunfish and small-bodied fishes together made up

20% of the energy per bolus. At Lox West in 2008, small-bodied fishes made up 22% of

the energy per bolus but the contribution was due to 2 diets being extremely heavy with

small-bodied fish prey. When the mean total kcal/bolus was calculated, Colony 73 had

the highest (6.56 kcal) and Lox West had the lowest (4.89 kcal). NC4 in 2009 had an

intermediate caloric value of 6.45 kcal/bolus.

Discussion

        Crayfish dominated the diets of White Ibis nesting in Loxahatchee in both a good

and a poor nesting year. Although total biomass was not different across years and diet

composition was similar across collections in 2008, I did find differences in diet

composition between the early and late collections in 2009. Kushlan (1979) made

scattered observations of White Ibis diets in 4 regions across South Florida and

suggested that ibis may feed on crayfish when landscape water depths are relatively high

and that fish are only accessible when the system is relatively dry. Dorn et al. (*in review*)

studied White Ibis diets in Loxahatchee and Water Conservation Area 3A in 2006 and

2007 and found that ibis diets can be quite variable throughout the nesting season. Compared to these earlier studies, I have large sample sizes from several dates from each colony in two years (Dorn et al. *in review*, Kushlan 1979). Large sample sizes and numerous collections across the nesting season allowed for a more comprehensive study than either Kushlan (1979) or Dorn et al. (*in review*) were capable of. Also, the methods employed here (and Dorn et al. *in review*) allowed me to reconstruct the biomass of most prey rather than simply recording presence or absence of prey or quantifying only whole prey (Findholt and Anderson 1995, Derby and Lovvorn 1997, Collins et al. 2002). The comprehensiveness of these results therefore allows me to consider the causes of variation in diets, the relative importance of different prey to nesting ibis and potential connections between bolus characteristics, environmental conditions, and nesting effort.

Variation in wetland water level is an important factor determining the availability of prey to nesting birds (Gawlik 2002, Ma et al. 2010). Wading birds are generally foraging over a small range of water depths and are limited by either leg length or bill length, depending on the specific foraging strategy (Gawlik 2002). Being a highly opportunistic feeder with a broad diet, the White Ibis is capable of switching quickly between different prey types depending upon prevailing hydrologic conditions (Kushlan 1979, Bildstein et al. 1990, Gawlik 2002). Previous research (Kushlan 1979, Dorn et al. *in review*) indicated that the diets of White Ibis may shift within the nesting season in response to low landscape water levels (i.e., depth-dependent diets) and the results here showed a similar decrease in the use of crayfish and an increase in the use of fish as the 2009 nesting season progressed and water levels dropped.

While crayfish dominated the diets in all of my collections in both years I observed a partial diet shift in 2009 from crayfish to fish prey as the wetland surrounding the colony became constricted and overall landscape water depths decreased. Whether the total amount of available habitat or the landscape water depth (i.e., concentration levels of fish and exposure of long hydroperiod sites) in the wetland was responsible for the observed switches was not entirely clear from the earlier work because landscape water depth and available habitat (km^2) were confounded over time (Dorn et al. *in review*). The same confounding occurs when looking at 2009 alone in this study; relatively higher water depths are associated with more foraging habitat around the colony earlier in the provisioning period. However the high use of crayfish and lack of fish use across a range of conditions in both years (2008 & 2009) suggests that the amount of habitat available is probably less important for switches from crayfish to fish than the actual depths of the lowest elevation portions of the wetland landscape (i.e., extremely low landscape water depths). The smallest amounts of available habitat for any given colony in my study came in 2008 when the landscape depths were at their highest (Table 1) and crayfish dominated the diets.

The lack of correlation between the amount of foraging habitat and landscape water depth across both years (Table 1) occurs because the amount of foraging habitat available to wading birds is expected to be unimodal with respect to landscape depths for any one colony (Fig. 5). Small amounts of available foraging habitat result from either extremely low or extremely high landscape water depths. When landscape water depths at the beginning of the nesting season are relatively high like in 2008, rainfall or water management that raises water levels further decreases the amount of available foraging

habitat, fish remain dispersed and only moderate or short hydroperiod locations at relatively high elevations on the landscape will be available. A decrease in available foraging habitat may also result from decreases in landscape water depth when depths were shallow to begin with (the left side of the hump in Fig. 5). When fish use was greatest, at the end of 2009, the amount of available habitat for those nesting birds was still higher than for any of the nesting birds in 2008 (Table 1). Assuming minimal location differences (note: all colonies had some access to the lowest elevation sites in Loxahatchee) the key difference between diets at the end of 2009 and all of 2008 is probably the actual landscape water depths; low landscape water depths at the end of 2009 resulted in the longest hydroperiod habitats becoming available for foraging and greater system-wide concentration of fish.

This leads to the question of why ibis switch from eating crayfish to fish when water levels drop. Hypothetically, there are two mechanisms that may be at play, either the crayfish are depleted by the end of the nesting season and ibis have no other choice but to feed on fish (i.e., crayfish are preferred, but unavailable), or fish become so highly concentrated in isolated pools that ibis switch their foraging tactics (i.e., fish are preferred, but not encountered at low densities), begin bill-sweeping (Heath et al. 2009) and focus on capturing fish (Kushlan 1979). Results by Stanek (2009) indicated that captive Scarlet Ibis (*Eudocimus ruber*) selected large crayfish (*P. alleni*) over fish (Eastern mosquitofish) prey over a range of "very low" to "high" fish densities (16-96 m^2). This suggests that in spite of the higher individual value of fish prey (Kushlan 1986, Appendix 2), ibis encounter them at lower rates than crayfish even when fish densities are "high". Perhaps Stanek (2009) did not use high enough fish densities to initiate a

switch in prey use. Though the fractional contribution of crayfish was lowest with the lowest water depths at the end of the 2009 nesting season, crayfish were still frequently consumed indicating that crayfish were still available. The higher use of fish at the end of 2009 probably indicates that some birds were switching tactics when encountering fish densities at high enough concentration levels (Gawlik et al. 2008). In contrast to 2009, the landscape water depths were even lower at the end of nesting in 2007 and foraging ibis showed a more complete shift to fish use when water depths surrounding the colony reached -18.8 cm (Dorn et al. *in review*). Depths did not approach those levels in 2009 and thus the switch to fish was only partial. Taken together these observations suggest that ibis feed on fish only when fish become highly concentrated at extremely low water levels in Loxahatchee. In other words, there is a relatively small window of opportunity for ibis to feed on fish (e.g., Fig. 5 hatched region); specifically, when average wetland depths around the colony (e.g., NC4) approach -12 to -19 cm. With further drying (depths < -20 cm) the Loxahatchee wetlands may become too dry for profitable foraging and birds may switch to terrestrial food sources (Dorn et al. *in review*).

While fish are not used consistently at higher landscape water depths a small fraction (24%) of foraging ibis did find fish at higher landscape water depths in 2009, and a couple of those diets were quite heavy with fish. This suggests that ibis have two foraging strategies at high water: most birds feed on crayfish and a small number can locate high concentrations of fish. Although fish were still less than 50% of the diet at the lowest landscape water depths in 2009 they may be more important in other nesting locations. For example Dorn et al. (*in review*) indicated that boluses were fish-dominated in a central Everglades colony at the end of the 2006 nesting season. In general, fish may

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be an important part of the diet of White Ibis when landscape water depths are low and long hydroperiod sites are available for foraging. Fish biomass and abundance is highest in wetlands that generally stay inundated for at least a year or more (Trexler et al. 2002, Ruetz et al. 2005) and those sites only become available when the landscape becomes quite dry. Kushlan (1979) suggested that fish diets are generally more profitable than other diets because of the high caloric value of fish and suggested that they become available at the end of the nesting season right when the ibis chicks are large and energetic demand is high. I found general agreement with the mean caloric size of fish diets being larger than non-fish diets (6.91 vs. 6.09 kcal, respectively); however the largest fish diets did not come at the end of the 2009 season and the comparison was not significant. Regardless of the nesting conditions in Loxahatchee, fish only accounted for 0.8 - 24% of the average energetic intake for a given colony (n = 3 colonies over both years).

Crayfish are an extremely important prey item for nesting White Ibis in Loxahatchee (this study, Dorn et al. *in review*), in north Florida (Nesbitt et al. 1975), and in other parts of the Everglades (Kushlan 1979). In this study, crayfish were the most frequently eaten prey item and contributed most to the total biomass on each collection date in both years and they dominated the energetics of the average bolus for each colony. Loxahatchee is a region of the Everglades with relatively high crayfish (*P. fallax*) densities (Davis et al. 2007), and more comprehensive diet studies will be necessary to determine which types of prey fuel the nesting colonies of ibis when ibis nest in other parts of the Everglades system.

Grass shrimp and aquatic insects were less important in the diets of White Ibis in Loxahatchee. Shrimp were used in two collections in 2009 ('09a and '09d, 32% and 24% occurrence respectively) and aquatic insects were used modestly in both years. However, both prey types contributed little to the total mean biomass (see Table 3) of the boluses and were unimportant in the diet composition differences between collections (see Table 5). Aquatic insects dominated 2 diets in 2008 but the total biomass of each of those boluses was rather small (< 100 mg). Kushlan (1979) found that aquatic insects were neither selected nor ignored by White Ibis. Although I cannot determine selection for or against any prey type, aquatic insects contributed 3% of the caloric content at Lox West in 2008. Aquatic insects have little importance for the energetics of the colonies; 2-3% of the colony energetic intake in 2008 and 3% of the colony energetics in 2009 and shrimp consistently contribute only 0-1% of the energy to a particular colony.

This leads to the question of how hydrologic management may enhance prey and therefore White Ibis nesting effort in Loxahatchee and in other parts of the Everglades. Gawlik and Crozier (2003) argued that the absence of frequent large nesting events and the longer time interval between those events implies that high quality foraging conditions are no longer being created because of current water management practices. Slough crayfish (*P. fallax*), the species found in Loxahatchee and in the diets, is more abundant in longer hydroperiod wetlands while the Everglades crayfish (*P. alleni*) is more abundant in short hydroperiod wetlands with frequent drying events (Hendrix and Loftus 1999, Dorn and Trexler 2007). The standing stock of fish can clearly be enhanced by water management practices that prevent frequent and severe droughts (Ruetz et al. 2004). Long and frequent dry periods can suppress both fish and crayfish populations

and prevent them from reaching the densities needed to sustain populations of wading birds during the nesting season (Trexler and Goss 2009). However, moderate drying and/or low wet-season water depths, similar to conditions in Loxahatchee, may actually enhance crayfish (Dorn 2008, Dorn and Trexler 2007), even *P. fallax* (Dorn and Volin 2009), by reducing aquatic predators. Frederick and Ogden (2001) found that large wading bird nesting events in the Everglades generally followed a year or two after a severe drought event and this observation is now known as the pulsed-production hypothesis. If crayfish densities are enhanced by moderately low water conditions or brief, infrequent drying events in the sloughs it would provide a mechanistic explanation for this hypothesis and the observed highly variable nesting effort of ibis across the ecosystem (Frederick and Ogden 2001). Nevertheless, these mechanisms will require further study. Once prey is produced and present, receding water during the dry season creates areas with high concentrations and availability of prey to nesting wading birds (Gawlik 2002 and Gawlik and Crozier 2003). Our results suggest that whatever the cause of production, consistent recession during the nesting season does result in higher use of aquatic prey.

Water depth is an important variable affecting the use of wetlands by waterbirds (Ma et al. 2010). Water depths can be managed effectively to meet the need of several species because different species forage most efficiently at different depths (Ma et al. 2010). For wading birds, foraging in shallow water increases food intake rates because prey are concentrated and decreases energy expenditure because prey are easier to capture and are more available. Deep water disperses prey and prey can escape both horizontally and vertically in the water column (Ma et al. 2010). Food preferences vary

greatly among species and individuals may switch between prey types depending on the availability of the most energetically profitable prey. Dekinga et al. (2001) found that Red Knots (*Calidris canutus*) prey on mollusks in the winter but switch to arthropods in the summer. Naef-Daenzer et al. (2000) showed that Great Tits (*Parus major*) switch from eating spiders to caterpillars when caterpillars became an abundant and profitable prey item. In the Everglades, seasonal shifts in the diet composition of White Ibis are dependent upon changes in hydrology that affect the availability of different prey types.

Although nesting effort and hydrologic conditions were variable between 2008 and 2009 the average biomass of prey and energetic content per bolus did not differ. Furthermore, crayfish dominated most ibis diets on every collection date and contributed the same proportion of the energetic content each year whereas other prey were relatively variable. If the diets were so similar then what conditions made nesting effort so different between years? If foraging conditions and nesting effort are directly related then they may or may not be related to composition of the boluses. If the most profitable prey are more available in one year than another then that may precipitate greater nesting effort. Therefore one explanation might be that foraging birds were finding more profitable individuals of their primary prey, larger crayfish, in 2009 than 2008, but in fact chicks were fed larger crayfish in 2008 than in 2009. It is also conceivable that Loxahatchee produced more crayfish in 2009 than in 2008, but our crayfish estimates suggest similar densities were available in the two years. Although some of the results suggest a tendency towards an increase in the use of terrestrial prey in 2008 and an increase in the use of aquatic prey in 2009 the direct statistical contrasts were not significant. All of these results suggest that diet composition and conditions of the

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primary prey (crayfish) in Loxahatchee were somewhat fixed and decoupled from total nesting effort across this range of environmental conditions.

Finally, it is possible that nesting effort reflects the evaluation by the ibis of the availability of crayfish prey on the landscape.   Because my results apply to successful birds (i.e., birds that decided to nest and hatched their eggs) it may not be surprising to see different nesting efforts and similar diets. Pre-nesting birds are likely sampling the areas around potential nesting colonies to determine the availability of prey and nesting effort proceeds accordingly (Kushlan 1976a, Kushlan 1979). The explanation for the annual differences in nesting effort may also relate to the recession rate, which was correlated positively with the amount of aquatic biomass in the diets. When average recession rate was calculated for each colony, the landscape water depths surrounding the 2008 colonies had net increases while the water depths surrounding NC 4 in 2009 decreased. Recession functions over short time scales and tends to be highly correlated with wading bird distributions (Russell et al. 2002) and locations of nesting colonies (Kushlan 1979). Steady recession rates produce conditions that are favorable for nest initiation and foraging (Cook and Herring 2007) because steady recession results in lower landscape water levels and isolated pools of water with high concentrations of fish. However, previous research did not find an effect of recession rate on foraging-site selection for White Ibis (Kushlan 1986, Gawlik and Crozier 2007, Herring et al. 2010). While crayfish do not necessarily concentrate in the same way fish do, steady recession rates decrease water depths to a level at which ibis can forage efficiently (Kushlan 1979), and recent work suggests that crayfish may concentrate, but perhaps at higher water depths (Cook and Herring 2007).

The observations of ibis diets in the northern everglades indicate that terrestrial foods are used regularly by a fraction of birds. The terrestrial insects and garbage together accounted for 8-37% of the total caloric intake of each colony. While no significant correlations were found between use of terrestrial resources and environmental variables it is possible that the variation in environmental conditions was too small to observe switches. Dorn et al. (*in review*) found that when water depths were extremely low and a vast majority of the wetland was dry, ibis diet composition was made up primarily of terrestrial prey (i.e. terrestrial insects and garbage). The 2009 nesting season did not experience extremely dry conditions or an extreme reversal like 2007 (Dorn et al. *in review*) suggesting that the response may be more of a threshold or a transient response to heavy rains and reversals. Although Suriname cockroaches were surprisingly high in caloric content cockroaches are relatively small (~0.05 g) and further, the birds must leave the marsh to feed on them. Foraging on terrestrial prey may present extra travel time costs if colonies are located near the interior of the marsh (Frederick and Collopy 1989). Terrestrial prey sources were 5.2 km away from NC 4 in 2009 but only 0.8 km and 1.6 km from Lox West and colony 73, respectively, in 2008. Nesting colonies may have been located closer to the edges of the wetland in 2008 in order to decrease the energetic costs of flying to urban areas to forage. High water and negative recession rates prior to nest initiation may lead to lower nesting effort, colonies being established on the periphery of the wetland, and a higher use of terrestrial prey. These factors may ensure reproductive success when fish and crayfish are less available.

White Ibis are tactile, nonvisual foragers and have a limited ability to choose between prey types (Kushlan 1979). The energy content of the average bolus at each

colony indicated that crayfish were a dominant fraction of the energy fed to growing chicks. These results and others (Kushlan 1979 and Dorn et al. *in review*) suggest that ibis are not switching to fish because of a behavioral or palatability factor, they switch because crayfish were encountered less often. Even though fish are higher in caloric content than crayfish, the high-energy diets were acquired because the preferred prey, crayfish, represented a small fraction of the available prey. However, birds are tracking seasonal prey production and availability when choosing initial foraging patches (Frederick et al. 2009). Diet shifts appear to be common in White Ibis (Kushlan 1979, Bildstein et al. 1990, Dorn et al. *in review*) and future research is needed to assess diet composition changes in other parts of the system where White Ibis nest. Managers ought to be aware of the mechanisms responsible for produce high quality foraging conditions when considering different restoration and management techniques.

Table 1. Bolus numbers, dates, and water depths around the nesting colonies for White Ibis nestling bolus collections made in 2008 and 2009.

Collection	Colony	n	Collection Date	Mean water depth[a] (cm) ± SD	Available habitat[b] (km²)	Recession rate (cm/day)	Per capita available habitat (km²/nest)
2008a	73	22	5/22/2008	10.7 ± 16.2	244	0.48	0.48
2008b	73	32	5/29/2008	14.9 ± 16.9	180	-1.05	0.35
2008c	West	21	6/10/2008	3.7 ± 13.5	227	0.04	0.06
2008d	West	12	6/17/2008	7.9 ± 13.1	198	0.00	0.06
2009a	NC4	25	4/17/2009	1.4 ± 9.4	363	0.39	0.09
2009b	NC4	34	4/24/2009	0.2 ± 9.4	367	-0.09	0.09
2009c	NC4	63	5/1/2009	-6.1 ± 10.1	345	0.52	0.08
2009d	NC4	23	5/8/2009	-12.9 ± 11.2	276	0.52	0.07

[a] The means were calculated using 2073-2518 equally spaced point estimates of wetland depth within 15 km of each colony. Depth measurements came from the EDEN model (Everglades Depth Estimation Network, U.S. Geological Survey).

[b] The available habitat was defined as the amount of preferred foraging habitat; area of wetland with EDEN water depths between -16 and +15 cm. Beerens (2008) indicated that foraging White Ibis selected these locations relative to all available locations in 2006.

Table 2. Percent occurrence for each prey type by collection in 2008 and 2009. N= number of boluses in each collection.

Prey Item	2008a	2008b	2008c	2008d	2009a	2009b	2009c	2009d
Crayfish	86	67	76	58	88	71	86	81
Small Fishes	9	0	14	0	24	3	22	67
Sunfish	0	3	14	0	8	3	22	33
Shrimp	0	0	5	0	32	0	8	24
Aquatic Insects	23	15	29	17	48	29	41	33
Terrestrial Insects	50	42	24	33	8	29	22	29
Vertebrates	0	3	0	0	0	3	0	5
Garbage	14	30	5	8	4	15	16	10
N	22	32	21	12	25	34	63	23

Table 3. Mean percent biomass by collection for each prey type in 2008 and 2009. N = number of boluses in each collection.

Prey Item	2008a	2008b	2008c	2008d	2009a	2009b	2009c	2009d
Crayfish	76.3	62.7	53.9	95.3	67.8	70.1	69.7	53.9
Small Fishes	0.9	0	33.7	0	25.2	0.2	5.7	14.2
Sunfish	0	0.4	2.5	0	2.2	0.6	3.9	12.0
Shrimp	0	0	0.3	0	2.2	0	0.2	2.2
Aquatic Insects	1.3	0.6	1.5	0.7	1.8	0.7	1.0	0.4
Terrestrial Insects	20.9	7.8	4.1	2.8	0.5	13.6	4.3	3.6
Vertebrates	0	0.4	0	0	0	2.3	0	2.6
Garbage	0.7	28	4.1	1.3	0.3	12.4	15.2	11.0
Avg. Total g / bolus (± SD)	2.15 (2.04)	1.58 (1.53)	1.39 (1.92)	1.38 (1.54)	1.50 (1.35)	1.39 (0.92)	2.15 (1.39)	1.70 (1.07)
N	22	32	21	12	25	34	63	23

Table 4. Percent contribution of crayfish to within-collection Bray-Curtis similarity at the time of each collection.

Collection	Percent contribution of Crayfish
2008a	86
2008b	75
2008c	93
2008d	80
2009a	89
2009b	83
2009c	90
2009d	66

Table 5. Relative importance (percent contribution) of each prey type to the dissimilarity between groups from the SIMPER analyses. Signs after the percentages indicate whether the first collection in the comparison had more or less biomass for that food type. Collection comparisons with significant compositional differences from the ANOSIM test are shown. Cray = crayfish, Smf = small-bodied fishes, Snf = sunfish, Shr = shrimp, AIns = aquatic insects, TIns = terrestrial insects, and Garb = garbage. P-values are uncorrected for multiple comparisons.

Comparison	Cray	Smf	Snf	Shr	AIns	TIns	Garb	*R*	*P*
'09a vs. '09d	33(+)	22(-)	12(-)	7(+)		8(-)	8(-)	0.09	0.006
'09b vs. '09c	43(-)	7(-)	7(-)			16(+)	19(-)	0.07	0.043
'09b vs. '09d	33(-)	16(-)	11(-)		4(+)	14(+)	14(+)	0.06	0.071
'09c vs. '09d	34(+)	18(-)	13(-)		5(+)	9(-)	14(+)	0.16	0.019
'08a vs. '09a	44(+)	14(-)		6(-)	8(-)	22(+)		0.08	0.012
'08b vs. '09a	41(-)	11(-)			7(-)	13(+)	17(+)	0.07	0.023
'08d vs. '09a	56(-)	13(-)		7(-)	8(-)	10(+)		0.17	0.034
'08b vs. '09c	43(-)	7(-)	6(-)			15(+)	23(+)	0.11	0.012
'08a vs. '09d	35(+)	16(-)	10(-)		5(+)	19(+)	8(-)	0.15	0.002
'08b vs. '09d	33(-)	16(-)	10(-)	4(-)		13(+)	18(+)	0.09	0.028
'08c vs. '09d	32(-)	22(-)	13(-)		5(+)	11(-)	9(-)	0.07	0.018
'08d vs. '09d	41(+)	17(-)	11(-)		4(-)	11(-)	9(-)	0.14	0.037

Table 6. Results of correlation analysis (coefficients and p-values) between average diet and environmental variables in 2008 and 2009. N = 8 points.

Variable	Mean Total Biomass	Mean Aquatic Biomass	Mean Terrestrial Biomass	Mean Caloric Content
Recession Rate	0.442 (0.273)	0.808 (0.015)	0.305 (0.462)	0.415 (0.307)
Landscape Water Depth (cm)	-0.127 (0.765)	-0.314 (0.449)	0.196 (0.642)	-0.237 (0.572)
Available Habitat (Km^2)	0.116 (0.784)	0.232 (0.581)	-0.106 (0.804)	0.149 (0.724)

Table 7. Energetic fraction (% of total kcal) of the average diet in each colony (time integrated) for each of the 8 prey groups and the mean total kcal for each colony.

Prey Item	Colony 73 (2008)	Colony Lox West (2008)	New Colony 4 (2009)
Crayfish	60	65	55
Sunfish	0.2	2	6
Small fishes	0.6	22	14
Shrimp	0	0.2	1
Aquatic Insects	2	3	3
Terrestrial Insects	22	4	6
Vertebrates	0.2	0	1
Garbage	15	4	14
Mean total kcal	6.56	4.89	6.45
N	54	33	145
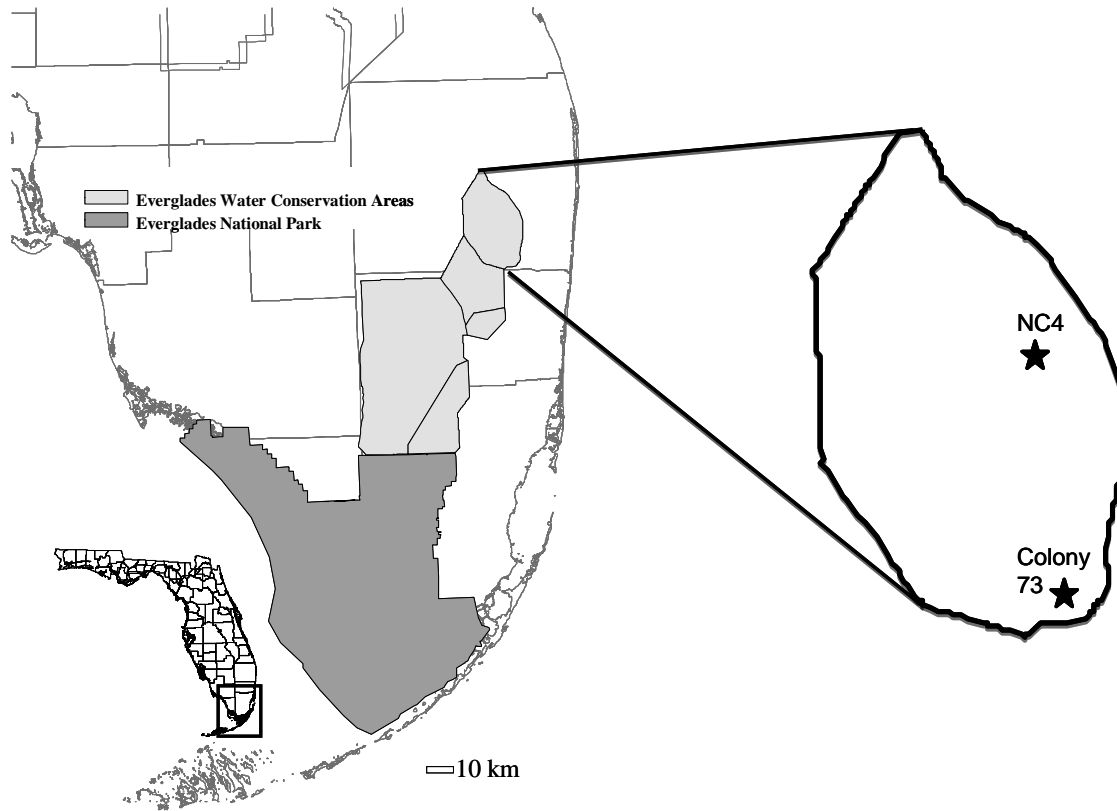
Figure 1. Map of the Everglades broken up into Water Conservation Areas and
Everglades National Park. The sampling areas for this study were in Loxahatchee (Arthur
R. Marshall Loxahatchee National Wildlife Refuge). Map of Loxahatchee National
Wildlife Refuge with sampled colony locations. Colony 73 and Loxahatchee West
Colony were sampled in 2008 while New Colony 4 was sampled in 2009.
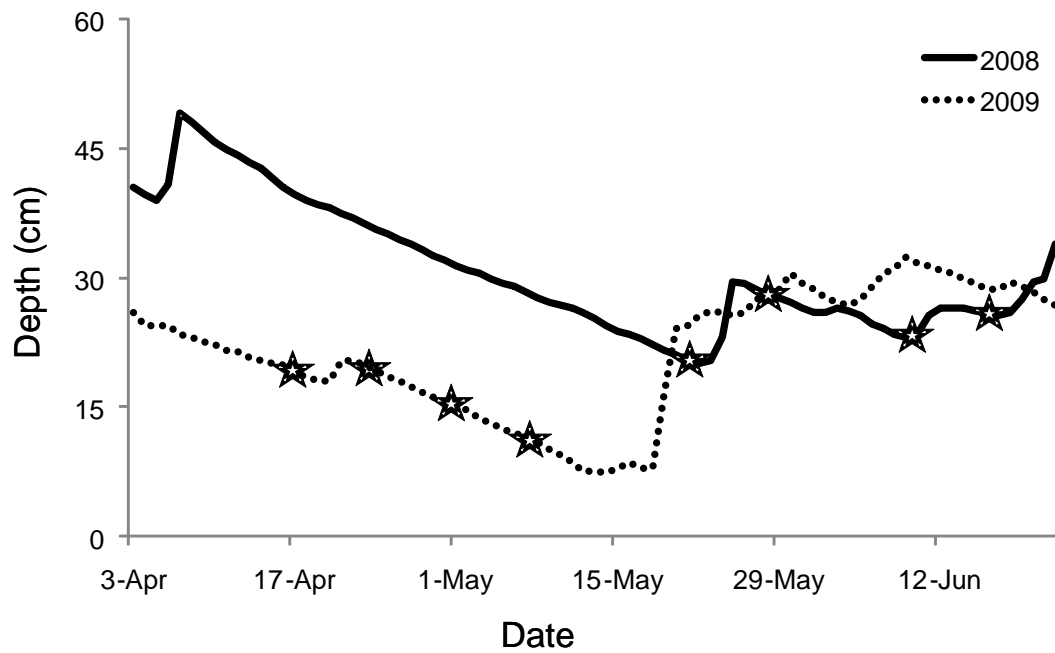
Figure 2. Water depths during the 2008 and 2009 nesting season. Stars indicate bolus

collection dates. The depths indicate relative landscape water depths as measured by a

continuous water gauge in the center of Loxahatchee (WCA1ME, Everglades Depth

Estimation Network, USGS).
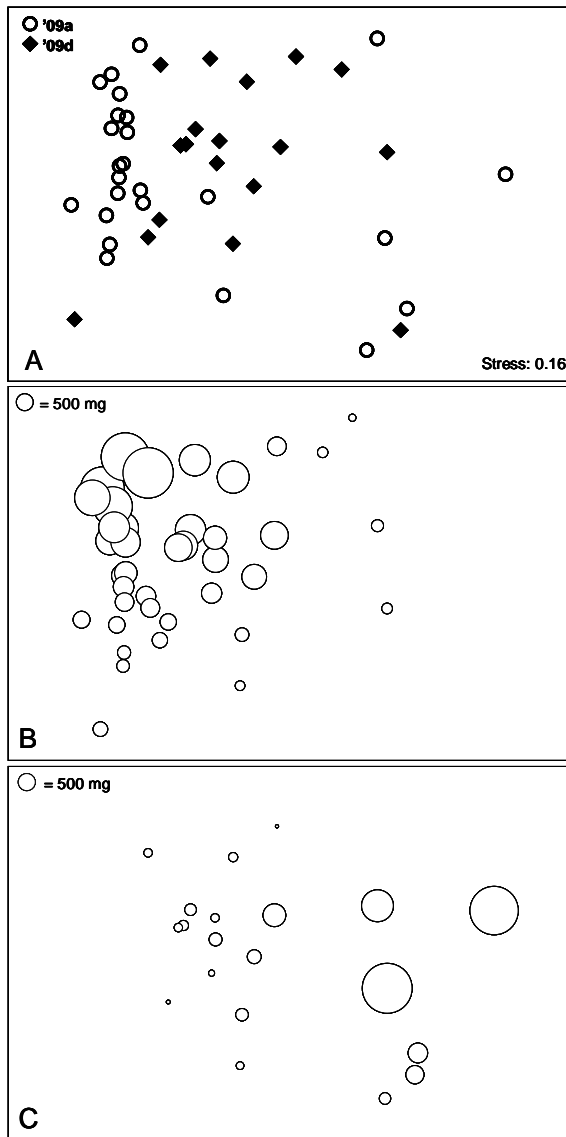
Figure 3. Prey composition of collections '09a and '09d illustrated by NMDS ordination of prey biomasses. A. Each point is a bolus and the proximity of points indicates the level of Bray-Curtis similarity in 2D space. Biomasses of B) crayfish and C) small fish are superimposed on the samples to indicate the relative abundances of prey in each cluster; larger circles indicate diets with relatively more biomass of the focal prey. Ordination of B and C is the same as A.
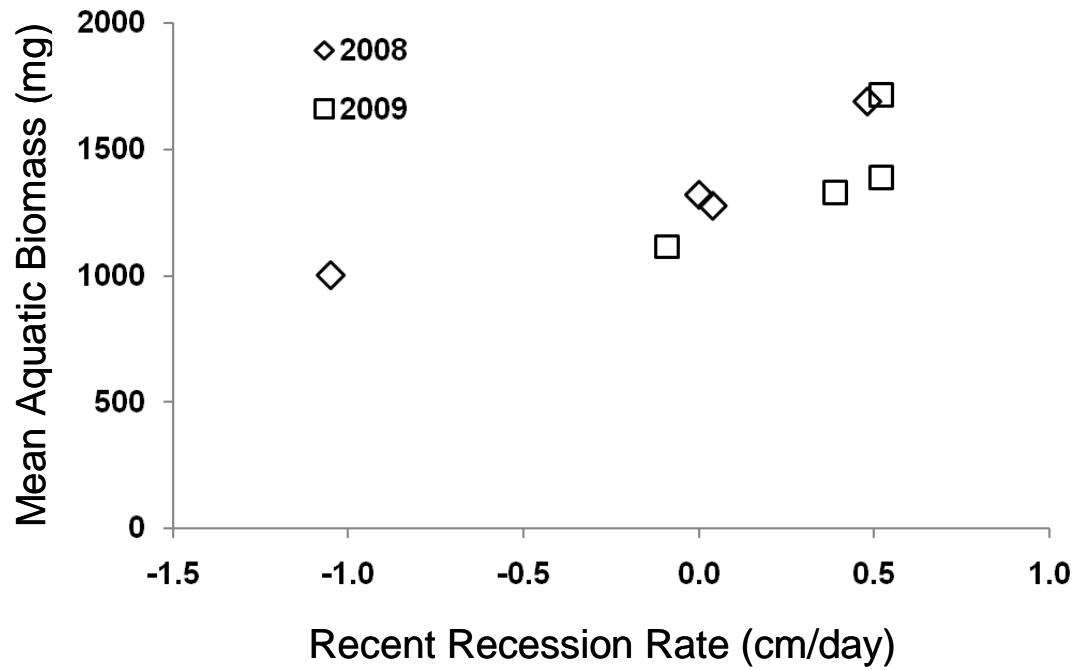
Figure 4. 2008-2009 Correlation between recent recession rates and mean aquatic

biomass. Positive values indicate falling water levels.
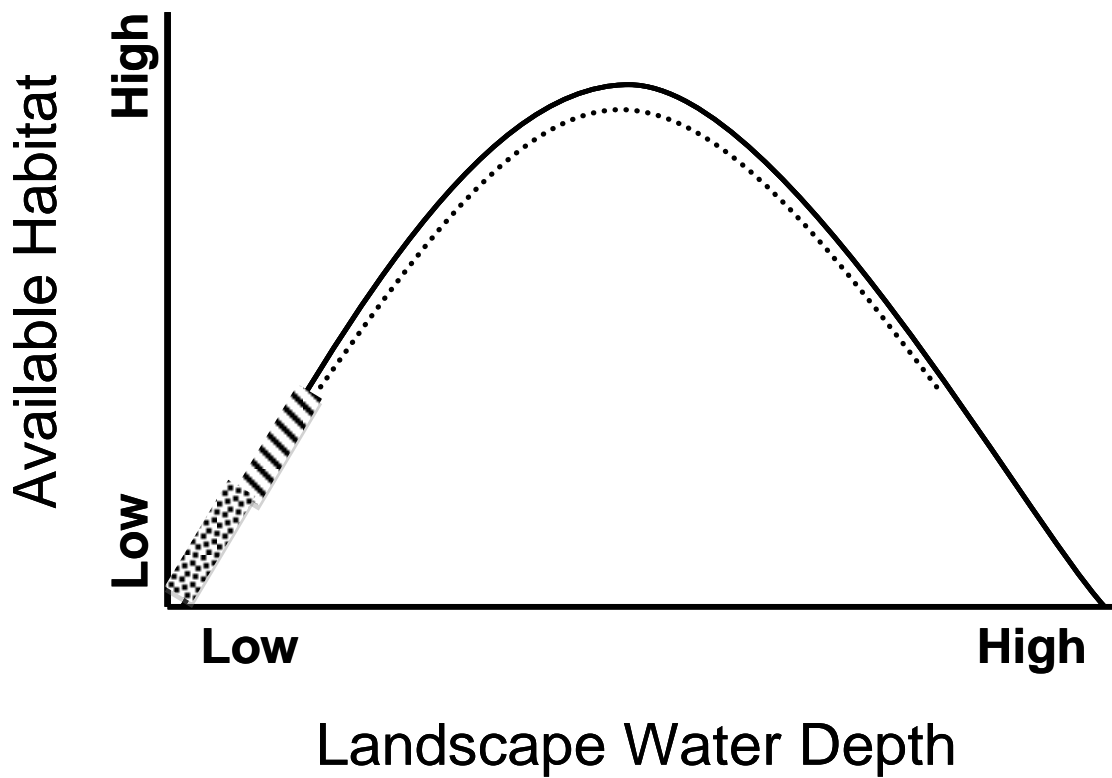
Figure 5. Hypothesized relationship between landscape water depth (average depth of surrounding wetlands) and total amount of available habitat (i.e., wetland area with preferred foraging depths) around a nesting colony in the Everglades. Hatched area represents a theoretical range of landscape conditions when ibis feed heavily on fish. Dotted area represents a range of landscape conditions when ibis leave the marsh and feed on terrestrial prey. The dotted line represents the range of landscape conditions when ibis feed on crayfish.

CHAPTER 3 - DIETARY NICHE RELATIONSHIPS OF THREE SPECIES OF CO-

OCCURRING WADING BIRDS NESTING TOGETHER IN THE FLORIDA

EVERGLADES

Abstract

Co-occurring nesting wading birds may be competing for prey or foraging in distinctive manners. The reproductive success of several nesting wading birds in the Everglades may be enhanced by hydrologic restoration, but that may depend on prey use and the responses of prey to hydrologic changes. Wading bird nesting colonies in the Everglades often contain several species, including White Ibis, Tricolored Herons and Snowy Egrets. The main objective of this study was to compare the diets of these species when they co-occur in colonies in the Northern Everglades.

In 2008, I collected 67 boluses from nestling White Ibis (n = 58) and Tricolored Herons (n = 9). In 2009, I collected 118 boluses from nestling White Ibis (n = 86), Tricolored Herons (n = 12), and Snowy Egrets (n = 20). All boluses were collected from colonies located in the Northern Everglades: Arthur R. Marshall Loxahatchee National Wildlife Refuge (hereafter Loxahatchee).

White Ibis diet was dominated by crayfish and was distinct from the diets of co-occurring herons and egrets. Small and large-bodied fishes dominated Tricolored Heron and Snowy Egret diets. Tricolored Heron and Snowy Egret diets were not different in taxonomic composition or size structure of fish eaten. Tricolored Heron diets varied

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significantly between 2008 and 2009, but the differences were consistent with greater use of canal-wetland edges in 2008 when the water depths in the sloughs were deeper. In 2008 Tricolored Herons ate more large-bodied fishes like largemouth bass and sunfish.

Differences in diet between these three species may affect how they respond to hydrologic restoration. Whether restoration will simultaneously enhance prey for both invertivores like the White Ibis and piscivores like the herons and egrets remains an important question.

Introduction

For most populations of breeding birds, food resources are a primary limiting factor affecting breeding success and population size (Martin 1987, Baker and Baker 1973) and studying the dietary niches of several species of birds will shed light on community structure and species interactions (Baker and Baker 1973). The composition of boluses fed to chicks can indicate diet quality, habitat use, and niche requirements for breeding birds (Willard 1977, Smith 1997, Martínez 2004, Eeva et al. 2005) and studying diet composition will also aid researchers in determining which prey types are fueling nesting colonies of wading birds.

Several groups of birds nest and/or forage in mixed species aggregations and may be competing for food or space. In the Great Lakes region of the United States, Maxon et al. (1996) recorded Ring-billed Gulls (*Larus delawarensis*) and Common Terns (*Sterna hirundo*) breeding at the same sites and Somers et al. (2007) recorded Herring Gulls (*L. argentatus*) and Double-crested Cormorants (*Phalacrocorax auritus*) breeding on the same island in Lake Ontario. On a barrier island off the coast of Senegal, Royal Terns (*S. maxima*), Caspian Terns (*S. caspia*), Slender-billed Gulls (*L. genei*) and Grey-headed

Gulls (*L. cirrocephalus*) nest in mixed-species colonies (Brasseur 2006). Among wading birds, sympatric nesting Scarlet Ibis (*Eudocimus ruber*) and Yellow-crowned Night Herons (*Nyctanassa violacea*) were shown to have similar diets (both species fed mainly on crabs) but significant differences in diet composition were found (Martínez 2004). Baker and Baker (1973) studied the niche relationships of 6 species of shorebirds that share both breeding and wintering grounds. They found that a birds' diet was influenced by foraging behavior and when more than one species had the same foraging tactic their dietary niches were more likely to have high overlap.

The large historical south Florida wading bird nesting colonies in the 1930s were dominated by White Ibis (*E. albus*), but several other species of wading birds co-occurred in those colonies, including Great Blue Herons (*Ardea herodias*), Great Egrets (*A. alba*), Snowy Egrets (*Egretta thula*), Tricolored Herons (*E. tricolor*), Little Blue Herons (*E. caerulea*), Cattle Egrets (*Bubulcus ibis*), Green-backed Herons (*Butorides striatus*), Black-crowned (*Nyctanassa nycticorax)* and Yellow-crowned Night Herons, Roseate Spoonbills (*Ajaia ajaia*) and Wood Storks (*Mycteria americana*) (Crozier and Gawlik 2003). The Snowy Egret and Tricolored Heron are two small-bodied egrets that that share similar foraging depth restrictions with the White Ibis. On the basis of that similarity alone the breeding numbers of these species may be expected to respond to hydrologic variation in similar ways (i.e., they require similar depths to forage, Ma et al. 2010). Hydrologic restoration may affect these species in similar ways and even more so if their dietary niches overlap. However the diets of these birds are generally thought to differ with the ibis being more of a generalist with crustaceans (crayfish) making up a large fraction of their diets in some cases (chapter 1, Dorn et al. *in review*) while the egrets are

more piscivorous (Smith 1997, Parsons and Master 2000). Dietary niche differences between the numerically dominant ibis and the egrets may become less pronounced when landscape water depths are low, fish densities are high and ibis switch to eating fish (Kushlan 1979, Dorn et al. *in review*). However the diets of all three species have not been carefully examined and compared in co-occurring colonies in the Everglades. Snowy Egrets and Tricolored Herons are ecologically similar species based on geographic range, body size, prey consumption, and foraging behavior (Strong et al. 1997). Strong et al (1997) compared the diet and habitat use of Tricolored Herons and Snowy Egrets in Everglades National Park and found that habitat selection between species was different in each year of the study, but diet composition and prey size were the same.

Snowy Egrets have a wide distribution, breeding in coastal and inland wetlands across the United States, Mexico, the Caribbean and South America (Parsons and Master 2000). Snowy Egrets utilize a range of foraging behaviors but are rather selective in their prey choice. They are visual foragers and capture prey using a variety of tactics including running, foot-stirring, hovering, pecking, foot probing, open wing feeding and foot-dragging (Parsons and Master 2000). Out of the 34 wading bird foraging behaviors described by Kushlan (1976b), Snowy Egrets have been known to exhibit 30 of them (Kelly et al. 2003). Snowy Egrets forage in water depths less than 20 cm (Willard 1977, Parsons and Master 2000). Smith (1997) and Strong et al. (1997) collected regurgitated prey from nestling Snowy Egrets and found that greater than 90% of their diet consisted of fish. Snowy Egrets have the ability to fly great distances (>30 km, Bancroft et al. 1990,

Strong et al. 1997) to obtain prey but their mean flight distance is less than 5 km (Smith 1995).

Tricolored Herons have a more restricted distribution breeding in coastal wetlands along the Gulf Coast of the United States and Mexico, the Caribbean and northern South America. Tricolored Herons also use a variety of foraging tactics but mainly eat fish (Frederick 1997). Tricolored Herons and Snowy Egrets forage at similar depths (18 cm maximum depth) and use similar foraging tactics. Out of the 34 wading bird foraging behaviors described by Kushlan (1976b), Tricolored Herons exhibit 25 of them (Kelly et al. 2003) including running, hovering, open wing feeding and foot stirring. Results from Smith (1997) suggested that Tricolored Herons eat almost exclusively fish; 95% of their diet contained small marsh fishes and larger sunfish prey. A small fraction of their diet also contained insects and spiders. Tricolored Herons have the ability to fly up to 27 km (Strong et al. 1997) to obtain food but their mean flight distance is ~5 km (Smith 1995).

The White Ibis is one of the flagship species of Everglades restoration efforts (Frederick et al. 2009). It ranges along the coastal areas of the southeast United States, the Caribbean, and the Gulf Coast of Texas and Mexico south to Belize. White Ibis are generalist probing foragers and have a broad diet. While the adults are often seen foraging close to the nesting colony (<15 km), they are able to fly >35 km to obtain prey (Smith 1995). In wetlands, ibis forage in water up to 25 cm deep (Beerens 2008, Heath et al. 2009) but typical depths are 5-10 cm. They use two principle techniques for capturing prey: bill sweeping is used when fish concentrations are high while tactile probing is used to extract crayfish, fiddler crabs (*Uca spp*.) and other aquatic invertebrates from the

sediments (Heath et al. 2009). Probing is also used in urban habitats while foraging for terrestrial prey (*personal observation*).

Since the 1930s it has been estimated that the number of wading bird nests in the Everglades has decreased by 70% (Crozier and Gawlik 2003). White Ibis nests have declined by about 87% and Tricolored Heron and Snowy Egrets by 66%. Much of this loss seems to be a result of decreased prey availability (Frederick and Spalding 1994, Gawlik 2002). While prey production across the south Florida landscape has certainly been affected by the 50% reduction in the size of the wetland (Davis and Ogden 1994, Rader 1999), highly altered hydrologic regimes also affect prey production (Loftus and Eklund 1994, Ruetz et al. 2005) and the availability of the prey to the nesting birds (Gawlik 2002).

Elsewhere (chapter1, Dorn et al. *in review*) the variation of White Ibis diets was compared within and between nesting seasons. White Ibis diets tended to become more fish-dominated as landscape water depths became lower and fish became more concentrated. Therefore the diet similarity between egrets and ibis may be higher in 2009 when the landscape was drier than in 2008 under high water conditions.

I compared diets of nestling White Ibis, Tricolored Herons and Snowy Egrets collected from the Northern Everglades within and between years in a relatively poor nesting year (2008) and a very good nesting year (2009). Specifically, my objectives were to: (1) compare the diets of White Ibis, Tricolored Heron and Snowy Egret chicks using a coarse scale analysis of diet composition and diet breadth measures. In this analysis prey were lumped into 8 broad categories, (2) compare the diets of Tricolored Heron and Snowy Egret chicks in 2009 using a fine scale analysis of diet composition

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and diet breadth with fish prey divided into distinct taxonomic groups, (3) compare the size structure (SL) of fish eaten by Tricolored Herons and Snowy Egrets in 2009, and (4) compare the diet composition of Tricolored Herons when nesting during high-water conditions (2008) and low-water conditions (2009).

Methods

Area of Study

Loxahatchee is located in Palm Beach County, Florida. The refuge is a 57,324-ha area of remnant Everglades wetland in the northern reaches of the Everglades ecosystem (Fig. 1). Loxahatchee is a peat-based wetland with seasonally fluctuating water levels and it is separated from other water conservation areas by a series of canals and levees (Brandt et al. 2000). The two nesting years were independently judged to be poor and very good respectively, based on nesting numbers and hydrologic patterns in Loxahatchee: 2008 had high stable water with reversals and 2009 had steady water recession and moderate-low water depths (Frederick and Simon 2008, 2009). There were ~6000 White Ibis nests in Loxahatchee in 2008 and ~500 ibis nests at the colony I sampled. In 2009 there were ~9300 White Ibis nests in Loxahatchee and ~4100 of those nests were located at the large colony I sampled in 2009. No Tricolored Herons or Snowy Egrets were reported nesting in either of the colonies I sampled (Frederick and Simon 2008, 2009), but I was able to locate egret nests that contained chicks in both colonies of ibis. Although the Tricolored Heron and Snowy Egret nests were far less abundant than White Ibis nests there were approximately 25-35 Tricolored Heron nests in the ibis

colony I sampled in 2008 and approximately 40-50 Tricolored Heron and Snowy Egret

nests combined in the colony in 2009.

Diet Collection and Analysis

I collected 185 boluses from White Ibis, Tricolored Heron and Snowy Egret

chicks in 2008 (n = 67) and 2009 (n = 118). In 2008 I collected 58 White Ibis boluses

and 9 Tricolored Heron boluses from 1 nesting colony in Loxahatchee, Colony 73. In

2009 I collected 86 White Ibis boluses, 12 Tricolored Heron boluses and 20 Snowy Egret

boluses from 1 nesting colony in Loxahatchee, New Colony 4 (hereafter NC 4, locations

in Fig. 1). Bolus collection dates, colony designations, mean water depths in the

wetlands surrounding the colonies and the total number of boluses collected during both

nesting seasons are shown in Table 1. Boluses were collected between 0800 and 1200

hours and total time spent on the colony did not exceed one hour in order to limit stress to

both the chicks and adults. Mean water depth surrounding the colonies was calculated

using the Everglades Depth Estimation Network (EDEN) and the xy Locator Tool (v1.4).

EDEN is an integrated network that uses both ground elevation and water surface data to

produce real-time water level data for the entire fresh water portion of the Everglades

ecosystem (400x400 m cell resolution). Using the EDEN grid and a GIS (ESRI

ArcMap$^{®}$ V 9.2) I selected the cells within a 15-km radius around each nesting colony.

Previous studies (Smith 1995 and Beerens 2008) indicated that the average foraging

distances of nesting White Ibis, Snowy Egrets and Tricolored Herons were less than 15

km from the nesting colony so wetland conditions within a 15 km radius should reflect

conditions experienced in more than 50% of the foraging trips. The xy Locator Tool was

then used to determine the depth of each cell on each collection date and the weighted mean depth of all cells within a 15 km radius was calculated.

Approximately 90% of boluses were collected from the ground after voluntary regurgitation from the chicks. Tracheal massage to induce regurgitation was used on chicks that appeared to hold a bolus in their crop. Approximately 15 nestlings were handled in 2008 in order to obtain a bolus; no nestlings were handled in 2009. All boluses were placed in plastic Ziploc® or Whirlpac® bags and placed on ice for transport back to the lab. In the lab the boluses were preserved in 80% ethanol until sorted.

In the lab I rinsed each bolus in a mesh net (0.63 µm), and sorted the prey remains under a magnifying lamp. Boluses were searched twice and all identifiable prey items or parts found were collected, counted and placed in labeled glass scintillation vials. For most prey items, excluding garbage and large terrestrial vertebrates, I used length-length and length-mass regressions to calculate dry mass. Other prey items were dried at 55°C to a constant mass and weighed to determine dry mass. Detailed methods for biomass determination and regression parameters can be found in Appendix 1.

Statistical Methods

To analyze diet composition and the size structure of prey eaten I used graphical and statistical multivariate techniques outlined by Clarke and Warwick (2001, PRIMER v6). These data are multivariate (biomasses of several prey types and counts of several size classes) and traditional multivariate analysis of the data (e.g., MANOVA) was impractical because of the large number of zero values. Biomass of each prey type in each bolus was square root transformed before calculation of the Bray-Curtis

resemblance matrix. Square root transformation was used in order to down-weight the influence of overly heavy and/or exceptionally dominant prey items (e.g., vertebrates or crayfish), which allowed me to detect both the major differences and more subtle differences in bolus composition. Using the resemblance matrix, diet similarity was visually inspected with 2-Dimensional and 3-D MDS (non-metric multi-dimensional scaling) plots while the ANOSIM test was used to determine if there were differences in bolus composition between collections. If statistical differences were detected then SIMPER analyses were run on the original transformed dataset to determine which prey types were most responsible for the similarity within and dissimilarity between collections. Frequency of occurrence of prey and average proportional contributions of each prey type to the boluses on each collection date were calculated and the tabular summaries were used to help interpret the multivariate results. Boluses were collected on 3 dates in 2008 and on 2 dates in 2009 but collections were pooled because of small sample sizes on each collection.

Coarse scale analyses of the data included diets from all three species. Prey items were lumped into 8 distinct prey categories or prey functional groups; crayfish (all identifiable individuals were *Procambarus fallax*), fishes with relatively large-bodied adults (sunfish; *Lepomis* spp. and *Enneacanthus gloriosus*, *Micropterus salmoides* and *Cichlasoma* spp.), the suite of small-bodied marsh fishes (*Gambusia holbrooki, Jordanella floridae, Poecilia latippina*, *Lucania goodie*, *Heterandria formosa*, *Fundulus chrysotus* and *F. confluentus*), grass shrimp, aquatic insects, terrestrial insects, garbage (mostly rotten chicken and dog food) and other vertebrate prey. These groupings are consistent with another analysis of diet data from the Everglades (Dorn et al. *in review*)

and are based on habitat type (terrestrial vs. aquatic foraging), adult prey size, and taxonomy (i.e., life history and/or functional relationships with water depths; Kushlan 1979).

I wanted to compare the diets of a tactile, nonvisual forager, the White Ibis, to co-occurring visual foragers, the Tricolored Heron and Snowy Egret to see if there were differences in diet. To evaluate dietary niche breadth of each species in each nesting year I calculated the Shannon-Weaver diversity index, H (Shannon 1948, Li et al. 2007, Christensen and Kleindorfer 2009):

$$H = -\Sigma \, (P_i * \ln \, (P_i))$$

where P_i is the proportion of each prey type in the diet. Mean niche breadth for each species each year was calculated using the niche breadth calculated for individual boluses. Values close to zero indicate a low diversity of prey types used. Dietary niche breadth was calculated for all 3 species based on coarse scale prey categories and for Tricolored Herons and Snowy Egrets based on fine scale prey categories (fish prey divided into distinct taxonomic groups). Parametric statistics were not appropriate for the data because the residuals could not be normalized so I used a nonparametric Wilcoxon test (Sokal and Rohlf 1995) to test for differences in diet breadth. White Ibis diet breadth was compared to Tricolored Heron and Snowy Egret diet breadth at the coarse scale and Tricolored Herons were compared to Snowy Egrets at the fine scale in 2009.

To test for differences in diet composition, White Ibis diets were compared to Tricolored Heron and Snowy Egret diets by combining the two egret species (*Egretta* spp.). White Ibis and *Egretta* species were compared two ways; first by combining nesting years and second by analyzing each year separately. I then compared the diets of

White Ibis, Tricolored Herons and Snowy Egrets to each other in years in which they co-occurred. Snowy Egret diets were collected only in 2009 so White Ibis diets were compared to Tricolored Herons in 2008 and 2009 but only to Snowy Egrets in 2009. The diet composition of Tricolored Herons and Snowy Egrets was compared at both the coarse and fine scales in 2009.

After the coarse scale analyses I repeated the analyses of diet breadth and bolus composition between the two egrets in 2009 with a fine scale analysis of the fish composition. A similar level of fish resolution was not possible for the ibis but was judged to be unnecessary after the coarse analysis of diet. Large-bodied fishes were divided into 3 categories; sunfish (*Lepomis* and *Enneacanthus* spp.), largemouth bass (*Micropterus salmoides),* and cichlids (*Cichlasoma* spp.). Small-bodied fish were divided into 6 categories: eastern mosquito fish (*Gambusia holbrooki*), sailfin molly (*Poecilia latippina)*, flagfish (*Jordanella floridae*), bluefin killifish (*Lucania goodie*), least killifish (*Heterandria formosa),* and *Fundulus* spp (golden topminnow; *F. chrysotus* and marsh killifish; *F. confluentus).*

After taxonomic analyses I also analyzed composition by size structure (standard length, SL) of all fish eaten by the Tricolored Herons and Snowy Egrets. The fish prey were divided into 5 size classes based on 1 cm increments and compared using similar multivariate analyses on the counts within each size class. A Bray-Curtis resemblance matrix was computed by the raw counts within each size class. Size class similarity was visually inspected with 2-Dimensional and 3-D MDS plots and an ANOSIM test was used to determine if there were differences in fish size eaten between species. Finally, the

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mean standard length of all fish in each bolus was calculated and the means were compared with ANOVA (SAS$^®$ V 9.2 PROC GLM; SAS Institute).

Results

Coarse-scale Diet comparisons of all three wading birds

With prey divided into 8 broad categories, diet breadth ranged from 0.19 to 0.36 (Table 2). There were no differences in the diet breadths of White Ibis and Tricolored Herons in either year (P-values = 0.962 and 0.239). In 2009 White Ibis had similar diet breadths to Snowy Egrets (P = 0.236) and Tricolored Heron diet breadth was similar to that of Snowy Egrets in 2009 (P = 0.743).

Crayfish dominated the diets of White Ibis while small and large-bodied fishes dominated the diets of Tricolored Herons and Snowy Egrets in 2008 and 2009. All multivariate comparisons between diets of White Ibis and Tricolored Herons or Snowy Egrets were statistically significant (all P-values < 0.01, Table 3). Average dissimilarity between Tricolored Herons and White Ibis diets were somewhat less in 2009 than in 2008 (Table 3), however the diet composition was still highly distinct. Visual inspection of the MDS prey biomass plots shows the clear distinction between White Ibis diets and the diets of Tricolored Herons and Snowy Egrets (Fig. 2). Differences were due to crayfish dominating the diets of White Ibis and small and large-bodied fish dominating the diets of Tricolored Herons and Snowy Egrets (Table 3). No differences were found between Tricolored Heron and Snowy Egret diets in 2009 (P = 0.798) and both species contained similar amounts of small-bodied fish prey. Three Snowy Egret boluses contained crayfish but were dominated overall by small and large-bodied fish.

Fine-scale analysis of Snowy Egret and Tricolored Heron diets in 2009

For fine scale analyses of egret diets, diet breadth ranged from 0.52 to 0.93 and was not statistically different between species in 2009 (Table 4). Diet composition of Tricolored Herons and Snowy Egrets was not different in 2009 ($P = 0.229$, Fig. 3). The size distributions of fish eaten by Tricolored Herons and Snowy Egrets in 2009 were not different when analyzed with ANOSIM ($P = 0.221$) and the mean fish length per bolus was also similar. The mean ($\pm$ SD) standard lengths of fish eaten by Tricolored Herons and Snowy Egrets in 2009 were 2.6 cm ($\pm$ 0.83) and 2.6 cm ($\pm$ 0.56) and they were not statistically different ($F_{(1,29)} = 0.05$, $P = 0.978$).

Variation in Tricolored Heron diets between years

No differences in diet breadth were detected between Tricolored Herons within the two years at either the coarse scale ($P = 0.181$) or the fine scale ($P = 0.721$) however there were differences in coarse scale diet composition of Tricolored Herons in 2008 versus 2009 ($P = 0.012$). In 2008, the diets of Tricolored Herons contained more large-bodied fishes (*Lepomis* spp., bass and cichlids) and the average biomasses and occurrence of small fishes was higher in 2009 (Fig. 4). No vertebrate prey were consumed in 2008, but 1 bolus in 2009 contained a Two-toed amphiuma (*Amphiuma means*) which contributed to 9% of the dissimilarity between years. Fine scale analyses produced similar results; diet composition of Tricolored Herons was different between years ($P = 0.005$) and 5 species of fish were responsible for 68% of the dissimilarity. Golden topminnow, eastern mosquitofish, and sailfin molly were more abundant in the 2009 boluses, and largemouth bass and *Lepomis* sunfish were more abundant in 2008 boluses.

The fish composition by length classes was not different between years ($P = 0.384$) nor were the mean sizes of fish per bolus ($F_{(1,19)} = 1.36$, $P = 0.257$). The mean ($\pm$ SD) sizes of fish eaten by Tricolored Herons in 2008 were 3.0 cm ($\pm$ 0.85) and 2.6 cm ($\pm$ 0.83) in 2009.

Discussion

The prey use of nesting ibis and co-occurring herons in Loxahatchee were highly distinct in both a wet year (nesting in the south of the system) and in a year with lower water when much of Loxahatchee was available for foraging ($276 - 345$ km^2 of available foraging habitat). The tactile foraging ibis ate mainly crayfish in both years whereas the egrets were primarily eating fish. This suggests that even when these species are found foraging together in wetlands during the nesting season they are targeting different prey species (Martínez 2004).

Considering the differences in foraging tactics (Kushlan 1979, Gawlik 2002, Dorn et al. *in review*), it may not be too surprising that the diet composition of White Ibis versus Tricolored Herons and Snowy Egrets was different. Although the differences between White Ibis and Tricolored Herons diets were consistent between years and were somewhat less dissimilar in 2009 than in 2008 as ibis fed on more small-bodied marsh fishes in 2009 (Table 5). Gawlik (2002) studied the giving up densities (GUD) of wading birds that nest in the Everglades. A GUD is the density of a prey item remaining in a patch after an animal quits feeding in it. GUDs for wading birds are a function of both prey abundance and water depth (Gawlik 2002). Tactile feeders, like White Ibis, seem to be more sensitive to falling fish densities than visual foragers such that White Ibis have

higher GUDs than either Tricolored Herons or Snowy Egrets at "medium" and "deep" water depths (Gawlik 2002). If these diets are generally representative of the wider Everglades then responses of these wading species may not be directly correlated unless densities of crayfish and fish are both enhanced by hydrologic restoration (Trexler and Goss 2009). Restoring long hydroperiod areas by reducing the frequency and severity of droughts would further lengthen the time of inundation and may increase the density and abundance of large-bodied fishes (Trexler et al. 2002, Ruetz et al. 2005, Trexler and Goss 2009). Trexler and Goss (2009) suggested that the density of small-bodied fishes could be somewhat suppressed by the presence of large-bodied fishes (6 – 8 cm) in long hydroperiod areas although small-bodied fish densities should remain relatively high. An increase in the prevalence of large fish could also affect the abundances of aquatic invertebrates, including crayfish. Dorn (2008) found that crayfish (*P. alleni*) biomass was highest when large-bodied fishes were absent from ponds in the Big Cypress of Florida and other studies suggest crayfish may be limited by sunfish and other large-bodied fishes (e.g., Roth et al 2007). However *P. fallax* (the crayfish in these ibis diets) can be found in long-hydroperiod wetlands (i.e., with multiple years of inundation) and relatively less is known about the way *P. fallax* responds to hydrologic variation (Dorn and Trexler 2007). Furthermore, the diet of ibis in Loxahatchee is well established (Chapter 1, Dorn et al. *in review*) but the diet in other parts of south Florida remains little studied. Whether densities of small prey fishes (2.5-3.0 cm SL) and crayfish, the principle prey of these two wading birds, will simultaneously be enhanced by hydro-restoration efforts is an important issue given the apparently large dietary niche differences of these species.

Tricolored Herons and Snowy Egrets are ecologically similar species that are thought to share similar dietary niches (Strong et al 1997, Gawlik 2002). While this study had modest sample sizes the results confirm that there are no clear differences in diet between the two species. There were no differences in the composition or sizes of fish eaten by the two species. The mean SL of fish eaten by Tricolored Herons and Snowy Egrets in 2009 was 2.6 cm, which is comparable to 3.8 cm total length (unpublished regressions). The range of sizes of fish eaten by Tricolored Herons and Snowy Egrets in 2009 was 1.25 – 4.32 cm and 1.18 - 5.79 cm total length which is similar to other studies of Tricolored Heron and Snowy Egret diets (Ogden 1977, Kent 1986, Bancroft and Jewel 1987, Post 1990). While differential habitat use can limit competitive interactions between species with similar prey characteristics (May and MacArthur 1972, Martin 1987, Strong et al. 2007) we do not know if there were habitat use differences in 2009 in Loxahatchee or whether the two species were feeding side-by-side in the sloughs. The principle niche differences between these species when nesting in the Southern Everglades, appears to one of habitat use (Strong et al. 1997). In Everglades National Park, Tricolored Herons did not select for any particular habitat type but fed mainly in mangrove-coastal and mangrove habitats. Snowy Egrets selected mangrove habitats; both species avoided inland marsh and slough habitats (Strong et al. 1997). Future research focusing on habitat selection of Tricolored Herons and Snowy Egrets in the northern Everglades would be useful considering the lack of mangrove and coastal habitats outside of Everglades National Park.

Tricolored Heron diet composition differed between 2008 and 2009 although the differences cannot be attributed clearly to year or location differences. The 2008 colony

was closer to canals on the southern boundary of Loxahatchee, water levels in the sloughs were higher, and the birds experienced several reversals. In contrast the nesting colony studied in 2009 was more centrally located and conditions were generally considered better for feeding in the wetlands due to moderate to low depths and steady recession rates. The higher frequency of large-bodied fishes (*Lepomis* spp., bass, and cichlids) suggests greater use of canal edges in 2008. Rehage and Trexler (2006) studied the fish communities in the central and southern Everglades and found that the densities of large fish (including largemouth bass and several species of sunfish) were greater within 5 m of a canal. The poorer wetland foraging conditions in 2008 may have led to greater use of canals and canal-wetland interfaces. Nevertheless, the lack of differences in the lengths of fish in the boluses suggests that Tricolored Herons were targeting the same size fish each year regardless of composition.

White Ibis, Tricolored Herons and Snowy Egrets are often found nesting and foraging in the similar wetland locations in S. Florida. However, the diets of White Ibis are drastically different than the diets of Tricolored Herons and Snowy Egrets. Because of the differences in diet and the different prey types that fuel successful nesting colonies, future research should focus on the responses of prey to hydrologic restoration. In turn, White Ibis, Tricolored Herons, and Snowy Egrets may respond differently to the same restoration effort if that hydro-restoration changes the availability of these prey types disproportionately.

Table 1. Bolus collection numbers by species, collection dates and associated water depths surrounding the colonies in 2008 and 2009.

Species	Bolus Collection Dates	n	Mean water depth (cm) $\pm$ SD	Available Habitat (km^2)
2008				
White Ibis	22 and 29 May, 6 June	58	13.2 $\pm$ 16.6	180 - 224
Tricolored Heron		9		
2009				
White Ibis		86		
Tricolored Heron	1 and 8 May	12	-8.7 $\pm$ 10.6	276 - 345
Snowy Egret		20		

Table 2. Frequency of prey types (% of boluses containing a prey type) in boluses of three species of wading birds in the Everglades during the 2008 and 2009 nesting seasons. N = the number of boluses included in the collection. *H* is the mean Shannon-Weaver diversity index; higher *H* values indicate a greater diversity of prey types used. Cray = crayfish, Smf = small bodied fishes, Lgf = large bodied fishes, Shr = shrimp, AIns = aquatic insects, TIns = terrestrial insects, Garb = garbage and Vert = vertebrates.

	Frequency of use (%)									
Species	Cray	Smf	Lgf	Shr	AIns	TIns	Garb	Vert	*H* (± SD)	n
2008										
White Ibis	78	3	2	0	15	42	22	2	0.24 (±0.28)	58
Tricolored Heron	0	78	67	0	44	11	0	0	0.19 (±0.58)	9
2009										
White Ibis	85	33	25	12	39	24	14	1	0.36 (±0.37)	86
Tricolored Heron	0	100	25	25	17	17	0	8	0.20 (±0.27)	12
Snowy Egret	15	90	35	40	10	10	5	0	0.22 (±0.27)	20

Table 3. Relative importance (% contribution) of each prey type to the dissimilarity between groups from the SIMPER analyses. Signs after the percentages indicate whether the first collection in the comparison had more or less biomass for that food type. All collection comparisons from the ANOSIM test are shown. Cray = crayfish, Smf = small bodied fishes, Lgf = large bodied fishes, TIns = terrestrial insects, Garb = garbage and Vert = vertebrates. Average dissimilarity ranges from 0 to 100 and is calculated in the SIMPER analysis. Aquatic insects and shrimp were not included because they did not contribute to 75% the compositional differences between species.

Comparison	Cray	Smf	Lgf	TIns	Garb	Vert	Average Dissimilarity	R	P
2008									
White Ibis vs. Tricolored Heron	33(+)	24(-)	25(-)	9(+)			98.6	0.686	0.001
2009									
White Ibis vs. Tricolored Heron	37(+)	32(-)	9(-)	4(+)	6(+)	5(-)	88.4	0.591	0.001
White Ibis vs. Snowy Egret	35(+)	33(-)	13(-)	5(+)	8(+)		85.2	0.557	0.001
Tricolored Heron vs. Snowy Egret							48.2	0.058	0.798

Table 4. Relative frequency of prey types used by Tricolored Herons and Snowy Egrets during the 2008 and 2009 nesting seasons. Sample size is the number of boluses included in the collection. *H* is the mean Shannon-Weaver diversity index; higher *H* values indicate a greater diversity of prey types used. Lep = *Lepomis* spp + *Enneacanthus*, Mic = largemouth bass, Cic = Poe = sailfin molly, Gam = eastern mosquitofish, Jor = flagfish, Luc = bluefin killifish, Het = least killifish and Fun = golden topminnow and marsh killifish.

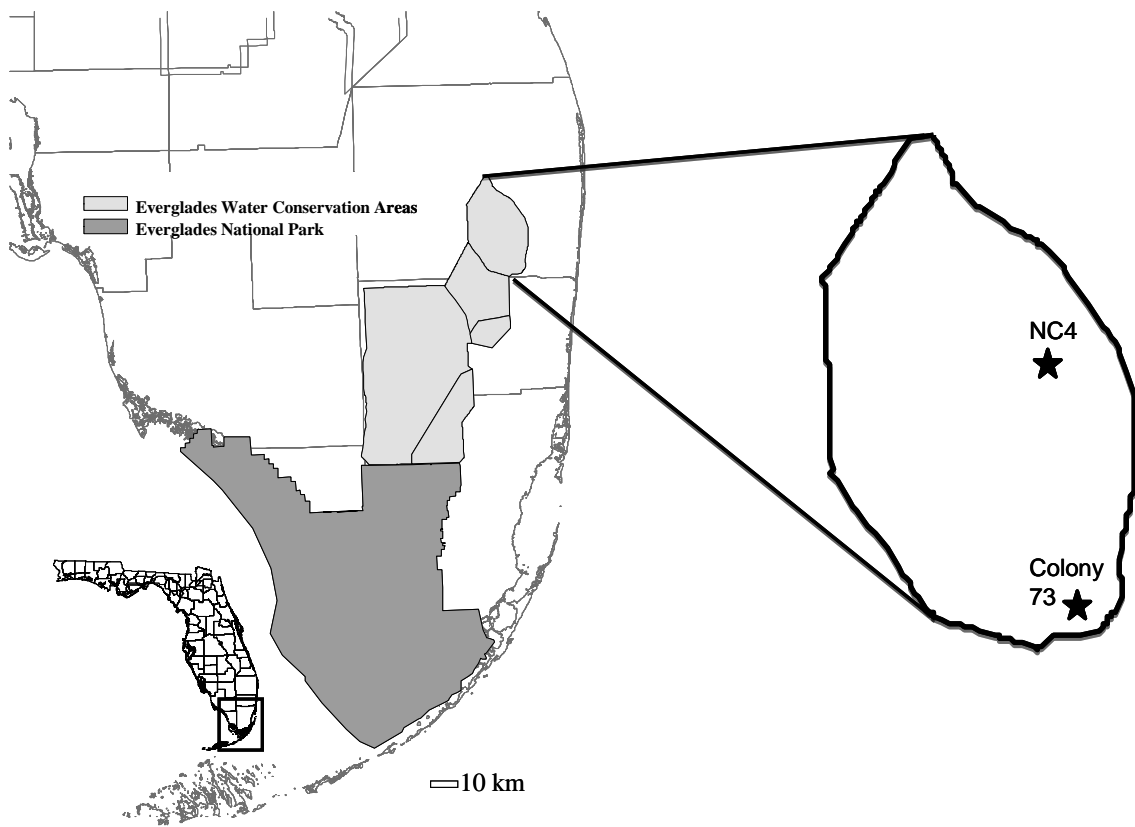|	Frequency of use (%)										
Species	Lep	Mic	Cic	Poe	Gam	Jor	Luc	Het	Fun	*H* (±SD)	n
2008											
Tricolored Heron	33	33	33	33	44	0	33	0	22	0.52 (±0.58)	9
2009											
Tricolored Heron	17	8	0	58	58	33	58	42	75	0.85 (±0.55)	12
Snowy Egret	35	0	0	85	50	45	30	40	60	0.93 (±0.44)	20

Figure 1. Map of the Everglades broken up into Water Conservation Areas and Everglades National Park. The sampling areas for this study were in Loxahatchee (Arthur R. Marshall Loxahatchee National Wildlife Refuge). Map of Loxahatchee National Wildlife Refuge with sampled colony locations. Colony 73 was sampled in 2008 and New Colony 4 was sampled in 2009.

Figure 2. Prey composition of White Ibis, Tricolored Heron and Snowy Egret diets in
2009 illustrated by NMDS ordination of prey biomasses. A. Each point is a bolus and the
proximity of points indicates the level of Bray-Curtis similarity in 2D space. B through
D. Biomasses of 3 of the 8 prey types are superimposed on the samples to indicate the
relative abundances of prey in each cluster; larger circles indicate diets with relatively
more biomass of the focal prey, but the scale (not shown) differs between panels. The
prey type in the top right ellipse is not shown in a separate figure but was composed of
terrestrial prey. Five other prey types are not shown because they were relatively less
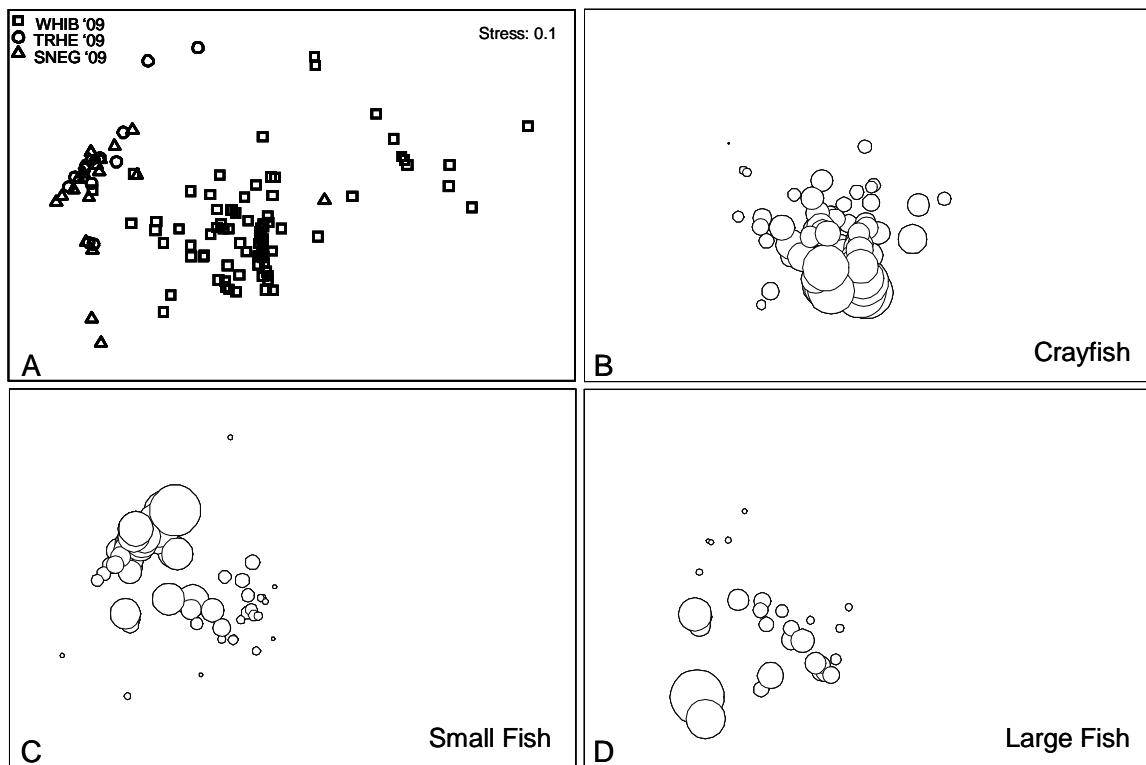important in differentiating diets among species.
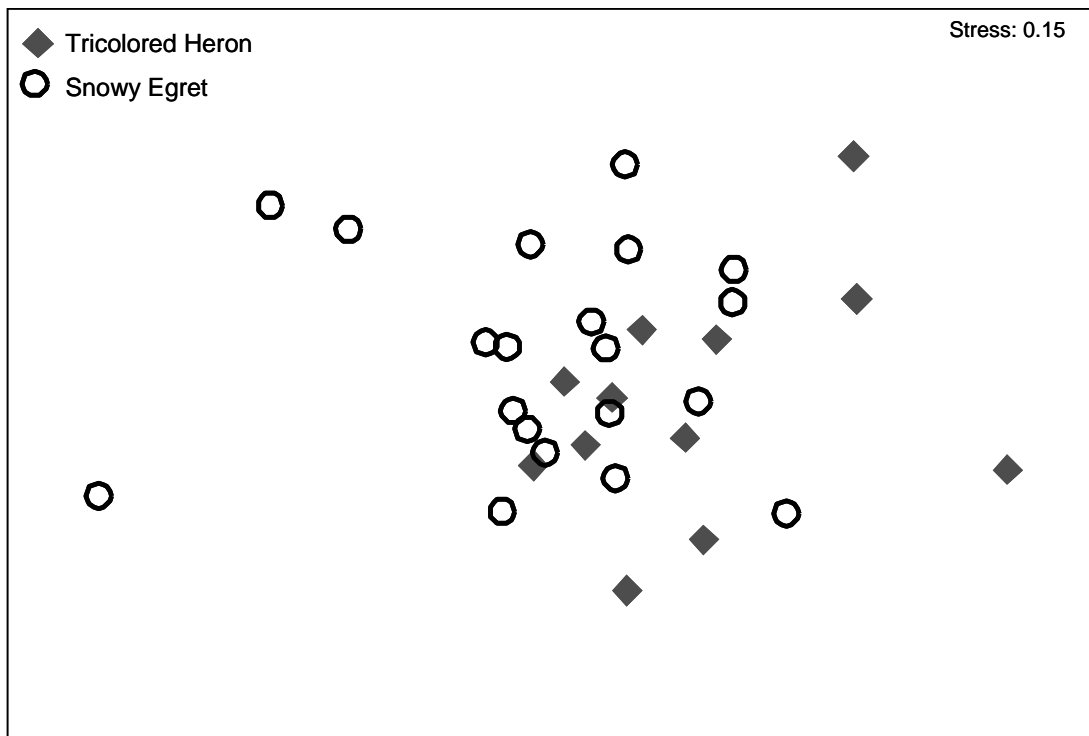
70

Figure 3. Prey composition of Tricolored Heron and Snowy Egret diets in 2009 illustrated

by NMDS ordination of prey biomasses. Each point is a bolus and the proximity of points

indicates the level of Bray-Curtis similarity in 2D space.
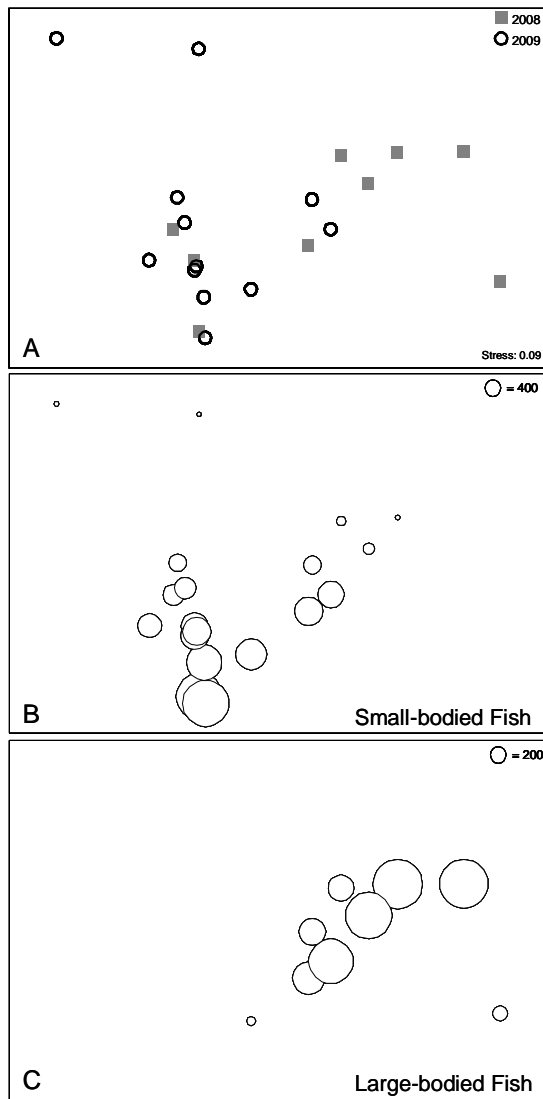
Figure 4. Prey composition of Tricolored Heron diets in 2008 and 2009 illustrated by

NMDS ordination of prey biomasses. A. Each point is a bolus and the proximity of points

indicates the level of Bray-Curtis similarity in 2D space. Tricolored Heron boluses in

2008 are represented by grey squares and Tricolored Heron boluses in 2009 are

represented by open black circles. B and C. Biomasses of small-bodied and large-bodied

fish species are superimposed on the samples to indicate the relative abundances of prey

in each cluster; larger circles indicate diets with relatively more biomass of the focal

prey, but the scale differs between panels.

APPENDIX 1

With collection help from staff of the South Florida Water Management District I

obtained 273 boluses from White Ibis, Tricolored Heron and Snowy Egret chicks during

the 2008 and 2009 nesting seasons. Boluses were collected from three colonies in

Loxahatchee. Boluses were collected between 0800 and 1200 hours. Total time spent on

the colony did not exceed one hour in order to limit stress to both the chicks and adults.

Adults were observed returning to the colony after we left. Approximately 90% of

boluses were collected from the ground after voluntary regurgitation from the chicks.

Tracheal massage to induce regurgitation was used on chicks that appeared to hold a

bolus in their crop. Chicks were handled for no more than three minutes and were

returned to the nest after the bolus was collected. All boluses were placed in plastic

Ziploc® or Whirl-pak® bags and placed on ice for transport back to the lab. In the lab the

boluses were preserved in 80% ethanol until sorted.

In the lab each bolus was poured through a mesh net (0.63 μm), washed, and then

I sorted the prey remains under a magnifying lamp. All identifiable prey items found

were collected, counted and placed in labeled glass scintillation vials. I searched each

bolus twice for crayfish rostrums, chelae, tails and gastroliths, fish otoliths and intact

fish/heads, as well as any other identifiable prey parts. Other animals and parts of

animals that were identified in the boluses included terrestrial prey like Surinam

cockroaches (*Pycnoscelus surinamensis*), mole crickets (*Scapteriscus* sp.), terrestrial

coleopteran adults and larvae (Scarabaeidae) as well as other aquatic prey; dragonfly naiads (Libellulidae and Aeshnidae), snails (*Planorbella* spp. and *Physa* spp.), aquatic coleopterans, grass shrimp (*Palaeomonetes paludosus*), and aquatic bugs (Belostomatidae and Naucoridae). In both years we found several boluses containing rotten chicken, dog food, and other unidentifiable tissues.

Crayfish were counted using rostrums, gastroliths, chelae, uropods, and other accessory crayfish parts like walking legs (Dorn et al. 2008). Crayfish counts were estimated by rostrums whenever rostrum estimates were equal to or greater than chelae or uropod estimates. If chelae or uropod estimates were larger than rostrum estimates, we used either the chelae or uropod estimate for final crayfish counts. Total chelae count was divided by two to provide an estimate of the number of crayfish in a bolus. In cases where we needed chelae estimates of crayfish sizes they were measured to the nearest 0.1 mm from the joint to the end of the propodus (immovable finger). Regressions were made to predict carapace length from either rostrum width or chelae length (Table 1). Uropods and walking legs were compared to reference collection crayfish and carapace length was recorded. Accessory parts, (i.e. walking legs) (Dorn et al. 2008), were used to estimate crayfish counts only when rostrums, chelae, or uropods were absent from the bolus.

Crayfish biomass estimates came from rostrum measurements unless chelae or uropod counts outnumbered rostrum counts and the chelae or uropod biomass estimate was 20% larger than the rostrum biomass estimate. Chelae biomass estimates probably suffer from greater error caused by the process of pairing and because the regression estimating carapace length from chelae length is not as strong as that for rostrums.

Estimates of carapace length were then used in another regression to determine dry mass (Table 2).

I used intact fish, fish heads, and sagittal otoliths to count fish in each bolus. Intact fish and fish heads were identified to genus or species (e.g., all *Jordanella* were presumed to be *J. floridae* as this is the only known species in the Everglades). I then measured the standard length (SL) of each fish. If only a head was present and the species known, I estimated the SL of the fish by comparing it directly to fish of various sizes in a reference collection. If identification was impossible from the head alone the otoliths were extracted for correct identification. I estimated the biomass of the intact fish/heads using regressions for each species/genus that predicts the dry mass from standard length.

Numerous fish are identifiable only by sagittal otoliths (Dorn et al. 2008) and so I also used otoliths in the boluses to determine the composition of fish present in each bolus. I developed a reference collection of otoliths for the most common species of fish in the Everglades (i.e., Eastern mosquitofish (*Gambusia holbrooki),* Bluefin Killifish *(Lucania goodei),* Flagfish *(J. floridae),* Sailfin Molly *(Poecilia latippina),* Golden Topminnow *(Fundulus chrysotus),* Marsh Killifish *(F. confluentus),* Warmouth *(Lepomis gulosus),* Dollar Sunfish *(L. marginatus),* and Spotted Sunfish *(L. punctatus*) for determination of otolith shapes. The sagittal otoliths found in the boluses were then compared to the reference collection of otoliths to determine what type of fish the otolith represented. The killifishes (*Lucania goodie* and *Fundulus* spp.) and sunfishes (*Lepomis* spp. and *Enneacanthus gloriosus*) could not be distinguished and were identified as killifish or sunfish. The otoliths appeared to be in good condition in all of the boluses

and the shapes were distinguishable. I then measured the absolute length (largest

dimension) of each otolith in each bolus.

Otoliths were paired together by species and size in each bolus. The number of

otolith pairs was rounded up to the smallest number of whole fish. Otoliths were paired

with the most similar sized otolith in the group, but otoliths of similar species that had a

difference in maximum width of more than 0.4 mm were counted as different fish. I then

averaged the lengths of the otoliths in each pair and used the average otolith length to

predict SL (Table 1). Standard lengths (mm) were converted to dry mass (mg) for each

fish using other regressions developed in the lab (Table 2).

I identified aquatic coleopterans by the presence of whole bodies in most cases

and intact leg pairs or heads (when bodies were missing) in a few instances.   I measured

total body length for whole prey and estimated total body lengths by comparing legs or

heads to intact references when only legs or heads were present. Using an independent

sample of aquatic coleopterans I constructed a regression that predicts total body length

from head width (Table 1) and dry mass from total body length (Table 2). Aquatic

coleopteran larvae were identified from a freshwater invertebrate manual and with the

assistance of staff at the South Florida Water Management District.

Unlike most of the insects and crayfish, grass shrimp do not have a uniform hard

part that was found intact and could be measured in each bolus. Shrimp tails were used

to estimate the number of shrimp in each bolus. Shrimp tails were compared to stock

samples of shrimp to determine the average sized shrimp in each bolus. The carapace

length of the reference shrimp was taken and was used to predict dry weight of the

average shrimp (regression in Table 2).

Aquatic bugs (*Belostoma* spp. and *Pelocoris* spp.), beetles (Coleopterans), dragonfly naiads (Aeshnidae and Libellulidae), adult scarab beetles (Scarabaeidae) and dipteran larvae (most likely *Musca domestica*) were counted and measured based on whole bodies, heads, and other parts (legs). Measurements of body lengths or head widths were used to estimate individual biomass from length-mass regressions (Table 2). Mole crickets were identified by the presence of a head, head and thorax, whole body, or legs. Only 3 mole crickets were found in the samples and were only present in the 2009 samples. A single intact mole cricket was dried and weighed and its mass was used as a representative for all mole crickets in the samples.

We identified and counted snails if they appeared to have been alive when eaten by the bird (i.e., soft tissues left in the shell). We did not measure or estimate the biomass of the snails that were found in the boluses, and they represented only 1.6% of all prey items found in the 2008 boluses and 0.2% of prey items in the 2009 boluses. Snails found in the boluses were identified as belonging to the families Planorbidae and Physidae.

Suriname cockroaches were the most abundant terrestrial insect in diets and were identified and counted based on the presence of heads and/or whole bodies. Adult Surinam cockroaches (*Pycnoscelus surinamensis*) were identified by the pale white band on the front edge of the pronotum and the presence of wings. Larvae were distinguished by the absence of the white band on the pronotum and the absence of wings. Cockroach heads that could not be distinguished as adults or larvae (due to the absence of a pronotum and body) were counted separately. Head widths or total body lengths were used to calculate individual biomass (Table 2).

One intact salamander was found in the 2008 samples. One ringneck snake (*Diadophis punctatus*), one unidentifiable anuran head, and one intact two-toed amphiuma (*Amphiuma means*) were found in the 2009 samples. The samples were dried at 55°C to a constant weight and then weighed to determine biomass.

Dog food, chicken, and other tissues were separated, dried (55°C for at least 24 hours or to a constant weight) and weighed. In this case the weights represent the weight after some unknown amount of digestion. This is different than most of our other measures of weight that are reconstitutions of prey biomass before digestion.

Table 1. Regression parameters and statistics for calculation of animal lengths (standard length, total length, carapace length) from small hard parts (e.g., otoliths, rostrums, heads) found in the boluses. The ranges indicate the standard lengths for fishes, but the sizes of parts for the invertebrates.

Species	Common Name	from	to	slope	intercept	R^2	N	Range
Lucania goodei, Fundulus chrystotus & Fundulus confluentus	Killifishes	8	1	1.1459	1.444	0.933	36	12.4-49.22
Gambusia holbrooki	Eastern Mosquitofish	8	1	1.4343	1.286	0.937	59	9.72-44
Heterandria formosa	Least Killifish	8	1	0.9187	1.319	0.926	13	9.79-16.2
Jordanella floridae	Florida Flagfish	8	1	1.0523	1.339	0.922	23	16.3-29.33
Lepomis spp.	Sunfishes	8	1	1.0232	1.210	0.891	63	18.4-80.76
Poecilia latipinna	Sailfin Molly	8	1	1.1155	1.366	0.953	38	11.8-51.37
Procambarus fallax	Slough Crayfish	9	10	17.121	16.844	0.941	37	0.55-1.9
Procambarus fallax	Slough Crayfish	11	3	0.7505	0.538	0.931	37	5.5-27
Pelocoris femoratus	Alligator Flea	7	4	1.0539	0.489	0.954	18	6-8.7
Coleoptera	Adult aquatic beetles	7	4	1.2636	0.432	0.999	6	2.33-6.8

Table 2. Length-mass regression parameters for fish, aquatic invertebrates, and terrestrial insects. The range indicates the lengths or widths (standard length, total length, head width, carapace length) of animals used (mm) to build each regression.

Species	Common Name	From	To	Slope	Intercept	R^2	N	Range
Lucania goodei, Fundulus chrystotus & Fundulus confluentus	Killifish	1	2	3.195	-2.6575	0.98	112	16.56-66
Lucania goodei	Bluefin Killifish	1	2	2.975	-2.3608	0.91	81	16.56-39.9
Gambusia holbrooki	Eastern Mosquitofish	1	2	3.596	-3.1538	0.97	89	11.9-46
Heterandria formosa	Least Killifish	1	2	2.739	-2.053	0.86	25	14.5-23.26
Jordanella floridae	Flagfish	1	2	3.921	-3.325	0.96	45	14.3-30.2
Lepomis spp.	Sunfish species	1	2	2.805	-1.788	0.92	56	24.8-66.5
Poecilia latipinna	Sailfin Molly	1	2	3.368	-2.736	0.95	54	13.9-45.8
Palaemonetes paludosus	Grass Shrimp	3	2	2.515	-1.227	0.87	136	5.1-16.3
Procambarus fallax	Slough Crayfish	3	2	3.227	-4.658	0.98	87	5.3-33.5
Pelocoris femoratus	Alligator Flea	4	2	2.207	-0.908	0.38	35	6.5-10
Stratiomyidae	Soldier fly larvae	4	2	2.441	-1.904	0.85	35	8.9-25.84
Coleoptera	Adult aquatic beetles	4	2	2.755	-1.351	0.90	67	4.5-31.9

Coleoptera	Larval aquatic beetles	4	2	0.038	-0.018	0.892	33	4.5-57.9
Belostoma spp.	Giant water bug	4	2	2.2539	-1.369	0.812	44	4-38.1
Anisoptera	Dragonfly naiad	6	2	0.0806	-0.112	0.530	85	8.5-18.5
Anisoptera	Dragonfly naiad	7	2	2.438	-0.495	0.561	84	2.2-6
Scarabaeidae larvae	Scarab Beetle Larvae	4	2	3.153	-2.53	0.91	13	14.5-58.5
Scarabaeidae larvae	Scarab Beetle Larvae	7	2	2.711	0.632	0.89	13	2.05-9.73
Pycnoscelus surinamensis	Surinam Cockroach	4	2	2.356	1.113	0.76	19	10.9-21.36
Pycnoscelus surinamensis	Surinam Cockroach	7	2	3.376	0.175	0.79	22	n.a.
Diptera	Fly larvae	6	5	1.280	-8.157	0.71	135	7.6-16.75

1 = log10 standard length (mm)

2 = log10 dry mass (mg)

3 = log10 carapace length (mm)

4 = log10 total length (mm)

5 = dry mass (mg)

6 = total length (mm)

7 = log10 head width (mm)

8 = log10 otolith maximum dimension

9 = ln rostrum width (mm)

10 = carapace length (mm)

11 = log10 chela length (mm)

APPENDIX 2

Caloric content for common prey items was determined and compared to Kushlan

et al. (1986a). Aquatic prey items were captured using minnow and throw traps and were

collected from various wetlands around the Water Conservation Areas. Fish were killed

using MS222 and were placed on ice, along with all other prey items, for transport back

to the lab. Prey items included eastern mosquitofish, bluefin killifish, flagfish, sailfin

molly, largemouth bass, dollar sunfish, golden topminnow, slough crayfish, dragonfly

naiads and grass shrimp. We also collected Suriname cockroaches from urban lawns to

calculate their caloric value. Samples were measured, dried at 60°C to a constant weight,

ground and dried again at 60°C to a constant weight. A total of 43 samples from 11

species (n = 1 to 6 individuals per prey species) were used to estimate the caloric content

of common prey items of White Ibis. The samples were placed in labeled vials and sent

to Auburn University (Dr. Dennis DeVries, Department of Fisheries and Wildlife) where

caloric content was determined using bomb calorimetry. Values for dog food,

herpetofauna, and chicken were taken from the literature (Smith 1976, Wever et al. 1978,

and Chizzilini et al. 1999).

Average caloric content values of common prey items are listed in Table 1. All

prey items analyzed had a lower caloric content than equivalent species listed by Kushlan

et al. (1986a). Suriname cockroaches had the highest caloric value (kcal/g) of any prey

item in the diets. Given their average size (17 mm), a typical cockroach has a caloric

content similar to that of a 30 mm (SL) eastern mosquitofish.

Table 1. Average caloric content values (kcal/g dry weight, ±SE) of common prey items found in White Ibis diets. N = number of samples of each prey type.

Prey species	N	Average kcal/g dry weight (±SE)	Kushlan et al. (1986) kcal/g dry weight
Fundulus chrysotus	3	4.27 (±0.07)	5.16
Jordanella floridae	3	4.49 (±0.12)	5.00
Lucania goodei	3	4.44 (±0.05)	5.50
Gambusia holbrooki	6	4.39 (±0.17)	5.51
Lepomis marginatus	3	4.30 (±0.08)	4.96 (*L. gulosus*)
Micropterus salmoides	1	4.43	NA
Poecilia latipinna	4	4.95 (±0.23)	NA
Palaemonetes paludosus	6	4.39 (±0.12)	4.70
Procambarus fallax	3	3.02 (±0.29)	4.31 (*P. alleni*)
Pycnoscelus surinamensis	6	5.27 (±0.21)	NA
Anisoptera	5	4.41 (±0.29)	5.00 (Odonata)
Dog Food*	-	3.66	NA
Mole cricket*	-	6.81	NA
Scarabaeidae*	-	4.48	NA
Chicken*	-	5.30	NA

* Caloric content values taken from the literature.

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