Research Article

Linking Wading Bird Prey Selection to Number of Nests

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ABSTRACT Establishing a link between food availability and productivity is often central to the recovery of declining populations; however, differences in prey selection may influence how populations are affected by changes in prey availability. We determined prey selection and prey availability for 3 wading bird species, and investigated the effects of prey availability on the number of nests initiated by 6 wading bird species in the Florida Everglades, USA. To determine prey selection, we compared food items recovered from tricolored heron (*Egretta tricolor*), snowy egret (*Egretta thula*), and little blue heron (*Egretta caerulea*) nestlings to aquatic prey availability from throw-traps across the Everglades landscape from 2012 to 2014. Tricolored heron and snowy egret prey composition was statistically similar across years, with the majority of prey biomass coming from relatively large (>1.9 cm) marsh fish. Little blue heron prey composition differed from the other wading bird species, and contained a higher percentage of grass shrimp (*Palaemonetes paludosus*) and exotic fish species. Numbers of small heron nests were positively influenced by the availability of large marsh fish across the landscape, whereas numbers of nests for other wading bird species (wood stork [*Mycteria americana*], great egret [*Ardea alba*], white ibis [*Eudocimus albus*]) were not. Our results suggest differences among wading bird species in their prey selection and availability. Although small heron foraging may seem restricted by their specialization on marsh fishes, their short nesting cycles allow for the phenological flexibility to delay nesting until foraging conditions are optimal. Conversely, wood storks with longer nesting cycles are more temporally constrained but have greater flexibility in prey items and foraging range. The annual number of small heron nests may be more robust to hydrological variability as a result of management action or global change than the number of wood stork nests. The temporal constraints of nesting by wood storks indicate that management of supporting wetland systems should provide continuous habitat availability during the nesting season. © 2016 The Wildlife Society.

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Food availability is a common constraint on population growth for many taxonomic groups (Martin 1987, Turchin and Batzli 2001, Ortega-Mayagoitia et al. 2011, Shine and Madsen 2012, Hanya and Chapman 2013). Access to food affects the survival of individuals within a population (Tveraa et al. 2003) and the ability of populations to produce recruits (Song et al. 2007, Haley and Rosenberg 2013). Effective foraging strategies directly affect population viability, particularly for populations with scarce or fluctuating food resources. Strategies include traveling to areas with higher food availability (Sekercioglu 2010, Mestre and Bonte 2012); switching food types based on trade-offs between accessibility, abundance, and quality (Ballard et al. 1997, Dorn et al. 2011, Flemming et al. 2013, Soininen et al. 2013); adjusting reproduction to match times

of high food availability (Butler 1993, Schlund et al. 2002); and even changes in physiology to survive times of food scarcity (Robin et al. 1988, Gardi et al. 2011).

Establishing the link between food availability and productivity is often central to the recovery of declining populations (Forcada et al. 1999, Wellicome et al. 2013, Ayers et al. 2014) and to broader ecosystem restoration and management (Lorenz et al. 2009). However, this relationship between food availability and productivity can be vague if prey selection patterns are unknown, or change depending on environmental conditions. Additionally, managing for species guilds can be further complicated if food selection preferences or foraging strategies differ among sympatric species. Because of this, successful species and ecosystem management plans depend on the specific knowledge of prey selection on a species-by-species basis, and how each species copes with limited food availability.

Wading birds (orders Ciconiiformes and Pelecaniformes) in the Florida Everglades provide a model system for studying food-limited populations, and how diet selection

and food availability influence reproduction. The Everglades is a well-studied wetland covering approximately 7,000 km² in south Florida, USA, and consists of sawgrass (*Cladium jamaicense*) ridges and freshwater sloughs, scattered with higher elevation tree islands. During the wet season (Jun–Nov), rainfall increases and the landscape is inundated. As water levels increase, aquatic faunal populations repopulate the marsh (Loftus and Eklund 1994). During the dry season (Dec–May), water levels fall and the inundated areas recede across the gradually sloped landscape, concentrating aquatic fauna in small isolated pools (Kushlan 1976, DeAngelis 1994, Botson et al. 2016). These isolated pools provide ideal foraging habitat for wading birds, and the high concentration of aquatic fauna provides a high abundance of accessible food (Gawlik 2002). The wading bird nesting season occurs concurrently with greater prey availability during the dry season (typically Feb–May). However, variable water recession rates and rain events affect the degree to which aquatic fauna are concentrated (Botson et al. 2016). Rain events can cause reversals in the drying pattern, allowing prey to disperse, which can lead to nest abandonment (Frederick and Collopy 1989). As a result, different years can be characterized by different hydrologic patterns, resulting in variable prey availability, wading bird nesting numbers, nesting success, and physiological condition. In addition to the evidence of relationships between prey availability and reproduction, there is also no evidence that nest predation, disease, or nesting habitat are limiting (Frederick and Spalding 1994). Because of this, prey availability is considered to be the prevailing limiting factor for wading bird populations in the Everglades (Kushlan 1986, Gawlik 2002, Herring et al. 2011).

Wading bird populations in the Everglades have decreased significantly since the establishment of levees and canals in the 1960s (Frohring et al. 1988, Ogden 1994). In light of such declines, wading birds were chosen as indicators of ecosystem health and function (Restoration Coordination and Verification 2005), with increasing wading bird nesting numbers being one of the primary objectives of the Comprehensive Everglades Restoration Plan (Restoration Coordination and Verification 2005). Several studies have examined the relationship between wading bird foraging locations or annual number of nests produced by wading bird populations and hydrologic parameters, identifying some general patterns relating to foraging habitat selection and impact of water reversal events (Frederick and Collopy 1989; Beerens et al. 2011, 2015; Lantz et al. 2011; Botson 2012). However, most of these studies used indirect measures of prey availability (e.g., hydrological conditions, modeled prey abundance). A recent study by Botson et al. (2016) investigated the role of hydrologic and landscape variables on prey availability during the wading bird nesting season. However, wading bird prey was broadly categorized as either fish, crayfish, or shrimp, without connecting these prey categories to the different prey selection behaviors of wading bird species. Such lumping of potential prey availability and wading bird species responses can result in ambiguous ecological relationships and species-specific responses.

Because of differences in body size and foraging strategies, it is reasonable to assume different wading bird species select different prey across the Everglades landscape. Thus, the annual number of nests produced by different species may be influenced in part by the population dynamics of different prey or foraging habitat availability. Recent research by Boyle et al. (2014) suggested the importance of crayfish for white ibis (*Eudocimus albus*) diets, and Dorn et al. (2011) demonstrated the ability of white ibises to switch diets between crayfish and urban food (i.e., garbage) depending on foraging conditions. Although prey selection is broadly described for wading bird species throughout their ranges (Coulter et al. 1999, Parsons and Master 2000, Heath et al. 2009, Rodgers and Smith 2012, Frederick 2013), there has been relatively little work on dynamics of prey selection within the Everglades ecosystem. Existing diet studies on tricolored herons (*Egretta tricolor*), snowy egrets (*Egretta thula*), and little blue herons (*Egretta caerulea*; i.e., small herons) are limited in sampling effort (Rodgers 1980, Strong et al. 1997, Boyle et al. 2012), whereas the most recent diet study for the wood stork (*Mycteria americana*) in the Everglades is now historical (Ogden et al. 1976). We conducted the first multi-year study of wading bird prey selection across the Everglades system, and investigated the link between prey selection and the annual number of nests for 6 wading bird species. More specifically, our study objectives were to 1) quantify small heron diets in the Everglades landscape; 2) determine small heron prey selection in comparison with aquatic prey availability in the landscape; 3) determine changes in small heron prey selection with hydrologic patterns; and 4) examine the relationship between selected prey, foraging habitat availability, and the annual number of nests produced by wading birds.

STUDY AREA

Our study took place in the freshwater regions of the Florida Everglades, USA, spanning approximately 7,000 km² (Fig. 1). The majority of the landscape was owned by federal and state agencies, with water storage, ecosystem conservation, and recreation as the primary landuse. Common vegetation in the ridge and slough system consisted of sawgrass, spikerush (*Eleocharis* spp.), bladder wort (*Utricularia* spp.), maidencane (*Panicum hemitomon*), and water lily (*Nymphea odorata*), scattered with cypress (*Taxodium* spp.), willow (*Salix* spp.), and pond apple (*Annona glabra*) trees on higher elevation islands. Common aquatic fauna consisted of mosquitofish (*Gambusia holbrooki*), grass shrimp (*Palaemonetes paludosus*), and crayfish species (*Procambarus alleni* and *Procambarus fallax*). Climate was sub-tropical, with the majority of precipitation occurring between June and November. Several levees and canals separated the ecosystem into 5 distinct water conservation areas in the northern Everglades. Everglades National Park comprised the southern portion of the Everglades, whereas Big Cypress National Preserve and dense urban areas bounded the Everglades system to the west and east, respectively.

We studied wading bird diet at 3 nesting colonies, specifically selected because of their range of hydrologic
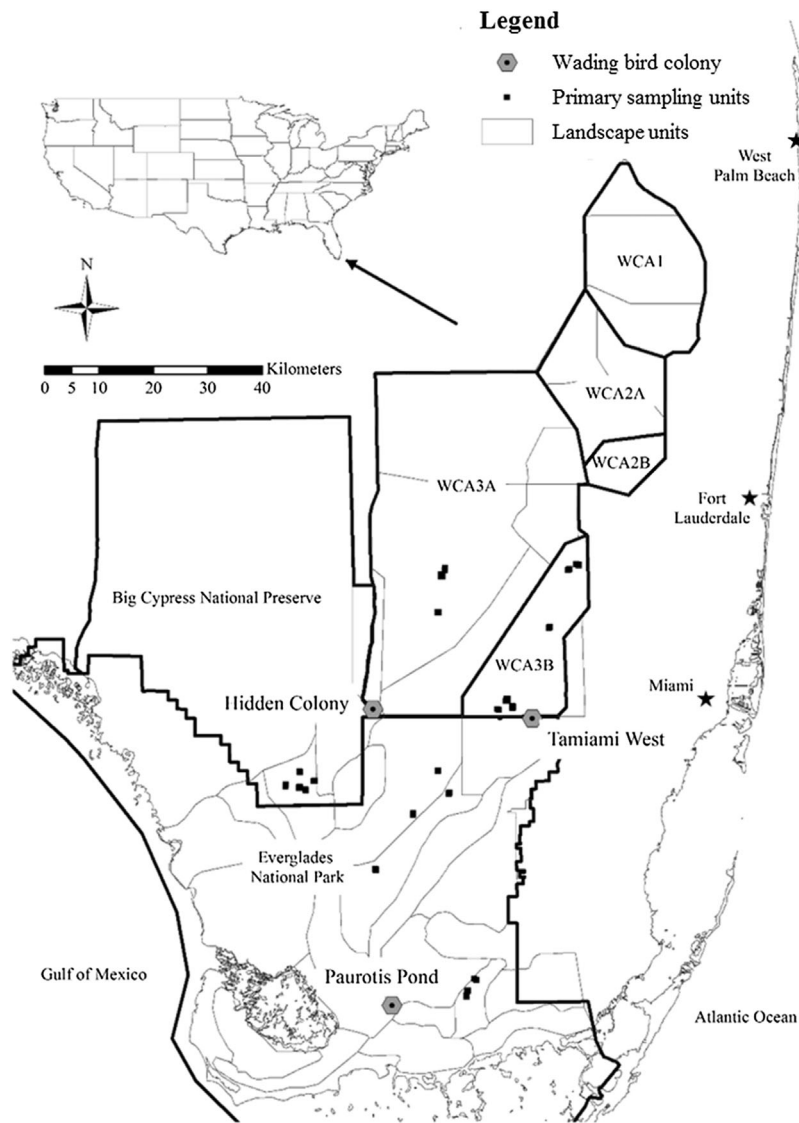
Figure 1. Sampled wading bird colonies and aquatic fauna sampling locations in the Everglades, Florida, USA, 2012–2014. National park and water conservation area (WCA) boundaries also shown.

conditions and history of repeated use by nesting wading birds. Hidden Colony (Water Conservation Area 3A, latitude 25.78, longitude −80.84) and Tamiami West (Everglades National Park, latitude 25.75, longitude −80.54) were located in the fresh water interior of the Florida Everglades, whereas Paurotis Pond (Everglades National Park, latitude 25.28, longitude −80.80) was located near the southern tip of Florida in a coastal brackish wetland (Fig. 1). Nesting colonies were located within tree islands of different nest tree species. Hidden colony was primarily composed of bald cypress (*Taxodium distichum*). Tamiami West was characterized by a mix of pond apple (*Annona glabra)* and willow (*Salix* spp.). Lastly, Paurotis Pond was primarily composed of large, mature red mangrove (*Rhizophora mangle*).

Hydrologic patterns affecting foraging habitat were fairly similar among years for the duration of our study (Fig. 2) in terms of water depth, recession rates, and reversal events. Compared to a 10-year average, the water depth at the

beginning of the dry season was moderate across the Everglades for all years (Botson 2012), and 2012 and 2013 experienced a steady recession with 1 mild reversal event in March. The 2014 dry season began with similar water depths, but it was marked with several reversals in the drying pattern throughout the first half of the dry season (Dec–Mar), followed by a steady and extended recession from April through June.

METHODS

Prey Selection

We collected regurgitated food boluses from nestling tricolored herons, snowy egrets, and little blue herons throughout the 2012, 2013, and 2014 nesting seasons (Mar–May). Heron capture, handling, and bolus collection techniques adhered to protocols approved by the Institutional Animal Care and Use Committee at Florida Atlantic University (permit number A12-03) and the Florida Fish
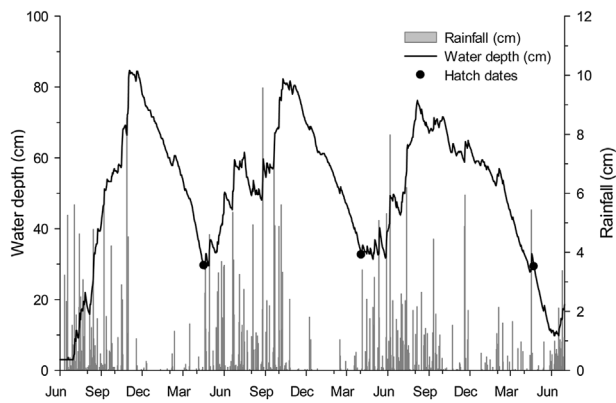
Figure 2. Water depth and rainfall within core foraging area of Hidden Colony and Tamiami West, from June 2011 to June 2014, derived from gage W2 of the Everglades Depth Estimate Network. Hatch dates denote the annual date in which most nests had hatched young in Hidden Colony and Tamiami West, Everglades, Florida, USA.

and Wildlife Conservation Commission (permit number LSSC-12-00012). To collect boluses, we visited each colony 1–2 times a week during the wading bird nesting season. Sampling trips within each colony lasted 1–2 hours; however, we moved locations frequently to ensure we did not disturb a nest for more than 10 minutes. Nestlings often regurgitate in the presence of a human, making bolus contents readily available. In the event a targeted nestling did not voluntarily regurgitate, we gently massaged its neck to encourage regurgitation. Once a nestling regurgitated, we placed the bolus contents in a plastic bag on ice for the duration of the sampling trip. Additionally, we re-fed the nestling bait fish to compensate for the loss of bolus contents. To maintain random samples, we placed a strip of flagging tape near the nest to ensure we did not collect boluses from a nest more than once. We rinsed and stored bolus contents in a color fixative (Prefer; Anatech Ltd., Battle Creek, MI) for 3 days, and then transferred the contents to a 70% ethanol solution for preservation.

To identify prey species, we poured each bolus through a 0.6 μm mesh net, rinsed it with water, and sorted prey remains under a magnifying lens. We identified each prey item to the lowest taxonomic group possible; this was often down to species for fish, crayfish, and shrimp, and order for other invertebrates. Additionally, we weighed each animal to 0.01 g and measured length to the nearest millimeter. We measured standard length and total length for fish species, carapace length and total length for crayfish species, and total length for shrimp and other invertebrates (Anderson and Neumann 1996). Lastly, because of differing states of digestion, we noted whether each animal represented a partial or whole carcass.

Prey Availability and Nest Counts

To determine available prey, we sampled aquatic fauna in marshes during the dry season (Dec–May) at various locations within the freshwater Everglades system (Fig. 1). This study was part of an on-going project that has monitored aquatic fauna since 2005. We used a multi-stage

sampling design (Cochran 1977) consisting of landscape units (LSUs), primary sampling units (PSUs), sites, and throw-trap locations (i.e., 1-m^2 box with mesh sides and an open top and bottom that allows sampling of aquatic fauna). Throw-traps accurately describe fish species and size classes present within several LSUs in the Everglades landscape (Jordan et al. 1997) and effectively sample invertebrate species (Freeman et al. 1984). Landscape units were delineated by hydroperiod and vegetative characteristics based on hydrological and vegetative gradients. Each LSU contained ≥7 500-m × 500-m PSUs randomly placed using ArcGIS 9.3 (ESRI, Redlands, CA). Each PSU contained 2 random points that varied for each sampling year. The sampling site was the closest suitable wading bird foraging habitat to the random points. Suitable foraging habitat was defined as an area with sparse to moderate vegetation that was <30 cm in water depth (Lantz et al. 2011). Once at the site, we selected a random bearing and distance within the suitable habitat for the throw-trap location, with the caveat that the second of 2 trap locations had to be ≥10 m away from the first throw-trap location.

After tossing the throw-trap to the determined location, we cleared aquatic fauna from the throw-trap with a bar seine until 5 consecutive sweeps yielded no faunal species. We transferred all species <15 cm to a labeled jar containing tricaine methanesulfonate (MS-222; Western Chemical, Ferndale, WA), a rapid euthanizing agent. We identified and measured larger faunal items in the field and released them. Once in the lab, we transferred all collected items to a color fixative (Prefer) for 3 days and then to a 70% ethanol solution for preservation. We sorted, identified, and measured each potential prey item using the same methods as bolus contents, described above.

We collected nest count data in conjunction with National Park Service staff for each nesting season from 2005 to 2014 via systematic aircraft surveys that covered the entire interior and coastal Everglades. Flights occurred monthly during the wading bird nesting season, and consisted of east-west transects spaced 3 km apart at an altitude of approximately 245 m. Once an active colony was located, 1–2 observers estimated numbers of nests by species and took digital photos. Observers later used photos to verify visual counts made during survey flights (Cook 2014). Both aquatic faunal sampling and colony nest counts followed protocols and guidelines related to the use of vertebrate animals in effect at the time the data were collected.

Statistical Analyses

We performed multivariate analyses as outlined by Clarke and Warwick (2001) to compare prey communities within bird species across nesting colonies and years, and among bird species. To analyze prey consumption patterns at the colony level and improve visual representation in non-metric multi-dimensional scaling (NMDS) plots, we combined bolus data collected from the same wading bird species within the same colony on the same date. We only included sampling dates in the multivariate analyses that contained ≥10 prey items from ≥2 separate boluses to minimize the

bias of dates with low sampling numbers. This created 1 sample point representative of the prey communities consumed by each wading bird species for each sampling location and date. We eliminated prey species that accounted for <1% of total prey composition biomass for each bird species from our analyses to prevent over-representation of rare species. To determine prey composition patterns, we calculated Bray–Curtis similarity matrices for each bird species on square-root transformed biomass data for prey species within boluses. Bray–Curtis similarity matrices provide an index of similarity between pairwise bolus samples, and the square-root transformation down-weights the influence of particularly dominant prey species. Based on the Bray–Curtis similarity matrices of each bird species, we ran an analysis of similarities (ANOSIM) among bolus samples from different nesting colonies and sampling years to determine the spatial and temporal consistency of prey consumption. An ANOSIM is a non-parametric permutation procedure that tests for differences among community samples based on the ranks of the pairwise similarities in the Bray–Curtis matrix. If no statistical differences occurred ($P > 0.05$), we combined all prey consumption data across nesting colonies and sampling years for each bird species to increase sample size and improve our ability to detect statistical differences. We ran an additional ANOSIM among bird species to determine whether prey consumption patterns differed by avian species. For diet comparisons among bird species, we also used NMDS plots derived from the Bray–Curtis similarity matrix to visually examine diet overlap based on prey composition. When statistical differences occurred ($P \leq 0.05$), we used a similarities percentage analysis (SIMPER) to determine which prey species were influencing those differences.

Similarly, we used the same multivariate analyses as described above to determine the consistency of prey communities spatially among nesting colonies and temporally among sampling years. We included only throw-trap samples that coincided both spatially and temporally with bolus sampling to represent the aquatic prey communities available to the wading birds used in our study. We included throw-trap samples only if they occurred within 30 km of each colony, the maximum foraging distance for small herons (Strong et al. 1997), and were sampled within the same date range as the bolus samples for each year. To analyze aquatic prey communities at the site level and improve visual representation in NMDS plots, we combined throw-trap data collected from the same site on the same date. If we did not detect a difference in prey communities among nesting colonies and sampling years (ANOSIM, $P > 0.05$), we combined prey availability data across all sampling locations and years. To determine prey species selection by wading birds, we performed the same multivariate analyses as described above to compare the prey communities consumed by each wading bird species (i.e., bolus samples) with the prey communities available in the landscape (i.e., throw-trap samples). Additionally, to determine prey size selection, we performed a 1-way analysis of variance (ANOVA) on ranks with SAS 9.3 (SAS Institute, Cary, NC) comparing the

median length of prey items within boluses and the median length of aquatic fauna available in the landscape as determined by throw-trap samples.

We performed a regression analysis in SAS 9.3 to examine the relationship between selected prey, foraging habitat availability, and number of wading bird nests across the entire Everglades landscape from 2005 to 2014. We calculated prey availability as the mean number of selected prey (defined as the prey taxa and size classes comprising 95% of small heron diet) individuals/m^2 averaged across all throw-trap samples within a year. Because of the large spatial extent of the Everglades, we coarsely defined foraging habitat availability as the number of km^2 that dried within the Everglades landscape during the dry season. Whereas this definition does not discriminate against dense vegetation cover, it provides a standard metric to compare year-to-year variations in the area of the Everglades that reached suitable foraging depths. To calculate foraging habitat availability, we used the Everglades Depth Estimate Network (EDEN), a real-time hydrologic monitoring network that provides daily water depths at a 400-m × 400-m spatial scale for the Everglades region (Telis 2006). If a previously wetted cell dried to a depth of zero between December and May, the cell contained water that was shallow enough to support wading bird foraging at some point throughout the dry season. Therefore, we considered that cell area available for wading bird foraging during that nesting year. We used the maximum nest count for a species within the nesting season, usually occurring in April, as an indication of annual number of nests. Maximum nest counts by species provides a comparable measure of annual landscape-wide nest counts without the additional time and resources required for individual nest monitoring (Crozier and Gawlik 2003, Frederick et al. 2009).

RESULTS

We collected 206 boluses from tricolored heron nestlings (37 in 2012 from 4 sampling dates, 47 in 2013 from 11 sampling dates, 122 in 2014 from 16 sampling dates), 113 boluses from snowy egret nestlings (29 in 2012 from 4 sampling dates, 15 in 2013 from 6 sampling dates, 69 in 2014 from 8 sampling dates), and 36 boluses from little blue heron nestlings (16 in 2013 from 2 sampling dates, 20 in 2014 from 4 sampling dates). Of the boluses collected, 95% were from Hidden Colony and Tamiami West. Mean fish length varied slightly among bird species but remained constant for each bird species across sampling years. Mean fish length in tricolored heron boluses was 2.8 ± 0.9 (SD) cm overall (2.7 ± 0.9 in 2012, 3.1 ± 1.0 in 2013, 2.8 ± 0.9 in 2014). Mean fish length in snowy egret boluses was 2.4 ± 0.9 cm overall (2.7 ± 0.8 in 2012, 2.4 ± 0.9 in 2013, 2.3 ± 0.9 in 2014). Mean fish length in little blue heron boluses was 3.1 ± 1.0 cm overall (3.4 ± 1.4 in 2013, 3.1 ± 1.0 in 2014).

There was no difference in prey composition for tricolored herons among years (R [ANOSIM test statistic] <0.26, $P > 0.21$), but there was a difference among colonies ($R < 0.26$, $P < 0.04$) in that boluses from Paurotis Pond contained more African jewelfish (*Hemichromis letourneuxi*)

than did the other 2 colonies. However, as evidenced by the small R, the biological difference among colonies was inconsequentially small, a possible effect of having many replicates for each colony (Clarke and Warwick 2001). There was also no difference in prey composition among colonies or years for snowy egrets ($R < 0.01$, $P > 0.53$) or little blue herons ($R = 0.29$, $P = 0.27$, only sampled at Hidden Colony in 2013 and 2014). Tricolored heron and snowy egret prey composition were similar ($R = 0.05$, $P = 0.17$; Fig. 3), and were characterized mainly by marsh fishes. The fish species comprising the majority of the biomass within tricolored heron and snowy egret boluses were flagfish (*Jordanella floridae*), golden topminnow (*Fundulus chrysotus*), marsh killifish (*Fundulus confluentus*), and sailfin molly (*Poecilia latipinna*; Table 1). Conversely, prey composition in little blue heron boluses was slightly different from tricolored herons ($R = 0.36$, $P = 0.01$) and snowy egrets ($R = 0.31$, $P = 0.02$; Fig. 3), and was characterized by grass shrimp, sunfish species (*Centrarchidae* spp.), and African jewelfish (Table 1).

We used 102 throw-traps (16 from 8 sites in 2012, 55 from 30 sites in 2013, 31 from 18 sites in 2014) to describe the aquatic prey available within the landscape. Mean fish length available in the landscape was 1.7 ± 0.7 cm over all species, and remained constant among years (1.6 ± 0.6 in 2012, 1.7 ± 0.7 in 2013, 1.8 ± 0.7 in 2014). There was no difference in available aquatic fauna communities among colonies ($R < 0.11$, $P > 0.05$) or years ($R < 0.05$, $P > 0.20$). Crayfish species and grass shrimp comprised 48% of aquatic prey biomass, whereas mosquitofish and bluefin killifish (*Lucania goodei*) were the most common fish species, representing 32% of fish biomass and >50% of fish individuals (Table 1). The prey composition of boluses from all 3 bird species was significantly different than the prey available in the landscape ($R > 0.68$, $P < 0.001$). Additionally, fish present in boluses were, on average, larger than those available in the landscape ($H_3 = 1,510$, $P < 0.001$) for all 3 wading bird species based on Dunn's pairwise multiple comparisons test. In particular, 95% of prey biomass within wading bird boluses were fish >1.9 cm standard length, whereas >70% of fish available in the landscape were <2 cm standard length (Fig. 4).

The consistency in small heron prey composition in boluses across our study years aligned with the consistency in hydrologic patterns and foraging habitat. The years 2012, 2013, and 2014 had similar hydrologic conditions (i.e., steady recession rates and minor to no disturbance by rain reversal events) once small heron colonies reached their peak numbers in active nests at colonies where we conducted bolus sampling. The peak nesting date (determined subjectively as the sampling date in which no. active nests was highest) for small herons at colonies with bolus sampling varied by year (17 Apr 2012, 3 Apr 2013, 26 Apr 2014). However, all dates coincided with water depths receding to approximately 30 cm in the open marshes that were within foraging distance of the colonies (Fig. 2). Additionally, the number of small heron nests across the Everglades system was positively related with availability of >1.9 cm fish within drying pools ($R^2 = 0.70$, $F_{1,8} = 18.6$, $P = 0.003$); fish density within drying pools had no correlation with the number of nests for other wading bird species (Fig. 5). Conversely, the number of small heron nests was not influenced by available foraging habitat ($R^2 = 0.06$, $F_{1,8} = 0.51$, $P = 0.495$). Available foraging habitat was not statistically related to the number of wood stork, great egret (*Ardea alba*), and white ibis nests (Fig. 6; $R^2 = 0.16$, $F_{1,8} = 1.53$, $P = 0.251$; $R^2 = 0.27$, $F_{1,8} = 2.97$, $P = 0.123$; $R^2 = 0.24$, $F_{1,8} = 2.49$, $P = 0.154$, respectively). However, the R^2 values for wood stork, great egret, and white ibis nests suggest a moderate biological effect, potentially limited statistically due to the lack of power from small sample size ($n = 10$ years).

DISCUSSION

The consistency in prey composition we found among years and nesting colonies suggests that tricolored herons and snowy egrets have consistent diets in average hydrological years. In more extreme hydrological years that are unusually dry or wet, small heron diet is also consistent. For example, the 2009 hydrologic year was quite different from our study period, with higher than average water depths at the beginning of the nesting season and an extensive dry-down across the landscape (Botson 2012). During the 2009 nesting season, tricolored herons and snowy egrets nesting in the northern Everglades selected fish >2 cm standard length with sailfin mollies and topminnows (*Fundulus* spp.) making up the majority of prey biomass (Boyle et al. 2012). This diet consistency is further supported by Strong et al. (1997). Similarly, under conditions of high rainfall and minimal recession rates (Botson 2012), tricolored heron and snowy egret diet was still heavily dominated by sailfin mollies and topminnows (Strong et al. 1997). This spatial and temporal diet consistency under widely different hydrological conditions suggests tricolored herons
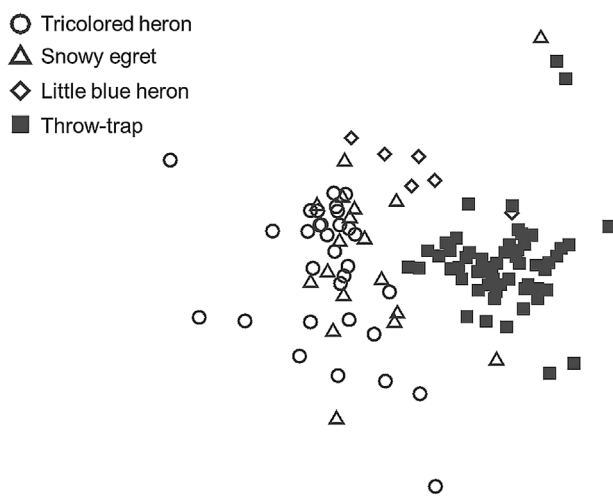

Figure 3. Non-metric multi-dimensional scaling ordination of prey biomass depicting prey composition of tricolored heron, snowy egret, and little blue heron boluses and throw-traps, Everglades, Florida, USA, 2012–2014. Each point is representative of the prey composition within boluses collected at the same colony on the same date, or throw-trap samples collected at the same site on the same day. The proximity of points indicates the level of Bray–Curtis similarity in 2-dimensional space.

Table 1. Percent biomass (% frequency) of prey species within small heron boluses and throw-trap samples, Everglades, Florida, USA, 2012–2014. We also present the number of boluses collected from each bird species or throw-traps to determine prey composition (*n*).

Prey species	Percent biomass (% frequency)			
	Tricolored heron	Snowy egret	Little blue heron	Throw-traps
Invertebrate species				
Insects (*Insecta* spp.)	1 (3)	1 (3)	1 (5)	4 (3)
Grass shrimp	1 (6)	4 (21)	7 (45)	22 (55)
Crayfish		1 (1)	5 (4)	26 (6)
Fish species				
Cyprinidae				
Coastal shiner (*Notropis petersoni*)		<1 (<1)		
Ictaluridae				
Tadpole madtom (*Noturus gyrinus*)			<1 (<1)	<1 (<1)
Esocidae				
Chain pickerel (*Esox niger*)		1 (<1)		
Cyprinodontidae				
Sheepshead minnow (*Cyprinodon variegatus*)	<1 (<1)			
Flagfish	14 (15)	9 (7)	3 (4)	7 (3)
Elassomatidae				
Everglades pygmy sunfish (*Elassoma evergladei*)		1 (2)		2 (2)
Fundulidae				
Golden topminnow	21 (15)	21 (10)	1 (2)	3 (1)
Marsh killifish	16 (9)	10 (4)	10 (5)	3 (<1)
Bluefin killifish	1 (5)	3 (10)	2 (7)	7 (10)
Poeciliidae				
Sailfin molly	26 (17)	15 (7)		4 (2)
Least killifish (*Heterandria formosa*)	<1 (4)	2 (12)	<1 (1)	2 (7)
Mosquitofish	8 (22)	12 (19)	1 (3)	7 (12)
Pike killifish (*Belonesox belizanus*)[a]	1 (1)			<1 (<1)
Centrachidae				
Bluegill (*Lepomis macrochirus*)		7 (1)		<1 (<1)
Spotted sunfish (*Lepomis punctatus*)	2 (1)	6 (1)	11 (6)	6 (<1)
Dollar sunfish (*Lepomis marginatus*)	2 (1)		9 (3)	<1 (<1)
Bluespotted sunfish (*Enneacanthus gloriosus*)		1 (<1)		1 (<1)
Cichlidea				
Black acara (*Cichlasoma bimaculatum*)[a]		1 (<1)	1 (<1)	
Mayan cichlid (*Cichlasoma urophthalmus*)[a]	<1 (<1)	<1 (<1)		
Jaguar cichlid (*Parachromis managuensis*)[a]		<1 (<1)		<1 (<1)
African jewelfish[a]	4 (2)	2 (<1)	37 (13)	
Amphibian species				
Siren (*Siren* spp.)				<1 (<1)
Salamander (*Salamandridae* spp.)				<1 (<1)
Frog (tadpole; *Anura* spp.)			4 (1)	3 (<1)
Frog (adult; *Anura* spp.)		1 (<1)	7 (1)	
n	206	113	36	102

[a] Non-native species.

and snowy egrets are diet specialists, actively selecting for larger marsh fish regardless of foraging conditions and nesting location. Additionally, strong prey selection for fishes is supported by other diet studies of tricolored herons and snowy egrets in Puerto Rico (Miranda and Collazo 1997) and Brazil (Martínez 2010).

Little blue herons have a similar body size and visual foraging strategy but selected considerably more grass shrimp than tricolored herons and snowy egrets. Smith (1997) reported similar proportions of grass shrimp in nestling diets at Lake Okeechobee, 40 km north of the Everglades. Little blue herons also consumed exotic fishes and sunfish to a larger extent than did tricolored herons and snowy egrets. Given the high proportion of grass shrimp available in the Everglades landscape, and a wider diversity of prey taxa consumed, our study suggests little blue herons have a more generalist diet than the other small herons, consuming prey items as they become available. This generalist diet and increased predation on crustaceans is further supported by several studies outside of the Everglades region (Miranda and Collazo 1997, Olmos et al. 2001, Martínez 2010). However, considering our study sampled little blue herons at 1 colony (Hidden Colony) with low nesting numbers, more research will be needed across the Everglades regions to determine the consistency of their diet.

Because of the high proportion of larger marsh fishes in small heron diets, it is not surprising that large fish (>1.9 cm standard length) density within drying pools is directly related to the number of small heron nests. Based on our 10-year dataset of fish densities and nesting numbers, large fish density within drying pools accounted for 70% of the variation in number of small heron nests, demonstrating the importance of these prey species on small heron populations within the Everglades. Additionally, our data set linking prey selection to nesting numbers highlights the importance of genus-specific analyses, and the unclear ecological
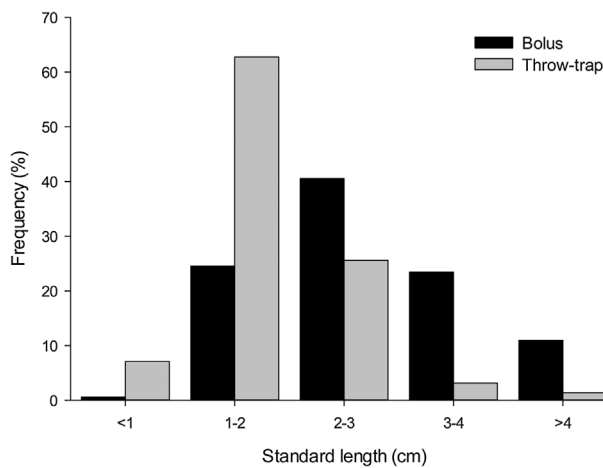
Figure 4. Distribution of fish sizes within small heron (i.e., tricolored heron, snowy egret, little blue heron) boluses and in throw-trap samples, Everglades, Florida, USA, 2012–2014. Numbers above bars denote the percent biomass within each size class.

relationships that may result from grouping sympatric species. For instance, if we pool the number of wading bird nests across species (wood stork, great egret, white ibis, tricolored heron, snowy egret, and little blue heron) and relate that number to a pooled measure of prey availability (i.e., fish, crayfish, shrimp combined), the explanation of annual nest number variation is minimal (see Fig. S1, available online at www.onlinelibrary.wiley.com; $R^2 = 0.19$, $F_{1,8} = 1.87$, $P = 0.209$), despite prey availability being a major limitation for Everglades wading bird populations. The comparatively

minimal effect of large marsh fish density on the number of wood stork, great egret, and white ibis nests leads to 2 possible explanations: either these wading bird species are selecting other food sources, or that these wading bird species are influenced by additional factors in combination with food limitation. Dorn et al. (2011) and Boyle et al. (2012) demonstrated the high proportion of crayfish in white ibis diets, with higher crayfish consumption linked with more successful nesting. Although wood storks were reported to primarily consume flagfish, sailfin mollies, and marsh killifish during the 1970s (Ogden et al. 1976), more recent research indicated selection of large (∼5 cm) sunfish species (Klassen and Gawlik 2014). Similarly, Frederick et al. (1999) reported that great egrets primarily consumed large (∼9 cm) sunfish species, and largemouth bass (*Micropterus salmoides*).

Our study and the work cited above also collectively suggest that prey density is not the only mechanism facilitating prey consumption by wading birds. Even at lower densities, high prey vulnerability can lead to high prey consumption. In the Everglades, fish become more vulnerable to capture as water levels drop and the landscape dries, concentrating fish into isolated, shallow pools. Thus, the more marsh area that dries in a given nesting season, the more foraging habitat becomes available. Birds with larger foraging areas or more efficient flight patterns (e.g., wood storks, great egrets, and white ibises; Bryan et al. 1995, Beerens 2008, Maccarone et al. 2008, Herring and Gawlik 2011), may be more likely to benefit from high availability of foraging habitat across the Everglades landscape than those that forage locally because they have the ability to access a wider range of foraging
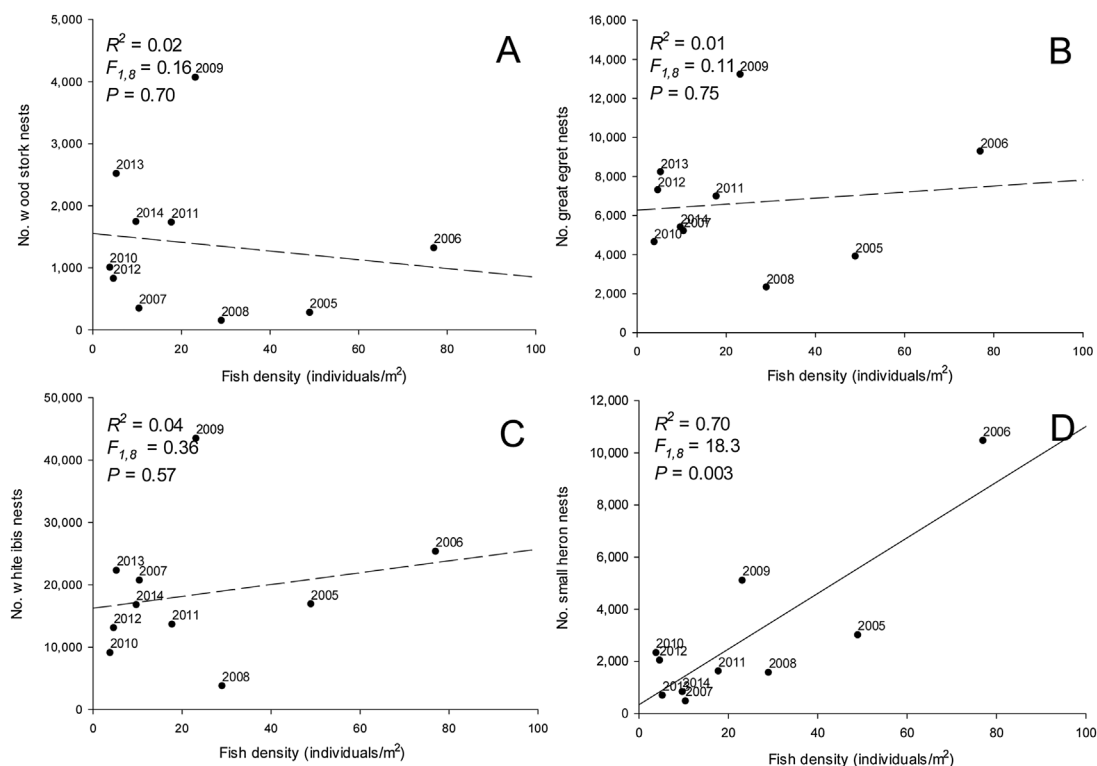

Figure 5. Regression plots between large fish (>19 mm) mean density in throw-traps and number of nests for wood storks (A), great egrets (B), white ibises (C), and small herons (i.e., tricolored herons, snowy egrets, and little blue herons; D) within the Everglades, Florida, USA, 2005–2014.
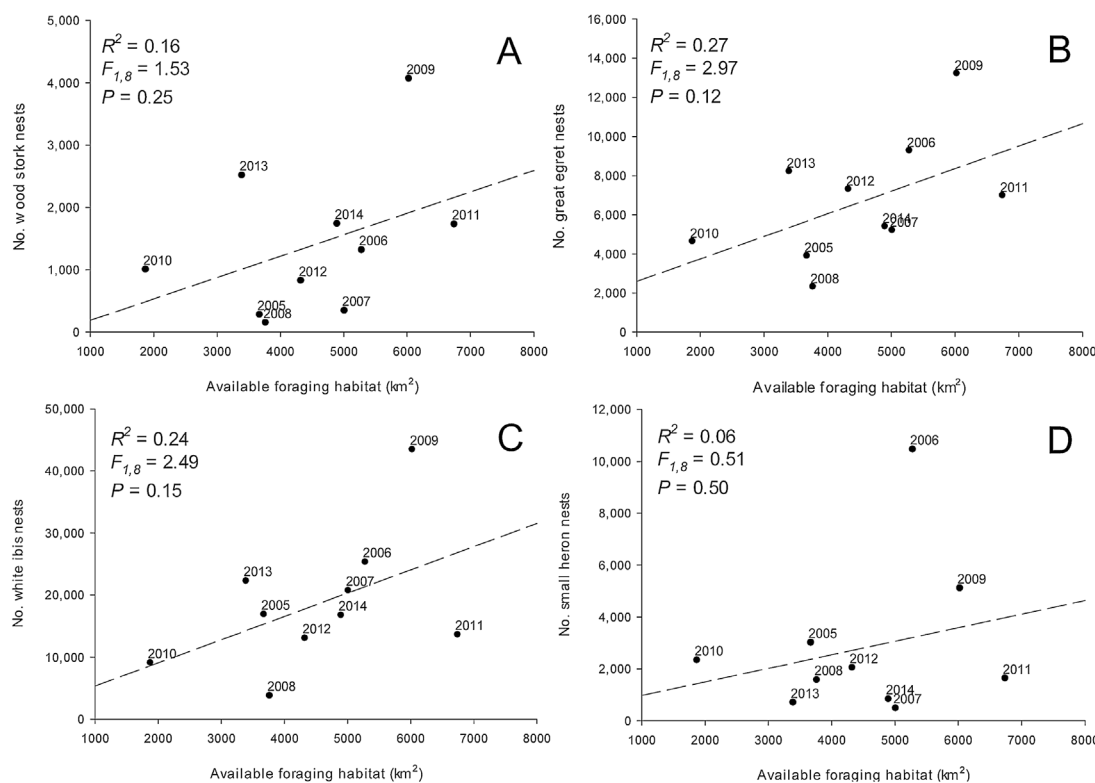
Figure 6. Regression plots of available foraging habitat within a nesting year and number of nests for wood storks (A), great egrets (B), white ibises (C), and small herons (i.e., tricolored herons, snowy egrets, and little blue herons; D) within the Everglades, Florida, USA, 2005–2014.

patches. Because there is a moderate biological effect of foraging habitat availability on the number of wood stork, great egret, and white ibis nests, these species may be partially influenced by habitat availability and local prey densities. Because foraging habitat availability and number of small heron nests were not related, small herons are likely more dependent on local quality of prey resources, than quantity of available foraging habitat.

The different relationships among wading birds regarding prey selection and habitat availability demonstrate that several strategies are employed by wading birds to cope with limited food availability within the same ecosystem. The specialization of small herons on a subset of marsh fishes may look restrictive at first, but small herons have the phenological flexibility to adjust nest initiation to times of optimal local foraging. Small herons need approximately 50 days of high prey availability to support a brood from hatching to fledging (Erwin et al. 1996, Frederick 2013). Considering dry season conditions last 5–6 months, small herons can delay nesting until conditions are most favorable and still have enough time to rear a brood before the onset of the wet season and decreasing prey availability. As such, wading birds with shorter nesting cycles have the ability to select the spatial resources and temporal window that would best support nesting, increasing the likelihood that only locally available prey are needed within the nesting period. Conversely, wading birds with long nesting cycles are likely to rely on foraging habitat that shifts in space over time. For instance, the wood stork has a long nesting cycle requiring

approximately 100 days to raise a brood to fledgling age (Kahl 1964). As water levels recede throughout the dry season, local foraging patches may dry and become devoid of prey before the end of the nesting cycle, thus increasing the need for alternate foraging locations. Because the Everglades is composed of different hydroperiod regions, suitable foraging locations may emerge tens of kilometers away from local nesting areas, requiring wood storks to use a greater area to sustain nesting activities. Therefore, wood storks rely on landscape dynamics to produce high prey concentrations and continual prey throughout the dry season. Despite the temporal nesting constraints for larger birds, wood storks and great egrets may be able to compensate by consuming different prey species from a wider range of foraging locations and wetland types within and outside the natural marsh.

MANAGEMENT IMPLICATIONS

There is good evidence that Everglades wading bird reproduction is influenced by prey availability, but specific characteristics relating to prey selection, foraging strategies, and nesting strategies differ on a species-by-species basis. Species with a long nesting cycle that must be completed within a narrow window of receding and low water depths are more likely to experience nest failure than species with the same hydrologic requirements but with a shorter nesting cycle. Thus, length of nesting cycle is a characteristic to consider in addition to habitat sensitivity (Frederick and Ogden 2003) when choosing an indicator species for tracking

ecosystem restoration and management. In reference to Everglades management, if water depths and recession rates are adequate for foraging wood storks, an indicator species with a long nesting cycle, then water depths and recession rates will also be adequate for small herons with shorter nesting cycles. Additionally, although extended landscape-wide dry-downs create large areas of foraging habitat across the nesting season, yearly dry-downs of the system can inhibit the production and quality of aquatic prey items. Fish species, in particular, require months of inundation to reproduce and grow to a size that is most selected by foraging wading birds. Therefore, if the objective is to encourage large nesting events, Everglades management plans should balance maintaining and drying long hydroperiod areas to increase the abundance and availability of larger-bodied fishes. Although food-limitations may be a common restriction on several wildlife populations, management strategies that alter food abundance or foraging habitat must take into consideration the degree to which each factor affects a particular species of interest. Additionally, the aspect in which species have the most flexibility in terms of diet and reproduction is important for predicting species responses to management regimes or environmental change.

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