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Author(s): Robin A. Boyle, Nathan J. Dorn and Mark I. Cook
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Nestling Diet of Three Sympatrically Nesting Wading Bird Species in the Florida Everglades

Robin A. Boyle[1], Nathan J. Dorn[1,*] and Mark I. Cook[2]

[1]Department of Biological Sciences, Florida Atlantic University, 3200 College Ave, Davie, FL, 33314, USA

[2]South Florida Water Management District, 3301 Gun Club Rd., West Palm Beach, FL, 33406, USA

[*]Corresponding author, E-mail: ndorn1@fau.edu

Abstract.—Wading bird (Ciconiiformes) nesting success is influenced by the availability of aquatic prey, but principle prey may differ among species. During an excellent nesting year (2009) 118 boluses were collected from nestlings of three species, White Ibis (*Eudocimus albus*), Tricolored Heron (*Egretta tricolor*) and Snowy Egret (*Egretta thula*) in a mixed colony in the northern Everglades. Although these species have similar foraging depths and foraging flight distances from nesting colonies, crayfish dominated the ibis boluses while small-bodied fishes dominated egret boluses. Fish prey species composition in Snowy Egret and Tricolored Heron boluses did not differ. Compared to available fish species from nearby wetlands, the *Egretta* spp. did not exhibit taxonomic selectivity but did feed selectively on larger (2-4 cm standard length) fish. Whether restoration activities in the Everglades, including hydroperiod lengthening, will simultaneously enhance prey for both invertivores like White Ibis and piscivores, such as the egrets, remains an open question. *Received 31 May 2011, accepted 27 October 2011.*

Key words.—avian diets, hydrological restoration, prey availability, wetland.

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Understanding which prey species are critical to waterbird reproductive success and how prey production and prey availability are influenced by environmental variation is essential for the effective management and restoration of waterbird populations (Gawlik 2002; Ma *et al.* 2010). Several groups of wading birds forage sympatrically in mixed species aggregations (Frederick and Collopy 1989; Smith 1995; Crozier and Gawlik 2003) and generally feed on similar types of prey, but the level of taxonomic resolution (e.g. species vs. family-level classification) of prey may determine whether differences in diet composition among waders are observed (Miranda and Collazo 1997; Martínez 2004. 2010). In the Everglades, nesting populations of wading birds (Ciconiiform) are being monitored for their response to restoration activities (e.g. hydroperiod lengthening, wetland reconnections) and hydrological variation (Gawlik and Crozier 2003; Frederick *et al.* 2009).

The Snowy Egret (*Egreta thulla*), Tricolored Heron (*Egretta tricolor*) and White Ibis (*Eudocimus albus*) are three species that share similar ideal foraging depths (Frederick 1997; Parsons and Master 2000; Gawlik 2002) and have been observed foraging in mixed species flocks (Smith 1995; Gawlik 2002; M. Cook, unpublished observations in 2009). On the basis of foraging considerations, the breeding numbers of these species may be expected to respond to hydrological variation in similar ways because prey access during the nesting season is largely determined by species-specific foraging depth limits (Gawlik 2002; Ma *et al.* 2010). While these species have similar foraging depth restrictions, previous diet studies suggest that prey use differs: the two egrets are piscivorous while the ibis have variable diets that often include crayfish (Smith 1997; Parsons and Master 2000; Heath *et al.* 2009; Dorn *et al.* 2011). The degree of the diet differences is not necessarily straightforward, as Gawlik (2002) observed ibis foraging on fish alongside egrets in impounded wetlands and diet studies suggest that nesting ibis will seasonally shift foraging towards fish when fish become highly concentrated (Kushlan 1979; Dorn *et al.* 2011). While there have been several studies looking at the dietary niche relationships of co-occurring Tricolored Herons and Snowy Egrets (Miranda and Collazo 1997; Strong *et al.* 1997; Smith 1997; Post 2008; Martínez 2010), none compare their prey use to sympatrically nesting White Ibis.

In this paper we compared the prey use of all three species from the same mixed-species colony in the northern Everglades during the 2009 nesting season; a year considered the best nesting season since the 1940's (Cook and Kobza 2009). Also, we compared the fish composition provisioned to egret nestlings to the composition of fish available in the surrounding wetlands to test for evidence of selective foraging.

METHODS

Arthur R. Marshall Loxahatchee National Wildlife Refuge (Loxahatchee NWR) is located in Palm Beach County, Florida. Boluses were collected from one nesting colony in Loxahatchee NWR, New Colony 4 (NC 4). During the 2009 nesting season 9,300 White Ibis nested in Loxahatchee NWR and ~4,100 of those nests were located at NC 4. There were approximately 600 Tricolored Heron and Snowy Egret nests (both species combined) within the sampled area of the colony.

We collected 86 White Ibis, twelve Tricolored Heron, and 20 Snowy Egret boluses on 1 May and 8 May 2009. All boluses were collected from the ground after voluntary regurgitation by the nestlings between 1000 and 1200 hours. These dates came near the end of the nesting season when surrounding water levels were near their lowest for the season (Boyle 2010).

The contents of each bolus were searched twice (in order to effectively remove all prey) in the lab and all identifiable prey items or parts found were collected, counted and measured. For most prey items, excluding garbage (rotting chicken pieces or dog food) and terrestrial vertebrates (e.g. reptiles), we used length-length and length-mass regressions (see Dorn *et al.* 2011) to calculate dry mass. Other prey items were dried at 55°C to a constant mass and weighed to determine dry mass.

White Ibis boluses contain several categories of aquatic and terrestrial food items and we compared all three bird species with a coarse-scale prey composition analysis (similar to Dorn *et al.* 2011). We calculated biomasses of prey items grouped into eight distinct categories; crayfish (*Procambarus fallax*), large-bodied fish (sunfish; *Lepomis* spp., *Enneacanthus gloriosus*, and *Micropterus salmoides*), small-bodied fish (e.g. *Gambusia holbrooki, Jordanella floridae, Poecilia latippina*, *Lucania goodie*), grass shrimp (*Palaemonetes paludosus*), aquatic insects, terrestrial insects, garbage (decomposing chicken and dog food) and other vertebrates. These groupings are based on habitat type (terrestrial vs. aquatic), adult size and taxonomy (i.e. life history and/or functional relationships with water depths; Kushlan 1979).

After the coarse-scale analysis, we compared fish composition of the two egrets with finer taxonomic resolution. A similar level of resolution was not possible for ibis, but was judged unnecessary after the coarse analysis. For comparisons of fish taxonomic composition, all prey were identified to species except for *Lepomis* spp. and *Fundulus* spp. After taxonomic analysis, we compared prey composition by fish length; fish were categorized by 1-cm standard length (SL) classes (0-1, 1-2, 2-3, 3-4, >4).

To compare taxonomic prey composition and the size structure of fish eaten by egrets, we used graphical and statistical nonparametric multivariate techniques outlined by Clarke and Warwick (2001, PRIMER v6). The data were multivariate (e.g. biomasses of several prey types) and parametric multivariate analyses were impractical due to the large number of zeros. For the comparisons of all three species, we calculated biomasses of each prey type in each bolus and square-root transformed the data before calculation of Bray-Curtis similarity. Square-root transformation of abundances was used to down-weight the influence of overly heavy or exceptionally dominant prey. Using the pair-wise similarity matrix, bolus-bolus similarity was visually inspected with NMDS (non-metric multi-dimensional scaling) plots, and ANOSIM tests (a non-parametric permutation procedure that randomly re-identifies the boluses) were used to determine if there were multivariate differences in prey composition between species. If statistical differences ($P < 0.05$) were detected we used SIMPER (a similarity percentage analysis) to determine which prey types were most responsible for the dissimilarity between species. Finally, the mean standard length of all fish in each bolus was calculated and the means were compared directly with ANOVA (SAS® V 9.2; SAS Institute).

To determine whether the egrets were selecting for certain species or size classes of fish, we compared the composition and size structure (by length) of fish consumed to the composition and size structure of fish available in the surrounding wetland. Data on available fish species composition and size-structure were taken from five 1-m^2 throw trap samples of fish collected in Loxahatchee NWR from 24 April to 6 May 2009; dates coincident to or just prior to bolus collection dates (D. Gawlik, unpublished data). Throw trap sample sites included areas within twelve km of the colony with water depths appropriate for wading bird foraging; distances between traps ranged from 0.3-9.6 km, traps were conducted in the mornings and three of the five were taken from sites where wading birds were actively foraging. The 1-m^2 throw trap is a box with mesh sides that encloses small animals in the water column; it is thrown into the marsh from 2-3 m away and aquatic animals are removed with nets. The fish taxonomic and size-class categories used in these analyses were the same as explained above. Because throw traps and boluses contain different absolute numbers of fish these analyses were run on proportions. The same multivariate techniques were used for these comparisons and we also conducted a chi-square goodness-of-fit test to compare observed fish sizes to expected sizes under a null-hypothesis of non-selective foraging.

RESULTS

The contents of White Ibis boluses were significantly different from those of both egrets (ANOSIM R-values > 0.56; P-values < 0.01). The majority of the dissimilarity was caused by crayfish dominating the boluses of White Ibis and small-bodied fishes dominating the boluses of Tricolored Herons and Snowy Egrets (Table 1, Figs. 1 and 2). No prey use differences were found between Tricolored Herons and Snowy Egrets (R = 0.14; P = 0.58). Three Snowy Egret boluses contained crayfish, but crayfish were absent from Tricolored Heron boluses. At least one fish was present in each of the twelve of the Tricolored Heron boluses and in 95% (19 of 20) of the Snowy Egret boluses.

The fish species that contributed most to the overall biomass for both Tricolored Herons and Snowy Egrets were Sailfin Mollies and *Fundulus spp.* (Table 2). The two egret species ate similar fish species (R = 0.04; P = 0.23, Fig. 3) and sizes (R = 0.05; P = 0.21). The mean fish length (cm) for Tricolored Herons (mean ± SD; 2.6 ± 0.8) and Snowy Egrets (2.6 ± 0.6) did not differ ($F_{1,29}$ = 0.05, P = 0.98).

The fish species composition in the throw traps was not different from the composition in the boluses of the egrets (R = 0.06, P = 0.29). However, egrets selectively fed on large fish (R = 0.28, P = 0.03; χ^2 = 206.10, P < 0.001; Fig. 4A). In particular, fish < 2 cm SL were underrepresented in boluses relative to the wetland, while fish >2 cm were overrepresented (Fig. 4B).

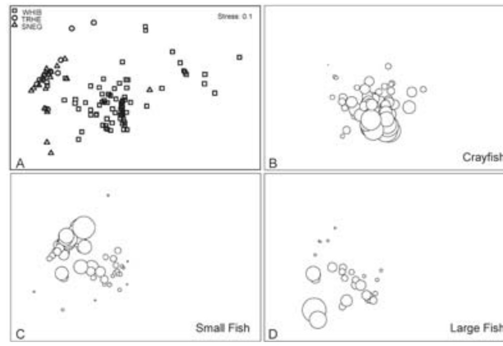

Figure 1. Prey composition of White Ibis (WHIB), Tricolored Heron (TRHE) and Snowy Egret (SNEG) boluses illustrated by NMDS ordination of prey biomasses. A. Each point is a bolus and the proximity of points indicates the level of Bray-Curtis similarity in 2D space. B through D. Biomasses of three of the eight 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. Five other prey types are not shown because they were relatively less important in differentiating between species. The stress indicates the degree of distortion in the two-dimensional plot relative to the actual multidimensional similarity between points.

DISCUSSION

Wading bird nesting numbers in the Everglades in 2009 were considered excellent; total nesting system-wide exceeded 73,000, and with more than 43,000 ibis nests this was considered an exceptional year by historical records (Frederick *et al.* 2009). During this excellent nesting year the prey use

Table 1. Frequency of prey groups (% of boluses containing a prey group) in boluses of nestlings of three species of wading birds in the Everglades during the 2009 nesting season. N = number of boluses included in the collection.

	Frequency of use (%)		
Prey Category	White Ibis	Tricolored Heron	Snowy Egret
Crayfish	85	0	15
Small-bodied fishes	33	100	90
Large-bodied fishes	25	25	35
Shrimp	12	25	40
Aquatic Insects	39	17	10
Terrestrial insects	24	17	10
Garbage	14	0	5
Other Vertebrates	1	8	0
N	85	12	20

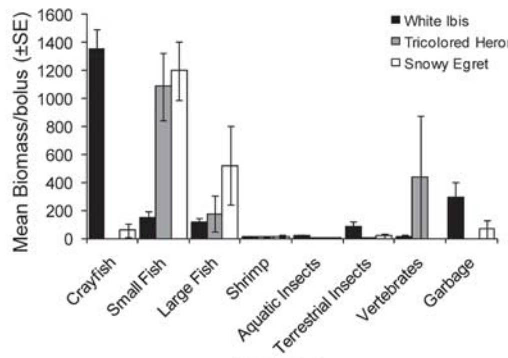

Figure 2. Mean biomass (± SE) of each prey group per bolus from White Ibis (n = 85), Tricolored Heron (n = 12) and Snowy Egret (n = 20) nestlings.

Table 2. Percent biomass of each prey species consumed by Tricolored Heron and Snowy Egret nestlings during the 2009 nesting season. N = number of boluses included in the collection.

Prey species	Percent Biomass	
	Tricolored Heron	Snowy Egret
Lepomis + Enneacanthus spp.	4	30
Micropterus salmoides	10	0
Poecilia latipinna	24	22
Gambusia affinis	16	4
Jordanella floridae	6	18
Lucania goodei	3	3
Heterandria formosa	4	2
Fundulus spp.	34	21
N	12	20

of nesting White Ibis was almost completely different from that of sympatrically nesting small egrets in Loxahatchee NWR (northern Everglades). The generality of this difference is limited by the single year and the short time frame of the study (eight days), but took place while water levels were at their lowest in 2009 and prey should have been most concentrated. Other diet studies of the ibis in this wetland (nesting seasons from 2006-2009) have given similar results (Boyle 2010) suggesting the characterization of the ibis diet appears to be fairly robust. The egret prey use was similar to prey use of these species from an older study conducted in the southern reaches of the Everglades (Strong *et al.* 1997). Whether the ibis and egrets chose different foraging locations on the landscape or whether they fed side-by-side is unknown, but egrets and

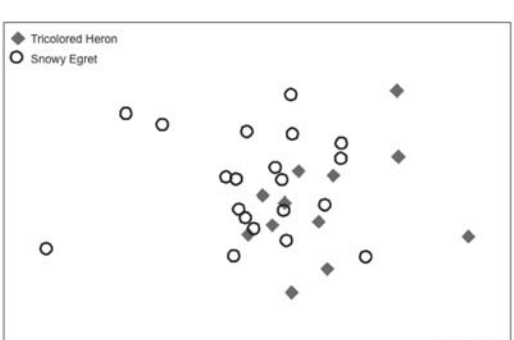

Figure 3. Fish composition of nestling Tricolored Heron and Snowy Egret boluses in 2009 illustrated by NMDS ordination of fish biomasses.

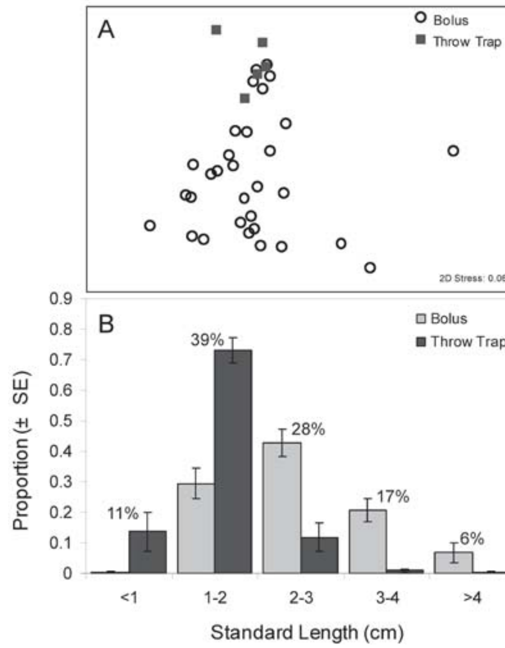

Figure 4. A. NMDS ordination of fish size class composition in nestling Tricolored Heron and Snowy Egret boluses and in the throw trap samples. Each point is either a bolus or a throw trap sample. B. Proportional contribution (mean [± SE], n = five throw trap samples, n = 32 boluses) of different fish size classes to boluses and throw trap samples (available fish). The percentages above each pair of bars indicates the contribution of each size-class contrast to the multivariate dissimilarity between groups (bolus vs. throw trap) as calculated from the SIMPER analysis.

ibis were observed foraging in mixed groups in 2009 (M. Cook, unpublished data).

While these species focused on different prey, it is not clear that fish and crayfish availability will both be enhanced by hydrological restoration (e.g. hydroperiod lengthening). Generally, long hydroperiods support high fish densities while moderate hydroperiods and water depths may be best for crayfish (Dorn and Trexler 2007; Trexler and Goss 2009). Nevertheless, the fact that all three species successfully fledged in 2009 in Loxahatchee NWR suggests that thousands of invertivorous ibis and some hundreds of piscivores egrets could be simultaneously supported with the same hydrological conditions.

The prey of the Snowy Egrets and Tricolored Herons were effectively indistinguishable in this study. Martínez (2010) studied the dietary niche relationships of these species in Brazil and found prey use differences; although the two species ate similar-sized prey, Tricolored Herons ate more shrimp (Penaeidae and Alpheidae), *Gobionellus* spp., and saltwater prey, while Snowy Egrets ate mostly mollies (*Poecilia* spp.). Given the similarity in breeding season prey use between these two species in the Everglades, other details of the ecology of the animals or the ecosystem must allow them to coexist/co-occur on the landscape. Strong *et al.* (1997) suggested differences in habitat use limited interference between these species. Habitat use differences or avoidance through spacing (Smith 1995; Tricolored Herons are more solitary) are possible in Loxhatchee NWR as well, but habitat use was not assessed in 2009. Exploitative competition between wading birds for prey fish is probably not important in these wetlands; fish production and availability are believed to be primarily driven by drying events (Trexler and Goss 2009) and recession (Gawlik 2002) rather than by consumer pressure from wading birds (i.e. weak dynamic feedbacks between predator consumption and prey availability).

Egrets showed no clear preference towards particular fish species, but they clearly preferred larger fishes. The lack of species-level selectivity was surprising as most Least Killifish (*Heterandria formosa*) are < 2 cm and they were abundant in several throw trap samples; the lack of significant avoidance may have been affected by the small number of throw trap samples. Small egrets appear to select fish according to their length regardless of species-level differences in fish behavior or morphology

White Ibis, Tricolored Herons, and Snowy Egrets are often found nesting and foraging in similar wetland locations in south Florida, but the principle prey of White Ibis (crayfish) was different from the prey of Tricolored Herons and Snowy Egrets (fish) when nesting sympatrically with good hydrological conditions in the northern Everglades in 2009. Based on these observed differences, future research should focus on the consistency of these results in space and time, as well as the hydrological mechanisms making both prey types available.

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