



Aquatic prey switching and urban foraging by the White Ibis *Eudocimus albus* are determined by wetland hydrological conditions

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Prey availability is known to limit reproduction of some species of nesting birds, but identifying the primary prey types of a species with a flexible diet can be challenging. For the White Ibis *Eudocimus albus*, a tactile feeding, medium-sized wading bird, nestling prey composition is suggested to depend on landscape water depths/availability of foraging habitat at the time of nesting and on historical drying events affecting prey production. We collected and compared inter- and intra-annual diet variation of White Ibis chicks reared in the Everglades over two years that were independently identified as being relatively good (2006) and poor (2007) nesting seasons. We collected 127 nestling boluses and analysed the temporal variation in biomass of eight functional prey groups using multivariate techniques. The boluses from 2006 in the central Everglades were dominated by fish, but in 2007, after fish had been reduced by the previous year of drying, the boluses from the same region were more variable and dominated by garbage (i.e. scavenging). Analysis of five different collections taken from a different colony in the northern Everglades indicated that boluses were characterized by crayfish and had fewer fish or less garbage when landscape water depths were relatively higher and more preferred habitat was available. At lower landscape water depths in 2007 the bolus composition shifted away from crayfish towards small fish and urban food (terrestrial insects and garbage). Our results support the suggestion of depth-dependent diets; prey composition depends on the current landscape water levels around the colonies, and also suggests that previous drying events can lead to increased reliance on alternative food sources. White Ibis partially compensated for unavailable aquatic prey with alternative urban foods, but their nesting success appears to have suffered.

Keywords: crayfish, diet flexibility, fish, prey availability, *Procambarus fallax*, refuse, roaches, wading birds.

Food availability for breeding birds is fundamental to somatic development, functioning and maintenance, and thereby exerts considerable influence on reproductive and population processes (e.g. Martin 1987, Byholm & Kekkonen 2008). Food

(hereafter prey) availability is a function of prey abundance and vulnerability, and these in turn are influenced by multiple characteristics of the environment, predator traits and prey characteristics (Gawlik 2002). It follows that the foraging strategy adopted by a bird will be influenced by interactions among characteristics of the prey types, prey availability within and among landscape patches, and fluctuating environmental conditions. While foraging strategies have been considered at the theoretical level in simple settings (Charnov 1976,

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Stephens & Krebs 1986), many birds face temporally variable prey abundance or patch quality (Naef-Daenzer *et al.* 2000, van Gils *et al.* 2006).

Success for some avian species depends on the synchrony between juvenile stages of the predator and developmental stages of particular prey (Naef-Daenzer *et al.* 2000, Pearce-Higgins & Yalden 2004), but many species of nesting wading birds are faced with hydrologically dependent prey availability (Gawlik 2002) that may result in variable diets within or between years. Wetland hydro-patterns are often actively managed for wetland birds in restoration initiatives, but principal prey types and their availability relative to hydrological variation are not always known (Trexler & Goss 2009, Ma *et al.* 2010). Finally, the relationship between prey use and breeding success of some opportunistic avian species living near urban centres or landfills has been complicated by the use of anthropogenic food sources (Belant *et al.* 1998, Annett & Pierotti 1999).

The Florida Everglades is an expansive, flat, hydrologically pulsed, oligotrophic wetland system with a rich assemblage of colonial wading bird species, including herons (Ardeidae), ibises (Threskiornithidae) and the Wood Stork *Mycteria americana* nesting in its marshes. The birds typically nest during the dry season (December–May) as water levels recede and prey become concentrated into smaller, shallower pools. During this period the available foraging locations change daily or weekly depending on recession rates and hydrological reversal events (e.g. local rainfall or water management). The substantial decline of Everglades wading bird nesting populations in the 20th century (Crozier & Gawlik 2003) is thought to be a consequence of hydrological alterations that reduced both the production and the seasonal concentrations of wetland fish and invertebrates (Gawlik 2002, Frederick *et al.* 2009). The White Ibis *Eudocimus albus* is the numerically dominant species in this assemblage and is a focal species in the restoration of the ecosystem (Crozier & Gawlik 2003, Frederick *et al.* 2009).

Ibises (Threskiornithinae) are probing foragers with broad diets (Bildstein *et al.* 1990, Soave *et al.* 2006, Heath *et al.* 2009), and whereas some studies suggest White Ibis feed primarily on freshwater crayfish or other crustaceans during nesting (e.g. Kushlan 1979, Bildstein *et al.* 1990), other observations clearly indicate that White Ibis will also feed on fish (Kushlan 1979, Gawlik 2002, Dorn

et al. 2008). Kushlan (1979) conducted a diet study in the Everglades in the early 1970s and suggested different aquatic prey were targeted at different landscape water depths, but he did not present any evidence suggesting that nesting ibis left the freshwater marsh to feed on non-aquatic prey. Since the time of Kushlan's study, the counties of southeast Florida (West Palm Beach, Broward and Miami-Dade) have collectively grown by more than 2.5 million residents and White Ibis can be observed feeding on soil arthropods in urban and suburban lawns during most seasons of the year (Heath *et al.* 2009, N.J. Dorn pers. obs.). The degree to which White Ibis on the wildland–urban interface currently use non-aquatic foods during nesting is not known and the principal prey types used by ibis to support their nesting colonies is still not clear, although aquatic prey are clearly important (Heath *et al.* 2009).

At least two aspects of hydrological variation can affect aquatic prey use patterns for wading birds. First, water depth in the year of nesting can affect prey availability by concentrating fish locally and making different parts of the wetland available for foraging (Kushlan 1979, Gawlik 2002). Secondly, extremely low water depths in the year(s) prior to nesting (i.e. drying events) can reduce the standing stocks of prey fish (Trexler *et al.* 2005, Trexler & Goss 2009).

We examine the foraging strategies of nesting White Ibis by quantifying and analysing the prey use variation of chicks over two years (Table 1, Fig. 1). The two years varied in hydrological conditions and nesting success of the White Ibis (Herring *et al.* 2010, 2011). Using data from colonies in the central Everglades (hereafter WCA 3A) and the northern Everglades (Arthur R. Marshall Loxahatchee National Wildlife Refuge, hereafter Lox) we looked for evidence of water depth-dependent diets (Kushlan 1979) and examined the correspondence between prey composition and nesting success between years.

METHODS

Field collections

We collected 127 boluses from White Ibis chicks in 2006 ($n = 23$) and 2007 ($n = 104$) in the major colonies of the central and northern Everglades (Fig. 1, Table 1). In 2006 we collected 11 boluses from the Alley North colony (26°11'N, 80°31'W;

Table 1. Bolus numbers, dates and water depths around the nesting colonies for White Ibis nestling bolus collections made in 2006 and 2007. The WCA 3A collections came from two different colonies that are separated by 7 km (Alley North and 6th Bridge) in the 2 years because the major colony shifted south in 2007. All Loxahatchee (Lox) samples came from the same colony used by the Ibis in both years.

Collection (area, year, group)	<i>n</i>	Bolus collection dates	Mean water depth ^a (cm) ± sd	Total available habitat (km ²) ^b	Per-capita habitat (km ² /per nest)
WCA 3A 2006	11	21 April–2 May	0.6 ± 26.1	328	0.024
WCA 3A 2007	20	4–5 May	−1.6 ± 23.9	230	0.022
Lox 2006	12	4–19 May	−0.2 ± 10.5	391	0.081
Lox 2007a	6	17–30 April	−7.9 ± 13.6	309	0.043
Lox 2007b	33	10–11 May	−18.8 ± 12.3	180	0.025
Lox 2007c	24	15 May	−20.3 ± 15.2	173	0.024
Lox 2007d	21	18 May	−8.7 ± 10.0	307	0.043

^aThe means were calculated using 2881–4163 equally spaced point estimates of wetland depth within 15 km of each colony. Depth measurements came from the EDEN model (Everglades Depth Estimation Network, US Geological Survey). Weighted means were calculated for collections with multiple dates.

^bThe available habitat was defined as the amount of preferred foraging habitat within 15 km of the colony; locations 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.

13 500 nests) in WCA 3A and 12 from New Colony 3 in Lox (26°31'N, 80°17'W; 4800 nests, Fig. 1). In 2007, we increased collection efforts, especially in Lox. In 2007, we collected 21 boluses from WCA 3A, but the major colony (6th Bridge colony; 26°07'N, 80°32'W, Fig. 1) was smaller (10 661 nests) and shifted to the south by 7 km because the entire Everglades dried out faster in 2007; there was no nesting at the Alley North Colony because the surrounding marsh was too dry during the breeding season. In Lox we collected 85 boluses over several dates from 17 April to 18 May 2007 at New Colony 4 (7207 nests); this was effectively the same colony location as in 2006 and is treated as equivalent in this paper. The location of the colony moved slightly between years (1.6 km), but because White Ibis forage on average about 10–12 km from a colony (Beerens 2008) both sites encompassed the same general foraging habitat. The two colonies between the water management areas were separated by at least 45 km so that overlap in feeding areas was unlikely to have been based on foraging flight distances (71% of 403 foraging flight distances were < 15 km in both years and < 2% were > 30 km; Beerens 2008, unpubl. data).

About 80% of boluses were voluntarily regurgitated by chicks from 15 to 40 days old and immediately picked up from the ground, and the rest were induced by massaging the oesophagus of hand-collected chicks. We assume that boluses were similar between those that were voluntarily provided and those that were massaged out of the

oesophagus. Almost all collections were made before 10:00 h and collection activity was similar between the 2 years. White Ibis boluses are regurgitations of partially digested food items fed to the chicks from the morning's foraging that include some whole prey and lots of prey parts. All boluses were placed on ice in the field and stored in 80% ethanol after transport to the laboratory.

In the laboratory, the bolus contents were poured through a 0.63-µm mesh and washed. The contents were sorted and picked under a magnifying lamp. We searched each sample twice and all identifiable prey items found were collected, counted and placed in vials. We followed the methods in Dorn *et al.* (2008) for counting and measuring crayfish in these boluses using rostrums and chelae pairs. For all animal prey except some of the large vertebrates (e.g. snakes) and other rare items we identified prey parts, measured them and used length–length and length–weight regressions to calculate dry biomass of each prey item. Further methodological and regression details can be found in Supporting Information Appendix S1. Tissue and bone remains of other vertebrates were found in a few boluses and represented large biomasses in some cases; most could not be easily measured or identified to a fine taxonomic level so we dried and weighed the remaining parts (55 °C for 24 h or to a constant weight) to estimate their biomasses. Urban refuse (*n* = 40 boluses) such as dog food, chicken meat and unidentified tissues (white gelatinous texture, not found with any other animal remains, i.e. no

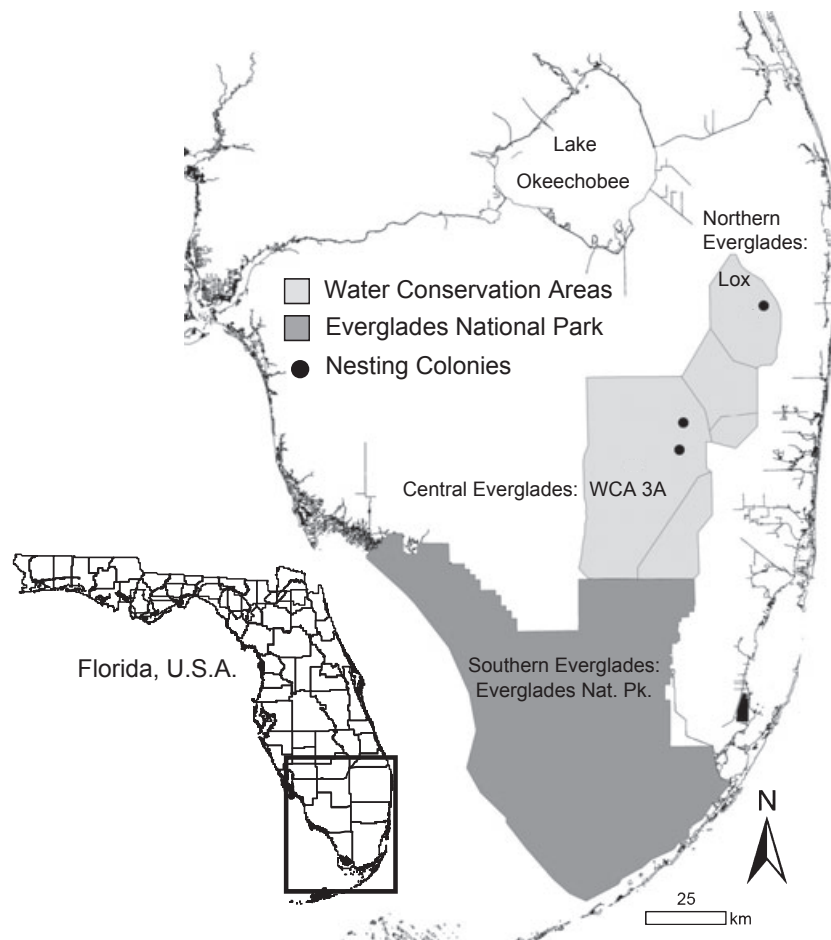


Figure 1. Map of the study area including the primary management areas and nesting colony locations in 2006 and 2007. The shaded portions of the map show the current extent of the Florida Everglades. In WCA 3A, the northern colony is Alley North Colony (2006) and the southern colony is 6th Bridge (2007). Lox indicates the location of the Arthur R. Marshall Loxahatchee National Wildlife Refuge, also known as WCA 1. The areas to the east are urban, suburban and agricultural parts of West Palm Beach and Broward counties.

scales, feathers or bones, but in one case found with remains of terrestrial insects, $n = 4$ boluses) were separated, dried and weighed. For analyses we aggregated the biomasses of different prey items into eight prey categories. Prey categories were based on major habitat types (e.g. aquatic/wetland vs. terrestrial), prey size and taxonomy. The categories were crayfish (the 10 identifiable crayfish of a total of almost 200 were all *Procambarus fallax*), small fishes (several species with relatively small adult sizes: *Gambusia holbrooki*, *Jordanella floridae*, *Poecilia latipinna* and killifish), sunfish (i.e. all centrarchids, but species could only rarely be discerned), grass shrimp (*Palaemonetes paludosus*), aquatic insects, terrestrial insects, garbage (primarily dog food and meat scraps), and other vertebrate prey.

Hydrological conditions for foraging

White Ibis commonly feed in water depths from 5 to 10 cm (Heath *et al.* 2009), but for individual chicks sampled in this study the exact foraging locations of their parents were not known. Instead, we quantified the wetness or dryness of the landscape consistent with Kushlan's (1979) observations using mean water depths and the amount of preferred foraging habitat within 15 km of the colonies (Beerens 2008). Deeper water around the colonies indicates that more of the shorter hydroperiod (i.e. higher elevation, inundation periods < 1 year) wetlands are flooded and the fish should be more dispersed. Mean wetland depths and area of preferred foraging habitat were tightly correlated for the single colony location in Lox

(Table 1) and this is to be expected in this flat wetland landscape. We obtained depth data from the Everglades Depth Estimation Network (hereafter EDEN; <http://sofia.usgs.gov/eden/>), which is a model of water surface for all wetland locations in the Everglades based on interpolation from a network of water-monitoring gauges. When combined with an elevation map (0.4-km grid) the model provides water depths relative to sediment surface for all of the Everglades at the scale of 16-ha grid cells. Because there is microtopographic relief at the scale of 1–100 m (i.e. alligator holes, tree islands, ridges, etc.) the EDEN depth values do not indicate the depth of all possible points within a grid cell; negative EDEN water depths do not necessarily indicate that every pond and slough is dry within a cell. Nevertheless, the EDEN water depths provided sufficient resolution to identify preferred foraging depths in a contemporaneous study of radiotracked adult ibis (Beerens 2008) in these colonies. The spatially extensive coverage of the depth estimates should provide good estimates of relative water depth and amount of available foraging habitat for each collection. We calculated the mean and standard deviation of depths of all wetland cells within 15 km of each colony for each bolus collection date (2881–4163 cells per colony). When boluses from several dates were lumped together, we weighted the average depths by the number of boluses collected on each date. We also calculated the amount of preferred foraging habitat using the resource selection results reported by Beerens (2008). In 2006, when foraging conditions were better system-wide, the adult ibis showed positive selection for cells with EDEN water depths from –16 to 15 cm. The selected depths in 2007 were more variable (–25 to 25 cm), but were still centred near 0 cm as in 2006 (Beerens 2008). To facilitate direct comparisons of available habitat between years, we quantified the amount of preferred habitat (km²) using the 2006 depth range results. We also report the per-capita availability of preferred wetland habitat (km² per nest) because the colony sizes varied in space and time (Table 1).

Data analysis

Individual boluses were treated as independent measures of prey use in our analyses. All boluses collected on a given date came from different chicks and because there can be high variation in bolus–bolus composition within and between

collections at the same colony, the assumption of independence would seem to be justified; different adults were making different assessments of habitat/patch quality and finding different prey to feed their young. Because most White Ibis feed in small flocks (Heath *et al.* 2009), some adults may have been foraging together on the landscape, but with several thousand adult birds in each colony, we consider this unlikely to be a large problem. Furthermore, some boluses contained prey from both terrestrial and aquatic habitat types, indicating that individuals or pairs were using multiple habitats when foraging. Given the large number of chicks (more than double the nest numbers) it is also unlikely that a single chick was sampled more than once in a given year.

We first calculated the biomass composition (%) of diets and the frequency of occurrence for each prey category in each collection and used these summaries for help with interpretation of the multivariate statistics. We then analysed the prey assemblages in the boluses with multivariate ordination techniques (e.g. Martin & Genner 2009); we conducted multivariate statistical and graphical analyses of similarity between prey biomass composition in boluses to look for diet shifts between collections. The multivariate nature of the data made univariate analyses unwieldy and MANOVA was not a viable option for these analyses because of the large number of zeros for every prey category. We therefore used the PRIMER-E software package (PRIMER v6., Clarke & Warwick 2001) to conduct the tests and visualize the data with non-metric multi-dimensional scaling (NMS). The biomass of each prey category for each sample was square-root-transformed to moderate the influence of relatively heavy prey types and Bray–Curtis similarity was computed for all pairs of boluses.

We explored the major underlying patterns in bolus composition with all boluses using a cluster analysis and evaluation of two-dimensional (2D) NMS plots. Cluster analysis was performed using a group-average link (Clarke & Warwick 2001). By inspection of the cluster diagrams we identified natural clusters of boluses and used the clusters to help in the graphical interpretation of the NMS plots. The stresses on some of our 2D ordinations were > 0.1 so we examined both 2D and 3D ordinations before describing the patterns graphically; however, the actual 2D stress levels were reasonable (0.11–0.12) and permitted fairly straightforward interpretations.

After describing the basic diet types using all of the boluses from both years and regions, we tested for differences in diet composition between collections using non-parametric permutation analyses (ANOSIM), which provide exact probabilities of observing the test statistic R (the average differences in similarity within vs. between groups) given the null hypothesis that bolus composition is equivalent for any pair of collections. Probabilities were based on 999 permutations for each comparison. When a comparison yielded compositional differences ($P < 0.05$) we conducted SIMPER analyses to quantify the contribution of the different prey types to the dissimilarity between collections. The P -values presented are uncorrected for multiple comparisons. We compared the multivariate dispersion in diets between collections using PERMDISP2 (Anderson 2004, 2006). This test analyses multivariate dispersion from a centroid with a permutation of residuals after re-ordering the sample identities 9999 times. The distance measure used was Bray–Curtis dissimilarity, which ranges from 0 to 100. We tested for dispersion differences because we thought the generalist feeding behavior (Heath *et al.* 2009) and high giving-up-density of the White Ibis (Gawlik 2002) may produce more variable prey use in years or dates with severe low water conditions, low aquatic prey densities or depth reversals (Frederick & Spalding 1994). Lower bolus–bolus prey use dispersion indicates greater diet similarity within a collection and may therefore indicate relative agreement among adult White Ibis about the habitat quality and prey availability, whereas high variation may indicate changing prey conditions (i.e. availability or unavailability of some prey type) leading to variation between adults in foraging strategies.

For the WCA 3A boluses we compared the bolus composition and dispersion between the two years directly. Because we had a greater sample size in Lox and because boluses were collected from one colony at different landscape water depths, we compared bolus composition and dispersion between all five sample dates (Table 1, Fig. 2). Using the estimates of slough water depth from the EDEN model, the analysis of Lox boluses allowed us to look for evidence of water depth-dependent diets as well as shifts in composition or dispersion following the rainfall and water reversal late in 2007 (Fig. 2). If prey use by nesting White Ibis is primarily determined by landscape water depth (or available habitat), then boluses collected

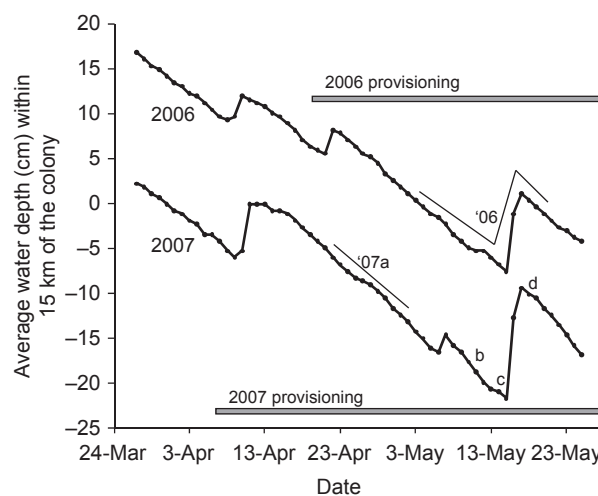


Figure 2. Average water depth estimates (cm), relative to wetland soil surfaces, according to the EDEN model in all wetland habitats within 15 km of the colony in the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Lox) in 2006 and 2007 during the White Ibis nesting seasons. The collection periods are indicated for each year and are referred to as 2006, 2007a, 2007b, 2007c and 2007d.

in 2006 should be most like the 2007a and 2007d diets (Fig. 2, Table 1). Boluses collected at times with the lowest landscape depths and constricted habitats, 2007b and/or 2007c, should contain more fish (Kushlan 1979). Although some contrasts had large discrepancies in sample sizes (e.g. 6 vs. 24) the probability of significant ($\alpha < 0.05$) differences being caused by individual variation and small sample bias, rather than temporal/environmental variation, in this dataset appears to be low (see Supporting Information Appendix S2).

RESULTS

We identified 557 prey items in 2006 and 2375 in 2007, excluding uncountable fragments of 'garbage' items such as rotten chicken and their associated maggots. Summary analyses of prey occurrences and mean biomass fractions are given in Tables 2 and 3. Besides fish and crayfish remains, other animals and parts of animals that were identified in the boluses included terrestrial animals such as Surinam cockroaches *Pycnoscelus surinamensis* (67% of all terrestrial insects), mole crickets *Scapteriscus* spp., terrestrial coleopteran larvae (Scarabaeidae), eastern garter snakes *Thamnophis sirtalis* as well as other aquatic prey: dragonfly naiads (Libellulidae), aquatic coleopterans,

Table 2. Percentage of White Ibis chick boluses containing various prey categories in seven collections from 2006 to 2007. *n* = number of boluses in each collection. Boluses were collected from colonies in Water Conservation Area 3A (Alley North and 6th Bridge) and Loxahatchee National Wildlife Refuge (Lox NC4). Some collections took place over several days but were lumped together for analyses (see Methods).

Prey item	WCA 3A 2006 (<i>n</i> = 11)	WCA 3A 2007 (<i>n</i> = 20)	Lox 2006 (<i>n</i> = 12)	Lox 2007a (<i>n</i> = 6)	Lox 2007b (<i>n</i> = 33)	Lox 2007c (<i>n</i> = 24)	Lox 2007d (<i>n</i> = 21)
Crayfish	45	40	83	67	42	21	43
Sunfish	91	10	17	0	39	8	0
Small fishes	73	10	17	0	58	21	14
Shrimp	82	15	0	0	39	13	5
Aquatic insects	45	15	33	33	27	4	33
Terrestrial insects	9	25	33	67	36	79	52
Garbage	0	55	0	0	36	54	29
Vertebrates	0	0	8	0	3	0	24

grass shrimp, aquatic bugs (Belostomatidae and Naucoridae) and soldier fly larvae (Tipulidae). In 2007, we found several boluses containing urban refuse.

Across all collections, crayfish were encountered in 21–83% of boluses (Table 2), and their contribution to the calculated prey biomass ranged from 6 to 66% (Table 3). Although fish collectively made up an average 0–15% of the total prey biomass in five bolus collection dates, they constituted 80% of the average prey biomass in WCA 3A in 2006 and 45% of prey biomass in one collection (2007b) from Lox (Table 3). In 2007, garbage and terrestrial insects were larger components of the White Ibis boluses in both colonies (Tables 2 and 3), together making up 37–80% of

the average biomass per bolus in every collection. Although aquatic insects and shrimp were found in many boluses (Table 2), their respective contributions to total biomass were relatively small (Table 3). Average total prey biomass per bolus (gram dry mass) varied more than threefold across the collections (Table 3), with the most massive boluses being the fish-dominated boluses from WCA 3A in 2006.

Multivariate cluster analysis of all diets resulted in six clusters with $\geq 33\%$ average Bray–Curtis similarity (hereafter ‘similarity’); this seemed to be a natural break in the cluster analysis and in the ordination (Fig. 3a). Ninety-six per cent of the boluses (122 of the 127) fell into four diet clusters (see ellipses in Fig. 3a), and five boluses made up

Table 3. Percentage dry biomass composition and total gram dry mass of prey in White Ibis chick boluses from seven collections taken in 2006 and 2007. *n* = number of boluses in each collection. Boluses were collected from colonies in Water Conservation Area 3A (Alley North and 6th Bridge) and Loxahatchee National Wildlife Refuge (Lox NC4). Some collections took place over several days but were lumped together for summary analyses (see Methods). Average total biomass per bolus is included in the last row.

Prey item	WCA 3A 2006 (<i>n</i> = 11)	WCA 3A 2007 (<i>n</i> = 20)	Lox 2006 (<i>n</i> = 12)	Lox 2007a (<i>n</i> = 6)	Lox 2007b (<i>n</i> = 33)	Lox 2007c (<i>n</i> = 24)	Lox 2007d (<i>n</i> = 21)
Crayfish	11.6	21.0	66.3	44.1	12.6	6.0	27.9
Sunfish	68.4	4.7	3.4	0.0	9.3	< 0.1	0.0
Small fishes	11.7	5.9	2.7	0.0	33.0	13.9	0.8
Shrimp	7.8	3.7	0.0	0.0	3.1	0.2	0.2
Aquatic insects	0.4	0.1	5.8	0.5	1.9	0.1	11.4
Terrestrial insects	0.1	10.0	18.0	55.4	8.7	37.0	23.6
Garbage	0.0	54.7	0.0	0.0	28.3	42.8	23.4
Vertebrates	0.0	0.0	3.8	0.0	3.0	0.0	12.6
Avg. Total g/bolus \pm se	6.32 \pm 10.18	4.32 \pm 00.86	3.11 \pm 1.05	1.86 \pm 0.63	4.26 \pm 0.72	2.18 \pm 0.24	2.79 \pm 0.82

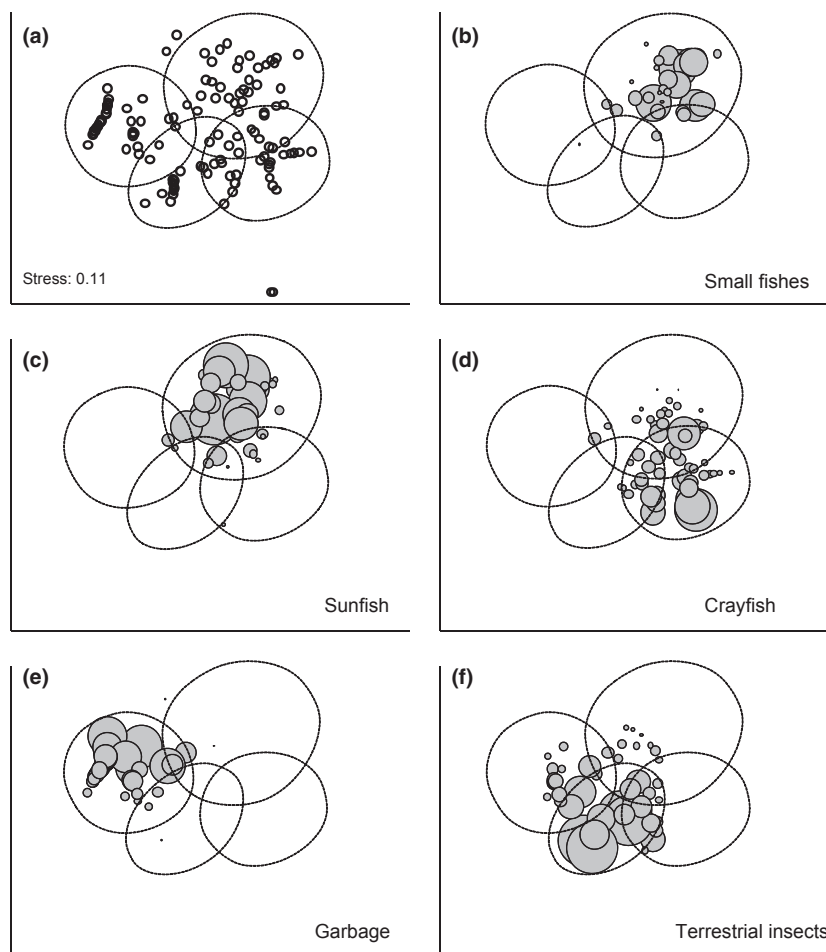


Figure 3. Prey composition of 127 White Ibis chick boluses in 2006 and 2007 from colonies in WCA 3A and Lox illustrated by NMS ordination of prey biomasses. (a) Each point is a bolus and the proximity of points indicates the level of Bray–Curtis similarity in 2D space. The ellipses envelop diets with $\geq 33\%$ average similarity from a cluster analysis. (b–f) Biomasses of five 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. The orientation of the four major clusters is the same in Figures 4 and 5. Two clusters not shown include the remaining five boluses: two boluses with a heavy non-fish vertebrate and three with low biomasses of only aquatic insects. The axes are unlabelled because they are a depiction of multidimensional differences between boluses in 2D space. The direction of change for the most important prey can be seen by inspection of the bubble plots. The stress indicates the degree of distortion in the 2D plot relative to the actual multidimensional similarity between points.

the other two clusters (ellipses not shown in Fig. 3a). Three of these ‘rare’ boluses were filled with a heavy vertebrate prey item (e.g. a snake), whereas the two boluses in the sixth cluster were extremely light and dominated by aquatic insects. The ellipses that envelop the four primary diet clusters overlap in 2D ordination space because of the multidimensional nature of the data, but each bolus plotted in Figure 3 falls into only a single cluster. By plotting relative biomass of the prey types on the ordination, we observe that small fishes (Fig. 3b), sunfish (Fig. 3c) and shrimp (not

shown) biomasses are high in boluses found in the upper right cluster (i.e. fish and shrimp diets). Crayfish biomass is high in boluses found in the lower right cluster (Fig. 3d), whereas garbage and terrestrial insects respectively dominate the clusters to the left side of the plot (Fig. 3e,f). Aquatic insects were not constrained to one cluster, but instead were found scattered in both the fish and shrimp diet cluster and the crayfish diet cluster (data not shown). The spatial orientation of the four clusters, representing the four diet types, is consistent in Figures 3–5.

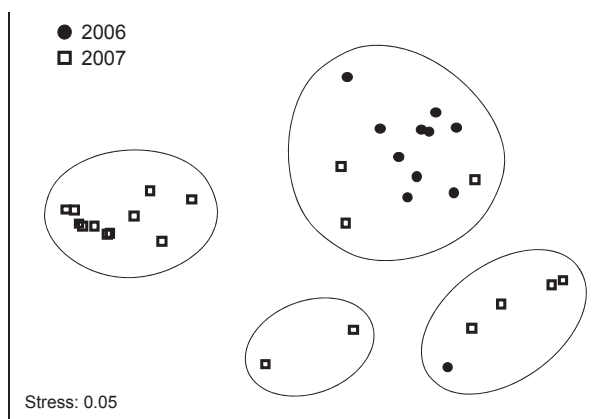


Figure 4. Prey composition of White Ibis chick boluses in WCA 3A colonies collected during the 2006 (black circles) and 2007 (open squares) nesting seasons, as illustrated by the first two dimensions of an NMS ordination based on prey biomasses. Individual boluses are represented by points and the proximity of points indicates the level of similarity in 2D space. The ellipses envelop diets with $\geq 33\%$ average similarity within the cluster. The orientations of the major diet types in the plot are the same as in Figure 3.

Depths and per-capita available habitat around the WCA 3A colonies were similar between years (Table 1), but at the times of our collections in both years there were still many locations around the colonies with water deeper (> 15 cm) and shallower (< -16 cm) than the preferred foraging depths. The composition of the boluses differed significantly between 2006 and 2007 (ANOSIM: $R = 0.35$, $P < 0.01$, Fig. 4). The 2007 boluses contained fewer sunfish (contribution to dissimilarity between years = 37.0%), more garbage (22.6%), fewer small fish (13.0%) and more crayfish (12.5%). Prey composition was also more variable between chicks (i.e. boluses had greater multivariate dissimilarity) in 2007 than in 2006 (mean dispersions: 31.0 in 2006 vs. 54.4 in 2007; PERMDISP: $P < 0.01$).

In Lox, the average landscape water depth varied widely between the five collections and was directly correlated with the amount of available foraging habitat (Table 1). When landscape water depths were at their highest (2006, 2007a, 2007d), the unavailable foraging locations were almost all on the dry side of the preferred range (< -16 cm EDEN water depth). Under the driest conditions in 2007 the total available habitat was constricted by at least 127 km² (~42%) relative to the deeper conditions.

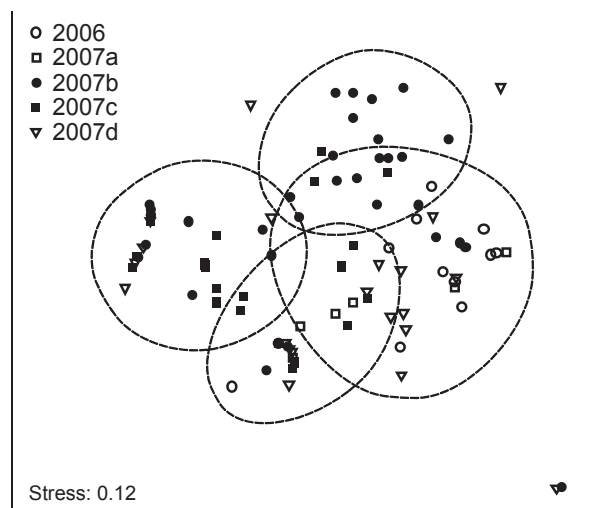


Figure 5. Prey composition in White Ibis chick boluses collected from Loxahatchee during 2006 and 2007 as illustrated by the first two dimensions of an NMS ordination of Bray–Curtis similarity. Each point represents a bolus, the proximity of points approximates the level of similarity in 2D space, and the shapes correspond to five collections made at different times during the 2 years; boluses within each collection share a common landscape water depth (see Fig. 1). Open symbols indicate three collections at higher landscape water depths for which there were no statistical differences in average prey composition (ANOSIM R -values < 0.08 , P -values > 0.22). All other pairwise comparisons of diet composition had significant differences (R -values 0.11–0.49, P -values ≤ 0.03). The ellipses envelop diets with $\geq 33\%$ average similarity within the cluster and indicate four major diet types (see Fig. 3).

Diet composition in Lox differed among the five collection dates (Global $R = 0.15$, $P < 0.01$) and bolus dispersion varied as well (Global PERMDISP test: $P < 0.01$). Seven of the 10 pairwise comparisons of bolus composition in Lox were statistically different (Table 4). All of the non-significant comparisons (P -values > 0.22) were between the three collections taken when landscape water depths were higher (mean depths > -9 cm) and more wetland habitat (> 300 km²) was available around the colonies (2006, 2007a and 2007d; Table 4, Fig. 5). These boluses generally included a significant crayfish component and few fish (Tables 2 and 3, Figs 5 and 6).

All six statistical comparisons between collections taken when the water was deeper (mean depths > -9 cm, Table 1) and one when the landscape was drier (2007b and 2007c) were significant (Table 4). Crayfish, small fishes and garbage were consistent contributors to the dissimilarity in those contrasts (SIMPER analysis in Table 4, Fig. 5). With

Table 4. Results of pairwise non-parametric permutation analyses (ANOSIM) for different bolus collections in Loxahatchee (*R* statistics and *P*-values) and the proportional contributions to dissimilarity between groups for each food type (for all diets with significant compositional differences).

Comparison	<i>R</i>	<i>P</i>	Cray	Smf	Sunf	Shr	Alns	Tlns	Garb	Vert
2006 vs. 2007a	0.06	0.22								
2006 vs. 2007b	0.18	< 0.01*	27 (+)	20 (-)	10 (-)		7 (+)	10 (+)	18 (-)	
2006 vs. 2007c	0.49	< 0.01*	31 (+)	8 (-)			6 (+)	22 (-)	24 (-)	
2006 vs. 2007d	0.04	0.23								
2007a vs. 2007b	0.19	0.03	18 (+)	21 (-)	9 (-)			23 (+)	20 (-)	
2007a vs. 2007c	0.21	0.03	25 (+)	10 (-)				29 (+)	31 (-)	
2007a vs. 2007d	-0.08	0.78								
2007b vs. 2007c	0.14	< 0.01*	10 (+)	23 (+)	8 (+)			21 (-)	28 (+)	
2007b vs. 2007d	0.13	< 0.01*	16 (-)	20 (+)	8 (+)			15 (-)	22 (+)	11 (-)
2007c vs. 2007d	0.11	< 0.01	19 (-)	10 (+)				26 (+)	29 (+)	10 (-)

Signs after the percentages indicate whether the first collection in the comparison had more or less biomass for that food type. The two collections with the lowest landscape water depths are indicated in bold.

Cray, crayfish; Smf, small fishes; Sunf, sunfish; Shr, shrimp; Alns, aquatic insects; Tlns, terrestrial insects; Garb, garbage; Vert, vertebrates.

Shrimp never contributed $\geq 5\%$ of the dissimilarity of any compositional differences. The listed *P*-values are not corrected for multiple comparisons, but asterisks indicate pairs that would still be considered significant (global $\alpha < 0.05$) after sequential Bonferroni correction.

lower landscape water depths and constricted available habitat, crayfish use decreased and small fish and garbage use increased. Terrestrial insects also contributed to the dissimilarity between the groups (Table 4), but the differences were more variable, particularly because terrestrial insect biomass was so high in boluses collected at the lowest water level (2007c, Fig. 5).

The prey assemblages in boluses collected under the two driest conditions were also significantly different (Fig. 5, Table 4). On 10–11 May (2007b) the boluses contained small fish and garbage, and were highly variable (Tables 2 and 3, Figs 5 and 6, mean distance = 55.0). Four days later (15 May, 2007d) when the water levels were at their lowest, the nestling diet shifted to terrestrial insects and even more garbage (Table 4, Figs 5 and 6) and bolus composition was less variable (mean distance = 44.0; 2007b vs. 2007c: $P < 0.01$) as the ibis abandoned the wetland. Following the 11-cm rise in average water depth, prey use shifted back towards crayfish, but dispersion increased again (mean distance = 56.0; 2007c vs. 2007d: $P < 0.01$) and several boluses still included garbage or vertebrate prey (Fig. 5, Tables 2 and 3).

DISCUSSION

Breeding White Ibis in southern Florida fed on four primary diet types and our results indicated they switched between prey types in 2007. For

some birds, seasonal prey switching is a response to the phenology of highly valuable insect prey (e.g. Naef-Daenzer *et al.* 2000, Pearce-Higgins & Yalden 2004), but switches by White Ibis seem to be driven by changes in an abiotic factor, namely landscape water depths. Our results in Lox generally support Kushlan's (1979) suggestion; ibis fed on crayfish at relatively higher landscape water

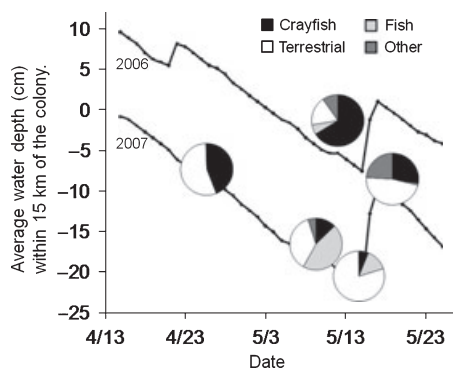


Figure 6. Average percentage contribution of different prey to boluses of White Ibis chicks in the Northern Everglades (Lox) superimposed on the hydrographs of average wetland depths (relative to soil surface) around the colonies during provisioning in 2006 and 2007. Terrestrial insects and garbage were combined as 'terrestrial' and the two fish categories were combined to highlight shifts between aquatic prey types and between aquatic and terrestrial/urban foraging. 'Other' prey includes grass shrimp, aquatic insects and vertebrates other than fish. Available preferred foraging habitat within 15 km of the colony is inversely correlated with lower landscape water depths over all illustrated water depths.

depths when more preferred habitat was available, and use of fish increased under drier conditions when the wetlands around the colony were simultaneously shallower and reduced in area. We do not know whether the switch from crayfish to fish was caused by increases in fish availability or a decrease in availability of crayfish. Bildstein *et al.* (1990) noted that shifts from crayfish to fish or crabs in coastal colonies of White Ibis occurred when freshwater wetlands were dry and crayfish were unavailable, but Kushlan (1979) argued that fish use in the Everglades depends primarily on fish availability. Probing non-visual foraging species like ibis seem to require high concentrations of fish to trigger a switch from crayfish to the more mobile prey such as fish (Kushlan 1986). Wading birds in the Everglades follow the receding water levels both locally (one to tens of metres) and regionally (thousands of metres) and may therefore feed in new areas every week as the wetland dries (Bancroft *et al.* 2002). As water levels become shallower, habitats with a longer hydroperiod at lower elevation are progressively exposed to foraging birds and fish become restricted to shallow pools. The longer hydroperiods and lower elevations should provide greater fish production and/or concentration (Trexler *et al.* 2002, 2005) and this could trigger a prey switch.

Jordan *et al.* (2000) indicated that crayfish (*Procambarus* spp.) were more abundant in wetland sites at higher elevation and with a shorter hydroperiod in central Florida. From 2007a to 2007b the available preferred foraging habitat decreased by 42% (127 km²), concomitant with a shift from crayfish to fish prey. This is consistent with a switch caused by the unavailability of crayfish, but we know relatively little about crayfish densities in the sloughs with the longest hydroperiod in Lox and cannot assess this mechanism directly. The two mechanisms are probably confounded and complementary because wetland drying forces crayfish to burrow even as fish are concentrating in shallow pools. Herring *et al.* (2010) noted that aquatic prey were less abundant in 2007 than in 2006, but that observation cannot provide an obvious explanation for the crayfish–fish prey shifts observed in Lox. The consistent use of crayfish at higher landscape water depths in Lox collections from both years (Fig. 6) appears to provide the best explanation, albeit correlative, for variable crayfish and fish use.

Although annual differences in prey abundance cannot explain the bolus composition differences

in Lox, the interannual diet variation in WCA 3A was probably caused by low prey abundances in the wetlands in 2007. Fish density is affected by time since the last drying event in wetlands like the Everglades (Trexler *et al.* 2005), and in response to the 2006 drying, the densities of concentrated fish during bird nesting were 61% lower in 2007 than in 2006 across the system, including in WCA 3A (Herring *et al.* 2010). Although the WCA 3A colony location shifted 7 Km south, the wetland depths around the respective colonies and the per-capita amount of preferred foraging habitat were similar between years (Table 1). Although the 2007 colony was slightly closer to more urban/terrestrial habitats, adults from either colony would have been forced to fly similar minimum distances (> 11 km) to forage in those habitats. Based on these observations we think it was unlikely that wetland depths, amount of available habitat around the colonies or spatial proximity to urban habitats could have been the primary determinant of prey use differences between the years. Low fish abundance, caused by the drying in the previous year, seems to be the best explanation for the garbage prevalence in the 2007 boluses in WCA 3A. Use of garbage and other terrestrial prey in Lox at the lowest landscape water depths (Fig. 6) could have been enhanced by relatively lower fish densities in 2007 (Herring *et al.* 2010), but we cannot address this hypothesis as ibis nesting did not occur at comparably low landscape water depths in 2006, when fish were more abundant.

Gulls (*Larus* spp.) are known to feed heavily on garbage around urban centres or landfills (Belant *et al.* 1998, Annett & Pierotti 1999, Weiser & Powell 2010), and a recent study suggests something similar for the Australian White Ibis *Threskiornis molucca* (Martin *et al.* 2010), but in these cases garbage use or urban foraging appears to be habitual for individuals or segments of the breeding populations. Although the effects of garbage feeding on individual long-term reproductive success of gulls has been debated (e.g. Annett & Pierotti 1999, Weiser & Powell 2010), populations of several gull species and possibly the Australian White Ibis seem to be growing on diets subsidized with garbage (Belant *et al.* 1998, Martin *et al.* 2010, Weiser & Powell 2010). In contrast, White Ibis use of garbage does not appear habitual, but opportunistic, and breeding is not obviously enhanced by the use of garbage

or terrestrial prey. Nestling condition and fledging success were poorer in the year of heavier urban/terrestrial prey use (Herring *et al.* 2010, 2011), reflecting poor wetland foraging conditions system-wide and we suggest that the use of garbage, and to some degree terrestrial insects, is an alternative strategy used when aquatic prey are scarce. However, the use of these prey types should be considered in future evaluations of breeding trends of this species living at the wildland–urban interface.

Restoration of breeding conditions for wading birds in south Florida has focused on the hydrological conditions making aquatic prey both abundant (Trexler & Goss 2009) and available (Gawlik 2002), but our observations suggest both fish and crayfish prey can be a part of the White Ibis diet during nesting. Populations of breeding White Ibis in Louisiana and South Carolina appear to be limited by the abundance of crayfish-producing wetlands (Bildstein *et al.* 1990, Fleury & Sherry 1995) and the success of this species may be related to the abundance and availability of crayfish in the Everglades as well. Considering the water depths (Fig. 6) during the better of the two nesting years in Lox (2006), it seems unlikely that the colony ever shifted to a fish-dominated diet, suggesting that high nesting success can be achieved without substantial use of fish. However, our collection of boluses in 2006 was rather small and a more comprehensive study of a good nesting year would be helpful before making strong conclusions. Because we did not collect bolus samples from early in the 2006 nesting season in WCA 3A we could not determine whether a shift from crayfish to fish occurred at that colony or whether fish were used consistently throughout the season. Additional work will be necessary to determine whether crayfish are indeed the principal prey type for Ibis throughout this or other wetland ecosystems.

Two hydrological aspects, landscape water depths at the time of nesting and drying events in the year prior to nesting, combine to determine aquatic prey use and scavenging prevalence of nesting White Ibis. While Ma *et al.* (2010) recently highlighted the importance of managing wetlands for appropriate water depths to enhance foraging by waterbirds, the influence of past hydrological conditions on animal prey abundance can also be significant (Trexler & Goss 2009) and wetland managers should be cognizant of both of these pro-

cesses whenever considering the optimal foraging conditions for birds.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Methods for prey identity, counts and size determination. Tables of regression parameters used to calculate prey biomass in diets of White Ibis chicks.

Appendix S2. Assessment of potential bias from comparisons of collections with unequal sample sizes.

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