

The Effects of Water Depth and Emergent Vegetation on Foraging Success and Habitat Selection of Wading Birds in the Everglades

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Abstract.—Wading bird foraging success and habitat preference can be greatly affected by prey availability, which encompasses both prey density and the vulnerability of prey to capture. Two components of prey vulnerability, water depth and emergent vegetation, were manipulated within 10 m × 10 m enclosures to determine the relative effects on foraging habitat preference for eight species of wading birds and foraging success for a subset of four species that strike their prey. All species showed a strong preference for shallow water, and within this water depth showed a preference for the sparse vegetation density treatment. The preference for foraging habitat with a sparse or intermediate vegetation density has been documented in other studies, and may represent a tradeoff between selecting more heavily vegetated areas, which have a higher prey density, and more open areas, where prey are more vulnerable to capture. Almost all foraging occurred in the shallow water treatment, suggesting that preferred water depths constituted high quality habitat for wading birds. The weaker selection for sparse vegetation density and lack of an effect of vegetation density on capture rate and capture efficiency ($p > 0.05$ for all tests, except Snowy Egret (*Egretta thula*) capture efficiency) suggested that emergent vegetation is of secondary importance to water depth as determinants of wading bird habitat quality. Received 15 December 2010, accepted 3 September 2011.

Key words.—Everglades, foraging success, habitat selection, Pelecaniformes, prey availability.

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Wading bird (Pelecaniformes and Ciconiiformes) populations in the Florida Everglades (Frederick and Spalding 1994) and other wetlands (Butler 1994; Hafner 1997) are limited by prey availability in some years (“prey availability hypothesis,” Gawlik 2002). The constraint can be expressed through changes in foraging habitat preferences (Frederick and Spalding 1994; Safran *et al.* 2000; Gawlik 2002), foraging success (Master *et al.* 2005) productivity (Herring *et al.* 2010) or levels of stress (Herring *et al.* 2011).

Characteristics of the environment that may affect prey availability are water depth and vegetation structure and density. Wading birds forage by standing or wading through the water and can be constrained physically by their leg length (Powell 1987) or bill length depending on whether they are tactile foragers. Emergent vegetation can influence wading bird foraging decisions, although the specific characteristics of vegetation that affect prey availability are not known. Hoffman *et al.* (1994) and Bancroft *et al.* (2002) used aerial surveys to show that the distribution of wading birds is related to vegetation at a coarse scale (2 km²). At

finer scales, the response by wading birds is mixed, with some studies showing that foraging wading birds prefer open water (Kersten *et al.* 1991), and others suggested that vegetated areas are preferred (Kushlan 1979; Lantz *et al.* 2010). Some variation might be explained by species-specific preference for either vegetated or open habitat (Dimalexis and Pyrovetsi 1997; Green and Leberg 2005a; Green and Leberg 2005b; Green 2005).

The management and restoration of wetland ecosystems increasingly relies on models that link wetland ecosystem drivers, like hydrology and nutrients, with species-specific responses (Gawlik 2006, Frederick *et al.* 2009). Such models require that we move beyond general bird-habitat relationships and identify the key components of habitat to which wading birds are responding and the pathways by which these responses are linked to ecosystem drivers. In this study we tested whether water depth and density of emergent vegetation influenced wading bird foraging habitat preference and foraging success and efficiency. Both treatment variables, which are a function of hydrologic drivers, rep-

resent components of prey availability that affect the vulnerability of prey to capture.

METHODS

Study Area

We conducted this study from January through March 2008 at the Loxahatchee Impoundment Landscape Assessment (LILA) project in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Boynton Beach, Florida (26°29.600'N, 80°13.000'W). LILA consists of four replicated 7-ha semi-natural wetland impoundments with a re-circulating water system that allows control over water depths. The impoundments (hereafter macrocosms) were designed to mimic the physical features of the Everglades, and consist of deep and shallow sloughs separated by shallower ridges (Fig. 1).

Experimental Design

To quantify the effects of water depth and emergent vegetation on wading bird foraging habitat selection and foraging success, an experiment was conducted at LILA with two replicates. We constructed three 10 × 10 m enclosures in both the deep and shallow sloughs of macrocosms 1 and 4 (M1 and M4, respectively). This size of enclosure was large enough to attract foraging wading birds (pers. obs.), but small enough to control vegetation densities and prey communities. Deep and shallow enclosures were separated by approximately 100 m, and enclosures within each slough were placed 15–20 m apart. Enclosures were constructed with 3 mm

mesh black knotless nylon, with a weighted line sewn around the bottom of the material and pushed into the sediment. Buoyant strips made from closed-cell foam were affixed to the top of the mesh.

Two water depth treatments were used to evaluate effects on wading bird foraging: 10 cm in the shallow slough and 25 cm in the deep slough (shallow and deep respectively). Depths were chosen based on maximum foraging depths of target wading bird species: Glossy Ibis (*Plegadis falcinellus*), Great Egret (*Ardea alba*), Great Blue Heron (*A. herodias*), Little Blue Heron (*Egretta caerulea*), Roseate Spoonbill (*Platalea ajaja*), Snowy Egret (*E. thula*), Tricolored Heron (*E. tricolor*), White Ibis, and Wood Stork (*Mycteria americana*). Wading bird foraging habitat preference was analyzed for all target wading bird species, whereas foraging success and capture efficiency were only analyzed for striking species (Great Egret, Little Blue Heron, Snowy Egret, Tricolored Heron) because these species more commonly forage on fish (Rodgers *et al.* 1995; Frederick 1997; Parsons *et al.* 2000; McCrimmon *et al.* 2001), for which densities were controlled, than on invertebrates in the soil, which were not excluded from enclosures.

Vegetation (spike rush; *Eleocharis* sp.) treatments created varying structural complexity among enclosures, with treatment levels including no vegetation (0 stems/m²), sparse densities of vegetation (46 ± 22.8 stems/m²), and moderate densities of vegetation (139.2 ± 32.8 stems/m²). These stem densities are characteristic of those found in the Everglades, and are consistent with other studies characterizing spike rush densities as sparse or dense (sparse 55.4 ± 1.6 stems/m², dense 113.2 ± 4.2 stems/m²; Karunaratne *et al.* 2006). Emergent vegetation was cleared in the “no vegetation” treatment enclosures, and thinned or transplanted from nearby sloughs in LILA as necessary in the other enclosures to meet our desired treatment densities. Vegetation treatments were established one week before the start of the experiments to ensure that transplanted vegetation took root and to minimize new growth.

We placed minnow traps in the enclosures four days prior to the experiment to remove any existing prey (fish and macroinvertebrates such as shrimp), and repeated this every day until prey captures were minimal. Enclosures were then stocked at a density of 20 fish/m² with Eastern Mosquitofish (*Gambusia holbrooki*; mean standard length = 24.4 ± 0.3 mm). The fish stocking density would be considered high in the Everglades in the wet season (Trexler *et al.* 2002), but is only one third of densities found in concentrated pools during the dry season (Gawlik unpubl. data). Fish were purchased from a commercial fish farm or caught within LILA using minnow traps.

Each morning of the experiment, wading bird decoys were placed in each enclosure in order to attract wading birds to the macrocosms to forage (e.g., Crozier and Gawlik 2003). We used decoy flocks consisting of 18 white plastic wading bird decoys next to each enclosure, and four white plastic decoys within the enclosure. Wading bird decoys were plastic lawn flamingos that were painted white to resemble White Ibis (e.g., Crozier and

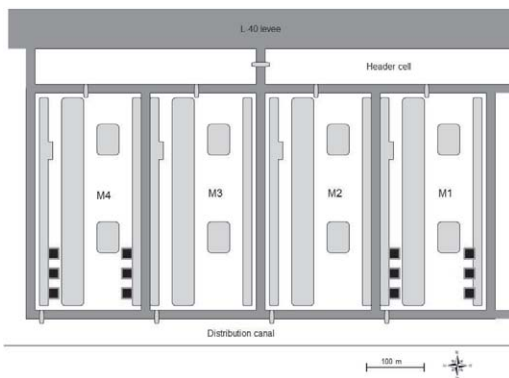


Figure 1. Loxahatchee Impoundment Landscape Assessment (LILA) project. Macrocosms are numbered 1–4, with enclosures represented by black squares in macrocosms 1 and 4. Rectangular macrocosms are separated by levees. Within each macrocosm, the shallow slough is to the south of the deep slough, separated by the center ridge, with additional ridges at both the north and south edge of each macrocosm. Water flows from the header cells through the macrocosms and out into the distribution canal.

Gawlik 2003). Additionally, two commercial Great Egret decoys were placed adjacent to each enclosure (e.g., Herring *et al.* 2008).

Observations were conducted from a vehicle on a levee adjacent to the shallow slough. The presence of a vehicle did not appear to change bird behavior, and studies have shown that wading birds are less disturbed by a vehicle than by visible observers (Stolen 2003). Days were assumed to be independent because all enclosures could be viewed simultaneously from the air by passing wading birds, thus allowing birds to reassess the macrocosm each morning (Gawlik 2002; Master *et al.* 2005). The first replicate of the experiment ran between 14 - 25 January ($n = 10$ days), and the second replicate ran between 26 February-11 March ($n = 14$ days). Data were combined between replicates for analysis because there was no significant difference between replicates.

We restocked the enclosures daily to ensure constant fish densities throughout the experiment by using mark-recapture methods to estimate the density in the enclosures after foraging observations. We marked fish in batches using six different colors (red, orange, yellow, green, blue, and pink) of visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, WA). Prior to marking, we anesthetized fish using 50 ppm of tricaine methanesulfonate (MS-222). We marked the fish by injection with a 1-2 mm line of VIE using 28 gauge insulin needles. Marking location was above the lateral line and anterior to the caudal peduncle. Marks persisted in mosquitofish in aquarium trials for at least one month (Lantz unpubl. data). VIE polymer is made of surgical quality plastic, with non-toxic dyes, that was not expected to impact the health of the marked fish or the wading birds ingesting the tagged fish (NMT Biological Support, pers. com.).

At the end of each day of observations, we placed bird netting over the enclosures to eliminate wading bird predation of fish, thus creating a closed population of fish within the enclosure. We released 200 marked fish (10% of the initial stock) into each enclosure and allowed them to disperse for at least 2 hours. We then recaptured both tagged and untagged fish using minnow traps baited with pellet fish food. Lincoln-Peterson population estimates (Williams *et al.* 2002) were used to assess population densities by comparing numbers of tagged and untagged fish. Additional fish were then added into the enclosures to return to original stocking densities.

Foraging Habitat

We quantified wading bird foraging habitat by identifying and counting the number of wading birds in each enclosure for all species. The observation period began at dawn and lasted approximately 3 h. All birds present were recorded, although some birds were not foraging for the entire duration in the enclosure. The arrival and departure of each bird was noted, thus maintaining continuous observations of the number of birds present and durations within each enclosure. Because of the potential influence of social-

ity, we summarized the enclosures as either used (1) or non-used (0) throughout the observation period. Birds were not treated as individuals because birds arriving and leaving in groups were most likely not making individual decisions on a foraging location. The number of minutes of use of each enclosure was summed each day. Wading bird use of the enclosures was compared to the availability of different habitat features to determine foraging habitat preference using Manly's selection index, which determines the probability that a resource, in this case water depth or vegetation density, will be selected if all resources are equally available (Manly *et al.* 2002).

Foraging Success

All wading birds were included in the foraging habitat preference analysis, but we included in the foraging success analysis only those species that forage visually on fish so we could eliminate any potential bias from invertebrates that might have been in the substrate. Foraging birds in the enclosures were recorded with a high resolution video camera and telephoto lens. Enclosures were videotaped separately, with the order chosen haphazardly. Birds were not marked, so some birds may have been videotaped multiple times if they left the study site completely and then returned. Foraging success was later quantified in the laboratory by analyzing recordings of foraging birds and constructing time activity budgets of foraging bouts. Because birds rarely foraged in the deep water treatment, only birds in the shallow water treatment were analyzed.

Videos were analyzed using EthoLog 2.2 (Ottoni 2000). Only birds that were actively foraging were analyzed; striking species [Great Egret, Little Blue Heron, Snowy Egret, Tricolored Heron] were considered to be foraging when seen looking at the water. Foraging activity was measured by recording the number of successful and unsuccessful strikes. Prey captures were apparent because striking birds were seen swallowing prey items. Capture rate was defined as the number of prey captured per minute of active foraging and capture efficiency was defined as the number of prey captured divided by the total number of attempts (#successful strikes/# total strikes). Both capture rate and capture efficiency were calculated for each striking species based on the treatment variables.

Data were tested for normality and equal variances prior to analyses. The square root of capture rate was the most appropriate transformation based on the slope of the linear regression of \ln variance versus \ln mean (Box *et al.* 1978). No transformation was necessary for capture efficiency. Data were analyzed using an analysis of variance (ANOVA) with vegetation density as the treatment variable and macrocosm as the blocking factor (PROC GLM, SAS version 9.1). To assure that the duration of foraging bouts did not influence the results we compared the analyses of foraging bouts with a minimum of 1-min, 3-min, and 5-min durations. Results were consistent across analyses so only results from the 1-min threshold are reported.

RESULTS

Foraging Habitat

Great Blue Herons, Great Egrets, Glossy Ibises, Little Blue Herons, Roseate Spoonbills, Snowy Egrets, Tricolored Herons, White Ibises, and Wood Storks were observed foraging within the experimental enclosures. Wading bird use at any given time ranged from 0-47 birds per enclosure (mean \pm SE, 3.6 ± 5.9 birds/enclosure).

Confidence intervals around the selection index showed that wading birds preferred the shallow water depth treatment over the deep water treatment (Table 1, Manly's selection index shallow = 0.914, deep = 0.086, and expected = 0.5). Within shallow water, foraging birds showed a preference for the sparse density of emergent vegetation, followed by the no vegetation treatment (Table 1). Birds strongly avoided deep water, but those that did occur in the deep treatment showed no preference for a vegetation density treatment, as evidenced by the overlapping confidence intervals (Table 1).

Foraging Success

We collected data from 212 foraging bouts totaling 957 min. Foraging durations ranged from 1-18 minutes (mean \pm SE, 4.5 ± 3.5), with capture rates and efficiencies showing high variability across treatments and species (Table 2). Capture rate did not vary significantly (all tests, $P > 0.08$) among vegetation densities (Table 3).

Capture efficiency for three of the four species was not significantly (all tests, $P > 0.12$) affected by the vegetation density

(Table 4). Only the capture efficiency of the Snowy Egret showed a significant ($P = 0.002$) effect of vegetation on capture efficiency. Although wading birds preferred the sparse vegetation treatment, the high variability in capture efficiency among treatments showed no obvious difference among vegetation densities (Table 2).

DISCUSSION

Wading birds preferred foraging habitat with shallow water and sparse emergent vegetation; however, water depth had a stronger effect, with preference for vegetation density only occurring in the shallow water enclosures. Pierce and Gawlik (2010) found that ideal hydrological conditions were more important to foraging wading birds than fine-scale environmental characteristics, although the importance of environmental characteristics such as emergent vegetation may be more prominent in years with poor hydrologic conditions because selectivity may increase when resource availability is low (Gaillard *et al.* 2010). For example, Bancroft *et al.* (2002) found that wading birds selected foraging sites based predominantly on water depth when water was limited, whereas they showed a stronger preference for vegetation types when ideal water depths were more available in the landscape.

The study adds to the growing evidence that wading birds respond to changing habitat conditions more strongly through habitat selection than they do through changes in foraging success (Lantz *et al.* 2010). Wading birds preferred the sparse emergent vegetation treatment, but their foraging suc-

Table 1. Manly's selection index with 95% confidence limits for wading bird foraging habitat selection in relation to water depth and emergent vegetation density. Wading bird use was compared to availability (0.167) across 6 enclosures in LILA. A selection index greater than the availability indicates preference, and less than indicates avoidance.

Water Depth	Emergent Vegetation Density	Used Sample Proportion	Confidence Intervals	
			Lower	Upper
Shallow	None	0.302	0.285	0.319
Shallow	Sparse	0.404	0.386	0.422
Shallow	Moderate	0.208	0.193	0.223
Deep	None	0.037	0.03	0.044
Deep	Sparse	0.03	0.024	0.036
Deep	Moderate	0.019	0.014	0.024

Table 2. Capture rates (CR, # cap/min) and capture efficiencies (CE, # successful strike/total strike attempts) for wading birds in shallow water, separated by emergent vegetation density treatments. Results are presented as mean \pm SE, with n indicating the number of birds for each treatment.

Species	Vegetation Density	CR \pm SE	n	CE \pm SE	n
Great Egret	None	0.17 \pm 0.24	2	0.13 \pm 0.18	2
	Sparse	0.66 \pm 0.40	9	0.34 \pm 0.19	9
	Moderate	0	1	—	
Little Blue Heron	None	1.18 \pm 0.90	24	0.51 \pm 0.27	24
	Sparse	1.16 \pm 0.96	46	0.41 \pm 0.28	44
	Moderate	1.77 \pm 1.35	16	0.61 \pm 0.25	15
Snowy Egret	None	1.27 \pm 1.08	25	0.41 \pm 0.27	23
	Sparse	1.35 \pm 2.08	49	0.20 \pm 0.25	49
	Moderate	0.78 \pm 0.46	18	0.39 \pm 0.26	17
Tricolored Heron	None	0.64 \pm 0.92	9	0.26 \pm 0.34	9
	Sparse	0.45 \pm 0.47	7	0.31 \pm 0.29	6
	Moderate	0.70 \pm 0.53	9	0.33 \pm 0.08	9

Table 3. Analysis of variance for capture rates of wading birds in shallow water in relation to emergent vegetation density, with macrocosm as a blocking factor.

Source	Error df	df	MS	F	P
Great Egret	9				
Vegetation		2	0.38	3.35	0.082
Macrocosm		0	—	—	
Little Blue Heron	81				
Vegetation		2	0.27	1.01	0.368
Macrocosm		1	0.07	0.26	0.612
Snowy Egret	86				
Vegetation		2	0.21	0.56	0.571
Macrocosm		1	0.15	0.41	0.526
Tricolored Heron	21				
Vegetation		2	0.08	0.31	0.734
Macrocosm		1	0.77	3.2	0.088

Table 4. Analysis of variance for capture efficiencies of wading birds in shallow water, in relation to emergent vegetation density, with macrocosm as a blocking factor.

Source	Error df	df	MS	F	P
Great Egret	9				
Vegetation		1	0.08	2.19	0.173
Macrocosm		0	0	—	—
Little Blue Heron	78				
Vegetation		2	0.15	2.12	0.127
Macrocosm		1	0.12	1.67	0.2
Snowy Egret	83				
Vegetation		2	0.37	7.01	0.002
Macrocosm		1	0.05	0.96	0.33
Tricolored Heron	20				
Vegetation		2	0.03	0.39	0.681
Macrocosm		1	0.22	3.15	0.091

cess and efficiency were, for the most part, not higher in this treatment. Thus, there is a temptation to conclude that wading bird density, the basis of habitat selection, is a misleading indicator of habitat quality (Van

Horne 1983; Bock and Jones 2004). However, in highly dynamic wetland systems where food limits wading bird populations in only some years (Herring *et al.* 2011), there may be only sporadic selection pressure on birds

to select habitats that provide the highest performance (Pierce and Gawlik 2010). Moreover, performance metrics, in this case foraging success and foraging efficiency, may not measure the response to a habitat component that is actually driving individual performance (Beyer *et al.* 2010; Gaillard *et al.* 2010). A plausible alternative explanation is that the adaptive value of habitat selection in unpredictable systems like wetlands is to reduce search time rather than to maximize prey intake rate. Wood Storks sometimes travel so far to foraging sites (Browder 1984; Herring and Gawlik 2011) that they do not have time to make more than one food delivery to a nest per day, even though their energetic budget would allow for it. Another indication that search time can be a limitation in dynamic ecosystems is that storks foraging in the Everglades use other white wading birds as a cue to find foraging sites much more than they do in tidal wetlands, where prospecting is more common (Bryan *et al.* 2002; Herring and Gawlik 2011), and the availability of foraging habitat occurs predictably around tidal cycles.

Studies investigating the correlation between vegetation and wading bird foraging have mixed results, with some studies showing a preference for foraging in open water habitat (Breininger and Smith 1990; Kersten *et al.* 1991; Dimalexis and Pyrovetsi 1997) and others showing a preference for foraging in vegetated areas (e.g., Smith *et al.* 1995; Surdick 1998; Pierce and Gawlik 2010). Some waterbird species appear to avoid foraging in areas of emergent vegetation to lower their risk of predation (Metcalfe 1984; Cresswell 1994). The birds in our study avoided the densest vegetation treatment, but it is unclear whether they were responding to increased predation risk or because prey were less vulnerable to capture in that habitat. Predation risk is known to be a strong selective force in shaping animal behavior (Brown 1999). However, in the Everglades, predation pressure does not seem to have a strong effect on wading bird nesting success (Frederick and Collopy 1989). Dense vegetation may reduce prey capture rates (Campos and Lukuona

2001; Richardson *et al.* 2001) and give fish refuge from avian predators (Batzer and Shurtleff 1999), perhaps explaining why aquatic prey densities are higher in vegetated areas than in non-vegetated areas (Dvorac and Best 1982; Diehl 1988; Rozas and Odum 1988; Stolen 2006; Stolen *et al.* 2009).

The tradeoff between low prey vulnerability but higher prey densities in vegetated areas as compared to non-vegetated areas may explain why wading birds sometimes prefer areas with intermediate amounts of vegetation (Lantz *et al.* 2010; Pierce and Gawlik 2010) or on the edge of dense vegetation. For example, Safran *et al.* (2000) showed that White-faced Ibises were more likely to forage in areas close to vegetation, presumably because of higher prey abundance. Stolen (2006) found that edge habitat (within 0.5 m of the boundary between vegetated and unvegetated habitat) was preferred by foraging wading birds. Although it is assumed that prey are more vulnerable to capture in open water than in vegetated areas, the presence of sparse emergent vegetation may calm the water surface in windy conditions, thus resulting in higher visual clarity for visually foraging birds (Hom 1983).

The pattern of wading birds foraging at the interface of vegetated and open areas or in sparsely vegetated areas, suggests that a fine scale habitat mosaic may provide a beneficial mix of heavily vegetated prey refuges and adjacent open areas where prey are more vulnerable to capture. Healthy wetlands tend to be patchy at fine scales because of frequent disturbances from fire and fluctuating water levels (Gunderson and Snyder 1994, Sklar *et al.* 2002); however, common anthropogenic stressors like eutrophication and water level stabilization often reduce diversity by promoting the dominance of a few plant species (Craft *et al.* 1995, Wood and Tanner 1990). Moreover, although fluctuating water levels could promote a beneficial vegetation community for foraging, only shallow water was the primary determinant of high quality habitat. The apparent paradox is reconciled in large wetlands or networks of wetlands through spatial variation in topography, which provides suitable wa-

ter depths somewhere in the system at any given time, but allows water levels at any particular site to fluctuate widely over time and sustain a diverse vegetation community.

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