

Wading Bird Foraging Habitat Selection in the Florida Everglades

RACHAEL L. PIERCE^{1,*} AND DALE E. GAWLIK²

¹South Florida Water Management District, Restoration Sciences Department, 3301 Gun Club Road, West Palm Beach, FL, 33406, USA

²Environmental Sciences Program, Florida Atlantic University, 777 Glades Road, Boca Raton, FL, 33431-0991, USA

*Corresponding author; E-mail: rapierce@sfwmd.gov

Abstract.—To determine how habitat structural complexity, which affects prey vulnerability, influences foraging habitat selection by wading birds, a habitat use versus availability study was conducted throughout the Florida Everglades in 2005 and 2006. Also, an experiment was conducted where structural complexity was manipulated and its effect on wading bird foraging efficiency quantified. Among-year differences in habitat selection were found, which corresponded to disparate hydrological conditions. In 2005, a poor hydrological year in terms of the seasonal recession, wading birds chose foraging sites that had less emergent vegetation, a thicker flocculent layer and higher prey density relative to random sites. In 2006, an optimal hydrological year, wading bird foraging locations were similar to random sites in all aspects. Submerged vegetation did not affect wading bird site selection in either year. The study indicated that hydrological conditions that affect prey density were more important to wading bird foraging success than fine scale variation in habitat characteristics. However, in years of poor hydrology factors that affect prey vulnerability may become increasingly important because the penalty for choosing low quality foraging habitat is greater than in years of more optimal conditions. Elucidating habitat characteristics which create high quality foraging sites will be beneficial in planning wetland restoration projects and gauging future restoration progress. *Received 2 October 2009, accepted 18 May 2010.*

Key words.—discriminant function, Everglades, foraging, habitat selection, prey availability, prey density, prey vulnerability, structural complexity, wading birds.

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Numerous studies have emphasized the importance of prey availability to the foraging success of wading birds and other avian predators. Early studies highlighted the correlation between prey density and the functional and numerical response of the predator (Holling 1959; Kushlan 1976a; Draulans 1987; Ogden *et al.* 1976) but more recent work has shown that predators and prey densities do not always coincide (Arengo and Baldassarre 1999; Gawlik 2002; Bennetts *et al.* 2006; Gwiazda and Amirowicz 2006). One reason for the lack of correlation is that predators are responding to the availability of prey, which reflects vulnerability to capture as well as prey density (Gawlik 2002). If prey occur in high densities, but are invulnerable to capture, predators will respond as if prey density is low. Thus, the ability to correctly predict the response of a predator to food abundance depends on understanding factors affecting prey vulnerability.

In the Florida Everglades, prey vulnerability varies seasonally in response to rainfall patterns. During the dry season, receding

water across the landscape concentrates aquatic prey in topographic depressions. Under these conditions, prey become highly vulnerable to capture and these high quality patches are strongly utilized by avian predators such as wading birds (Kahl 1964; Kushlan 1976a; Gonzalez 1997). In the pre-drainage Everglades, this seasonal dry-down is believed to have occurred predictably in time and space. The current managed Everglades is not only smaller in size (reduced foraging area), but also exhibits less predictability in drydown patterns due to water management operations that support regional flood control and water supply requirements. The unpredictable manner in which prey now becomes available throughout the landscape may have contributed to as much as a 78% decline of some species of Everglades wading birds (Crozier and Gawlik 2003a).

Although wading birds in the Everglades forage and nest sympatrically, individual species respond differently to changes in prey availability (Frederick and Collopy 1989; Crozier and Gawlik 2003a). Gawlik (2002)

showed experimentally that some species of wading birds, termed searchers, most notably Wood Stork (*Mycteria americana*), White Ibis (*Eudocimus albus*) and Snowy Egret (*Egretta thula*), are influenced more strongly by changes in prey availability than other species. These species select the highest quality patches (i.e. high prey density and high prey vulnerability) throughout the landscape and abandon patches quickly as prey availability declines (Charnov 1976; Gawlik 2002). Therefore, changes in landscape scale habitat characteristics that affect prey availability (e.g. water depth, topography, and vegetation) should be especially important to these species, and it is these species that have shown the greatest declines in breeding populations (Crozier and Gawlik 2003a).

Water depth has been repeatedly demonstrated to be an important determinant of habitat quality (Kahl 1964; Kushlan 1976a; Powell 1987; Bancroft *et al.* 2002) but little data exists describing the effects of other habitat characteristics, most notably, vegetative structure. In aquatic ecosystems smaller aquatic prey avoid predation by larger piscivorous fish by seeking refuge in structurally complex habitats such as emergent or submerged macrophytes (Crowder and Cooper 1982; McIvor and Odum 1988; Jordan *et al.* 1996; Snickars *et al.* 2004). However, little is known about how habitat characteristics like structural complexity affect prey vulnerability in aquatic systems where predators include avian piscivores. Factors contributing to increased prey vulnerability may be one reason wading birds forage disproportionately within more open habitat (Surdick 1998; Bancroft *et al.* 2002; Stolen 2006). Studies have attempted to describe how habitat variables such as vegetation density or vegetation type influence the foraging decisions of wading birds (Hoffman *et al.* 1994; Smith *et al.* 1995; Bancroft *et al.* 2002); however, they have done so at a coarse spatial scale with broad environmental categories. While these studies have been integral to understanding the preferred habitat of wading birds in the Everglades, they do not offer an explanation of the mechanisms underlying

foraging habitat selection decisions made by birds occurring at finer spatial scales.

In this study, our objectives were to identify fine scale habitat features related to structural complexity that are important to wading bird foraging and to test how specific habitat features affect prey vulnerability. To test for the importance of foraging habitat attributes to wading birds we conducted an observational study (hereafter habitat selection study) in which we compared habitat characteristics at random sites throughout the Florida Everglades to wading bird foraging sites. We predicted that if structural complexity decreased prey vulnerability to avian predation, birds would choose to forage in more open habitat. We also conducted an experiment (hereafter prey vulnerability experiment) in which we manipulated water depth and structural complexity in three enclosures in a shallow marsh to quantify their effects on wading bird foraging success. We predicted that structural complexity would decrease prey vulnerability to avian predation; therefore, wading bird foraging success would be greater in enclosures with more open habitat.

METHODS

Study Area

The habitat selection study was conducted throughout the freshwater marshes of the Everglades during January - May of 2005 and 2006. The Water Conservation Areas (WCA-1, WCA-2A and 2B, WCA-3A and 3B), Everglades National Park (ENP), and Big Cypress National Park (BCNP) were all included in this study (Fig.1). Sampling occurred predominantly in slough and wet prairie habitats. Slough communities were typically dominated by White Water Lily (*Nymphaea odorata*) and were common in the WCAs, whereas wet prairie habitats were dominated by Spikerushes (*Eleocharis* spp.) and Maidencane (*Panicum* spp.) and were typically encountered in ENP, BCNP, and the western portion of WCA-3A.

The prey vulnerability experiment was performed concurrent to the habitat selection study during the dry season (January-February) of 2006. This study was conducted within the Loxahatchee Impoundment Landscape Assessment (LILA) facility at the Arthur R. Marshall Loxahatchee National Wildlife Refuge in Palm Beach County, Florida. LILA is situated directly adjacent to WCA-1 and is an experimental facility consisting of four replicate 7-ha impoundments (hereafter macrocosms) with topographic features that mimic key physical attributes of the Everglades. A re-circulating water system allowed the water levels in each macrocosm to be

manipulated. The advantage of conducting this study in LILA rather than in the Everglades was the control over water depth and the large number of free-ranging wading birds at the site.

Experimental Design

Habitat Selection Study. A multi stage sampling design was implemented in this study consisting of four strata levels; landscape units (LSU), primary sampling units (PSU), sampling sites, and 1-m² sub-samples. The landscape units and primary sampling units remained fixed throughout the duration of the project and were sampled repeatedly throughout the two years. The sampling sites and the sub-samples were randomly selected each year. The landscape units were pre-defined and were delineated based primarily upon hydroperiod (the number of days an area is inundated with water) and vegetation type.

Within each LSU, five PSUs 500 m × 500 m were randomly selected. Two random points within each PSU were located by helicopter and the closest suitable habitat to those points was chosen as the sampling locations. In this study, we were not interested in comparing used sites with random sites that were obviously unsuitable wading bird foraging habitat (based on earlier studies; Kushlan 1976a; Hoffman *et al.* 1994; Smith *et al.* 1995; Bancroft *et al.* 2002). Therefore, we defined suitable habitat, *a priori*, as areas of sparse to moderate vegetation that had a third of the surface area covered with water and a water depth of ≤20 cm. Thus, not all LSUs were sampled each year because annual differences in rainfall did not always produce suitable habitat.

The physical features of each random site were characterized by measuring a suite of habitat characteristics in 0.5 m² quadrants every 5 m along a transect passing through the site. Transects extended in each bearing direction (E and W) for a maximum transect length of 100 m. Habitat characteristics measured included: the density of emergent and submerged vegetation, the height of the emergent plant above the surface of the water, the thickness of the flocculent layer (a loose aggregation of unconsolidated organic matter; hereafter floc), and the percent of floating periphyton mat. Vegetation density was characterized using the point-quarter method (Cottam and Curtis 1956), where the 'nearest-neighbor' distance is inversely related to vegetation density (i.e. large nearest neighbor distances represent more open habitat). In addition to measuring fine scale habitat characteristics, the mean density of fish and invertebrates at each site was estimated using a 1-m² throw trap; a mesh box open at the top and bottom which encloses a known volume of water when it is thrown. This sampling method has been shown to provide statistically precise density information and has proven to be the best method for sampling small fish in shallow marsh habitats (for review see Kushlan 1981b; Chick *et al.* 1992).

We evaluated wading bird foraging sites by sampling at locations with large aggregations of foraging birds. Flocks of mixed species wading birds (>30 birds) were located by helicopter within the same landscape unit in which random sampling was being conducted. Across all LSUs, the distance between foraging and random sites averaged a minimum of 2.7 km and a maximum of 9.8 km (range 213 m to 25.6 km). Random and foraging sites were sampled within

the same timeframe (±1 wk) to ensure that hydrology and vegetation structure was similar at both sites in order to make relevant comparisons. We sampled the area in which the foraging aggregation was most heavily concentrated. Habitat characteristics were measured in the same manner described for random sites.

Prey Vulnerability Experiment. To determine the effect of structural complexity on prey vulnerability, we constructed three 5 m × 5 m enclosures, 50 m apart from one another in one of the LILA macrocosms. Each enclosure was constructed with polyethylene mesh which was attached to a frame and buried beneath the sediment so that each enclosure was self-contained. Bladderwort (*Utricularia* sp.), one of the most common submerged plants in the Everglades, was added to each enclosure at a stocking rate of 0 L/m², 2 L/m², or 5 L/m². Treatments were randomly assigned to the enclosures and remained the same throughout the duration of the experiment. Each enclosure was stocked with 1,500 fish (60 fish/m²), a moderate density in the natural Everglades system during the dry season. We used Eastern Mosquitofish (*Gambusia holbrooki*), one of the most abundant fish species in the Everglades (Trexler *et al.* 2002) and one that is important in the diet of many wading birds (Jenni 1969; Smith 1997). Only fish ≥2 cm were used because this is the size typically preferred by wading birds (Niethammer and Kaiser 1983; Kent 1986; Kushlan and Bildstein 1992). Existing resident fish, as well as any vegetation, were removed before stocking.

The effects of structural complexity on prey vulnerability can be mediated by water depth. As water depth decreases during the dry season, submerged vegetation collapses, creating a mat of vegetation. Dense vegetation can confound visual perception and reduce the foraging efficiency of some predators (Jordan *et al.* 1996; Priyadarshana *et al.* 2001). Conversely, structural complexity at low water depths may increase prey vulnerability to predation by inhibiting prey movement. This relationship between structural complexity and water depth has the potential to benefit the predator or the prey and could affect how wading birds select a foraging patch. Consequently, this experiment was conducted at three different water depths; 10 cm, 16 cm, and 22 cm. The 10-cm depth treatment was chosen as the minimum because, in a pilot study, shallower water depths induced fish mortality due to high water temperature and low dissolved oxygen (R. P., pers. obs.). The 22-cm depth treatment was chosen as the maximum because we did not want to eliminate smaller herons from the study due to treatments exceeding their maximum foraging depth capacity. Further, a depth threshold exists beyond which deep water provides fish refuge from avian predation (Gawlik 2002).

To attract wading birds to the experimental site, we used 1-2 white wading bird decoys per enclosure (Crozier and Gawlik 2003b). Birds foraging within the enclosures were observed using a 60x spotting scope from the nearest levee of the macrocosm and the time interval (sec) between captures was measured and averaged for each foraging bout. The observation session for each animal continued for as long as that individual remained in the area unless another bird stopped to forage (Altman 1973). Then, observations lasted for a minimum of 15 min at which time the other individual was observed. The number

of birds observed on any day ranged between one and five, for a total of 20 birds observed throughout the duration of the experiment. Observations were considered independent because there was never an instance when there was more than one bird foraging within the same enclosure at the same time and there was never an instance where more than two birds were foraging at the site at the same time. We observed foraging birds for three consecutive days at each of the three water depth treatment intervals for a total of nine experimental observation days.

Statistical Analysis

Habitat Selection Study. Discriminant function analysis (DFA; PROC DISCRIM; SAS Institute 2003) was used to determine which habitat characteristics were important to foraging site selection by wading birds. The analysis was conducted on the 2005 data only since small sample sizes in 2006 precluded the use of this procedure. All habitat variables were assessed for equal variance (Levene's homogeneity of variance test) and univariate normality (Shapiro-Wilks test statistic). Homogeneity and normality were not violated and the original variables were used in all analyses. Multicollinearity problems were detected using the Pearson correlation procedure. The F-values of intercorrelated variables were compared and the variable with the larger value remained in the dataset.

To establish the optimal combination of discriminating variables to be used in the DFA we utilized a stepwise-selection procedure (PROC STEP; SAS Institute 2003). All groups met the minimum sample size requirements ($N \geq 3P$, where P is the number of discriminating variables; Williams and Titus 1988) and the normality of the canonical scores was assessed. Validation of our results was determined using the jackknife resampling procedure (PROC DISCRIM; SAS Institute 2003). Since a certain percentage of samples in any dataset can be expected to be correctly classified based upon chance alone, we applied Cohen's kappa statistic which provided a chance-corrected classification measure and supplied a more realistic measure of discrimination (Cohen 1960; Titus *et al.* 1984).

In addition to the DFA, we also present means and 95% CI for all measured variables to identify interannual differences in habitat characteristics and wading bird responses during both years. Means represent a single pooled estimate for all LSUs combined. To calculate the means and variance, we used PROC SURVEYMEANS (SAS Institute 2003) because this procedure takes into account that the sites were clustered in space due to the stratified sampling design. PROC SURVEYMEANS uses the Taylor expansion method to estimate error, which has the benefit of being able to handle unbalanced data, unlike the traditional methods of variance estimation.

Prey Vulnerability Experiment. To determine the effect of structural complexity and water depth on wading bird foraging efficiency we used a two-way factorial ANOVA (PROC GLM; SAS Institute 2003). The response variable was the mean time interval between captures and the fixed effects were water depth, vegetation density, and the interaction between water depth and vegetation. Capture intervals were square root transformed to meet the assumption of normality. We assumed that the data obtained between days was

independent because wading birds have been shown to reassess foraging conditions on a daily basis (Gawlik 2002; Master *et al.* 2005).

RESULTS

Habitat Selection Study

In 2005, we conducted a total of 95 transects at 69 random sites and 27 foraging sites (Fig. 1) distributed throughout twelve and seven landscape units, respectively. In 2006, we characterized sites along 72 transects at 59 random sites and 13 foraging sites (Fig. 1) in seven and six landscape units, respectively.

The discriminant function analysis revealed clear differences in habitat characteristics between used and random sites in 2005 (Fig. 2). The canonical discriminant function explained 41% of the variation in the data and the overall correct classification

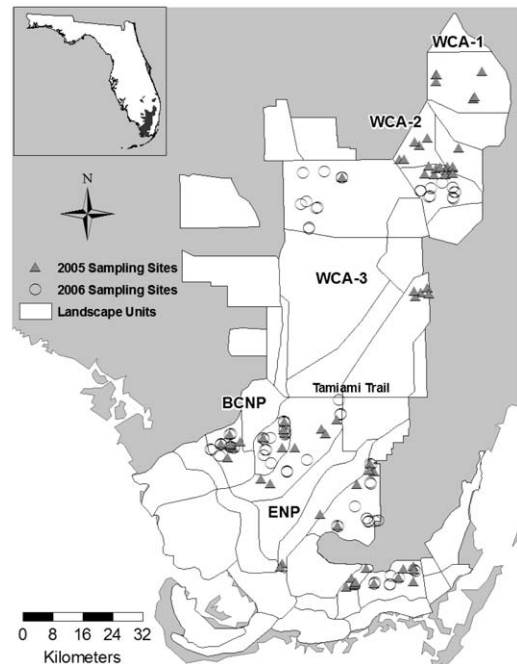


Figure 1. Spatial extent over which sampling occurred during the dry seasons (Jan-May) of 2005 and 2006 in the Florida Everglades. Sampling sites north of Tamiami Trail are part of the Water Conservation Areas (WCA) and south of Tamiami Trail are part of Everglades National Park (ENP) or Big Cypress National Park (BCNP). Sampling sites include both random and foraging locations.

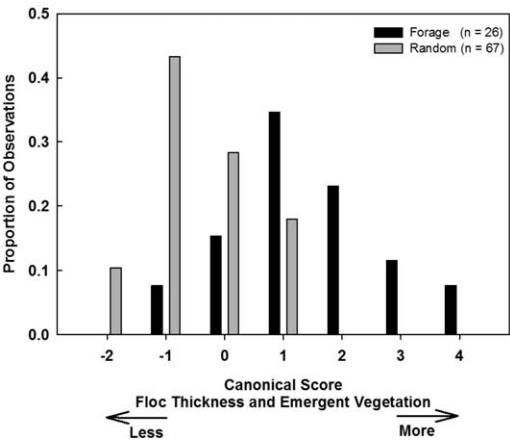


Figure 2. Distribution of discriminant function canonical scores for random and foraging sites in the dry season of 2005 in the Florida Everglades. Larger canonical scores are associated with habitat characteristics that had larger measurements. Floc thickness and emergent vegetation are listed (in order of importance) because they contributed the most to group separation (loadings ≥ 0.57).

rate was 81%, which was 37% better than chance alone. Three of the four discriminating variables that entered the model were identified as being the most important to group separation; these were the thickness of the flocculent layer, emergent stem density, and prey density (Table 1). Foraging sites had thicker floc layers, less emergent vegetation, and higher prey densities than did random sites.

Interannual Differences

A comparison of means (\pm 95% CI) indicated that in 2005, wading birds selected for-

aging sites with a thicker floc layer than at random sites [\bar{x} = 2.2 cm \pm 0.8 (random) and 5.0 cm \pm 1.6 (forage)]. In 2006, overlapping confidence intervals indicated that there was no significant difference in floc thickness between foraging and random sites [\bar{x} = 0.5 cm \pm 1.2 (random) and 1.7 cm \pm 2.1 (forage)], but it tended to be greater at foraging sites, as it was in 2005 (Table 2).

Birds selected foraging sites with significantly less dense emergent vegetation than random sites [\bar{x} = 9.1 cm \pm 0.9 (random) and 13.6 cm \pm 2.5 (forage)]; larger values represent more open habitat] in 2005; in 2006, the density of emergent vegetation was similar between random and foraging sites [\bar{x} = 13.0 cm \pm 1.1 (random) and 13.6 cm \pm 3.7 (forage)]. In both years birds selected foraging sites with identical vegetation densities (Table 2).

In 2005, birds selected foraging sites with a higher mean prey density than at random sites, but the high variability resulted in overlapping 95% confidence intervals [\bar{x} = 81 prey/m² \pm 27 (random) and 184 prey/m² \pm 196 (forage)]. In 2006, birds selected sites with a prey density similar to random sites [\bar{x} = 142 prey/m² \pm 70.8 (random) and 126 prey/m² \pm 70.5 (forage)]. However, prey at random sites was considerably higher in 2006 than in 2005 (Table 2).

Similar to the DFA, a comparison of the mean density of submerged vegetation between random and foraging sites indicated that there was no major difference in 2005 or 2006 [2005: \bar{x} = 24.1 cm \pm 13.5 (random) and 20.4 cm \pm 8.6 (forage); 2006: 11.9 cm \pm 4.3 (random) and 8.8 cm \pm 4.7 (forage)]; larg-

Table 1. Habitat variables for wading bird foraging sites and random sites throughout the Florida Everglades with the corresponding correlation coefficients for the canonical discriminant function. Bold values represent significant differences between the two groups.

Habitat Variables	Forage Sites (N = 26) ^a	Random Sites (N = 67)	DFA correlation coefficient ^b
Floc Thickness (cm)	5.0 \pm 1.6^c	2.2 \pm 0.8	0.91
Emergent Vegetation (cm) ^d	13.6 \pm 2.5	9.1 \pm 0.9	0.57
Prey Density (prey/m ²)	183.7 \pm 196	80.6 \pm 27	0.44
Floating Periphyton (%)	4.8 \pm 3.9	1.8 \pm 1.3	0.34

^aSample size.
^bCoefficients < 0.44 were deemed unimportant.
^cMean \pm 95% Confidence Interval.
^dHigher values for emergent vegetation = more open habitat.

Table 2: Means (\pm 95% CI) for measured habitat characteristics at random and foraging sites throughout the Everglades in 2005 and 2006.

Habitat Variables	2005 Sites		2006 Sites	
	Random (N = 69)	Forage (N = 27)	Random (N = 59)	Forage (N = 13)
Emergent Vegetation (cm)	9.1 \pm 0.9	13.6 \pm 2.5	13.0 \pm 1.1	13.6 \pm 3.7
Submerged Vegetation (cm)	24.1 \pm 13.5	20.4 \pm 8.6	11.9 \pm 4.3	8.8 \pm 4.7
Floc Thickness (cm)	2.2 \pm 0.8	5.0 \pm 1.6	0.5 \pm 1.2	1.7 \pm 2.1
Emergent Height (cm)	45.4 \pm 2.3	40.8 \pm 5.5	36.4 \pm 2.7	30.7 \pm 5.8
Floating Periphyton (%)	1.8 \pm 0.6	4.8 \pm 1.9	6.0 \pm 2.0	8.3 \pm 4.9
Prey Density (prey/m ²)	80.6 \pm 27	183.7 \pm 196	142 \pm 70.8	126 \pm 70.5

er values represent more open habitat]. However, the nonsignificant tendency was similar in both years; the trend being that birds chose foraging sites that had more submerged vegetation.

Prey Vulnerability Study

Over the observation period of nine days, the Snowy Egret (N = 20) was the only species to consistently forage within the experimental enclosures so our analysis was restricted to this species. We were unable to detect a difference in Snowy Egret capture intervals among any of the submerged vegetation treatments ($F_{2,30} = 2.27$, $P = >0.05$) or the water depth treatments ($F_{2,30} = 1.41$, $P > 0.05$; Fig. 3).

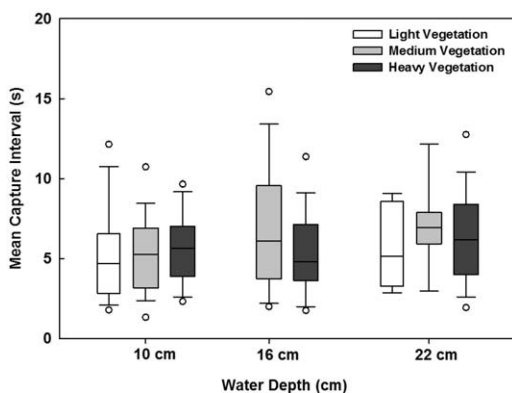


Figure 3. Mean time interval (s) between captures made by Snowy Egrets (n = 20) foraging within three vegetation treatments at three different water depths. Black bars within each box plot denote the median; boxes encompass 50% of the data while whiskers (SE) encompass 90% of the data; open circles represent the 5th and 95th percentile outliers. The missing box plot at the 16-cm water depth indicates that no birds foraged within the open vegetation treatment.

DISCUSSION

Field observations demonstrated that, in addition to coarse scale habitat selection documented by other studies (Hoffman *et al.* 1994; Smith *et al.* 1995; Bancroft *et al.* 2002), wading birds also select habitat characteristics at fine spatial scales. The discriminant function analysis indicated that wading birds selected foraging sites with a thicker floc layer and less emergent vegetation than that generally available in the landscape. Despite support for fine scale habitat selection, the canonical scores also revealed that there was similarity between random and foraging sites. This similarity exists because of how available habitat was defined in this study. We chose sites based on prior knowledge of the habitat in which wading birds typically forage (Hoffman *et al.* 1994; Smith *et al.* 1995; Bancroft *et al.* 2002). The predefined criteria precluded sites that were unsuitable foraging habitat so that within each LSU all sampled locations were similar to each other in regard to hydrology and vegetative structure. Therefore, the differences that were detected among these similar sites are more likely to be biologically meaningful instead of an artifact of a random sampling design.

The response of birds choosing foraging sites that had thicker floc layers is counterintuitive and the opposite of what was expected (e.g. that increased floc thickness would reduce foraging site quality by decreasing prey vulnerability). Prey species appear to use the floc layer to reduce their visibility and decrease the likelihood of capture (R. P., pers. obs.). One explanation for the con-

tradictory response by birds is that the thickness of the floc layer is indicative of other factors that increase the quality of a foraging site. Flocculent material is rich in organic matter and has been shown to be an important source of nutrients in an oligotrophic system (Wood 2005) and nutrient rich areas in the Everglades have higher aquatic animal densities (Turner *et al.* 1999; McCormick *et al.* 2004; Rehage and Trexler 2006). Further, parts of the system having the thickest floc layers are often open slough areas that are associated with intermediate to long hydroperiod marshes (Leonard *et al.* 2006). Increased hydroperiod has been linked with increased fish densities and increased fish biomass (Loftus and Eklund 1994; Trexler *et al.* 2002; Chick *et al.* 2004). Many studies have documented that birds use visual cues within the landscape to reduce search time when choosing foraging locations (Kushlan 1976b; Custer and Osborn 1978; Gawlik and Crozier 2007; Master *et al.* 2005). Thus, the thickness of the floc layer could act as a visual cue indicating favorable foraging habitat. Another explanation could be that sites that had the thickest flocculent layers were found in parts of the system that had increased microtopographic variation (e.g. ridge and slough habitat, peat pop-ups, or solution holes). These areas often become densely concentrated with prey as the landscape dries. In this case, wading birds may not be responding to floc thickness, but instead to the increased microtopography, which was a parameter not considered in this study.

In both study years, wading birds selected foraging sites with less emergent vegetation than random sites and with similar densities of emergent vegetation despite the fact that this habitat characteristic varied greatly in the landscape. These results are consistent with other habitat selection studies that have suggested that emergent vegetation is an important variable for foraging habitat selection at coarse (Hoffman *et al.* 1994; Smith *et al.* 1995; Bancroft *et al.* 2002) as well as fine spatial scales (Surdick 1998). Wading birds may be selecting areas of sparse emergent vegetation to reduce the risk of predation (Metcalf 1984; Cresswell 1994). However,

healthy adult wading birds are rarely preyed upon and the explanation for this lack of predation, to date, has never been tested (Kushlan 1981a). It is more likely that wading birds avoid areas of dense emergent vegetation because they inhibit foraging success by reducing the vulnerability of prey. Studies of wading birds foraging in rice fields have indicated that birds expend more energy per unit time in this habitat type and also have decreased capture rates as a result of the dense nature of these plants (Campos and Lukuona 2001; Richardson *et al.* 2001). Batzer and Shurtleff (1999) found that a pond being managed for feeding Wood Storks was underutilized by this species because stocked prey sought refuge in nearby macrophyte beds and were not vulnerable to capture.

Conversely, some species of waterbirds have been found to forage at the interface of open water and vegetation (Safran 2000; Bennetts *et al.* 2006; Stolen *et al.* 2007) and to preferentially select low stature wet-prairie habitats despite the existence of more open areas (Smith *et al.* 1995). If wading birds are responding to availability, they must assess prey density and prey vulnerability simultaneously. Therefore, if birds choose to forage in or near highly vegetated areas, prey density must be high enough to offset reduced prey vulnerability.

Unlike the response to emergent vegetation, birds seemed to be inhibited little by submerged vegetation. This variable did not enter the discriminant model as being a significant contributor to group separation nor was there any difference in either 2005 or 2006 in the mean density of submerged vegetation between random sites and sites selected by birds. Further, this result was also supported experimentally; we were unable to detect an effect of submerged vegetation on capture intervals of foraging Snowy Egrets. This suggests that prey vulnerability was not sufficiently decreased due to increased submerged structural complexity to affect foraging efficiency. These results were consistent with other studies that have shown that wading bird foraging success is not negatively affected by submerged vegetation (see Safran 2000; Adams and Frederick 2008; Lantz 2008).

The lack of a response to submerged vegetation in our studies may be the result of several factors. Submerged vegetation may not provide enough structural complexity to inhibit foraging success. Gawlik (2002) and Master *et al.* (2005) demonstrated that wading birds respond strongly to habitat with active and accessible prey. Submerged vegetation likely does not prevent the birds from recognizing disturbance of the water's surface caused by surface breathing fish or an escape response by fish to an approaching wading bird. Coupled with the fact that prey are easily flushed from cover by the typical egret behavior of foot-stirring, this could allow wading birds to be effective foragers in areas of dense submerged vegetation. Papa-kostas *et al.* (2005) found that Squacco Herons (*Ardeola ralloides*) had higher success rates foraging in open water with submerged vegetation relative to other microhabitat types, suggesting that submerged vegetation may be beneficial to foraging wading birds. In addition, birds are probably highly visible to their prey in open water habitats. Submerged macrophyte beds may act as a buffer against moving water caused by herons' wading which may allow birds to approach closer to prey without being noticed (Matsunaga 2000).

The comparison of means between the two study years indicated apparent differences in interannual habitat selection. In 2005, wading birds appeared to be selecting foraging sites that were different from what was available in the landscape; in 2006, birds selected sites that were more similar to the landscape. One explanation for this was the disparate hydrological conditions between the two years. The 2005 dry season experienced several rainfall events which resulted in the reversal of the seasonal water recession. In 2006, ideal hydrological conditions existed throughout the dry season. In years with ideal hydrology, high densities of prey throughout the landscape are probably more important to wading bird success than fine scale variations in habitat characteristics. However, in years with poor hydrological conditions the penalty for choosing a low quality foraging site may be much greater

than in years with more optimal conditions. Under these conditions, habitat structure would become an increasingly important component of habitat quality.

Species that reside in highly dynamic, patchy environments must rely heavily on social and environmental cues to locate high quality foraging habitat (Weins 1976; Green and Leberg 2005; Gawlik and Crozier 2007). This study identified specific fine scale habitat variables that are important to wading bird foraging site selection and also identified landscape characteristics which may act as visual cues guiding birds to higher quality foraging sites. Although strong habitat selection was apparent in this study, it is still unclear how these habitat variables may influence foraging success. Habitat preference is thought to be adaptive and affect fitness (Pulliam and Danielson 1991; Martin 1998). Therefore, it is likely that birds benefit from choosing foraging locations having specific habitat characteristics even though these benefits have not yet been quantified. The advantage of foraging at sites with specific habitat characteristics may not be realized until foraging conditions are sub-optimal, such as they are during times of high water conditions, extreme drought, or in areas with low prey density.

Wading birds are considered to be an indicator of ecosystem health. Thus, many restoration plans, including the Comprehensive Everglades Restoration Plan (CERP), use healthy wading bird populations as a target for restoration success. However, before wading birds can be reliably used as a performance measure it is necessary to have a clear understanding of the linkage between wading birds and the ecosystem processes that are being restored (Gawlik 2006). Knowledge of the type of habitat characteristics that create high quality wading bird foraging sites in the Florida Everglades is an important step in beginning to elucidate this linkage. Incorporating this type of information into continually evolving conceptual models in an adaptive management framework will assist managers in gauging future restoration progress.

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