

THE EFFECTS OF WATER DEPTH AND SUBMERGED AQUATIC VEGETATION ON THE SELECTION OF FORAGING HABITAT AND FORAGING SUCCESS OF WADING BIRDS

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Abstract. Successful foraging by avian predators is influenced largely by prey availability, which encompasses not only the density of prey but also its vulnerability to capture. For wading birds (Ciconiiformes), habitat features such as water depth and density of vegetation are thought to affect the vulnerability of their aquatic prey. In January and April 2007 we experimentally manipulated the depth of water and density of submerged aquatic vegetation (SAV) in enclosures (10 × 10 m) with equal densities of fish to determine their effects on wading birds' selection of foraging habitat and foraging success. Analysis of the results with Manly's selection index showed that wading birds preferred habitat with shallow water and SAV. The two habitat components had little effect on the birds' foraging success, however, as capture rate did not vary with water depth or SAV density. Capture efficiency did not vary by SAV density and was actually lower in shallow water, contrary to our expectations. Our results suggest that birds selected habitat on the basis of environmental cues such as water depth and SAV but that these factors did not affect foraging success strongly. We hypothesize that wading birds were selecting habitat with shallow water and SAV because of an anticipated benefit to foraging through elevated density and vulnerability of prey, but the relatively high and uniform density of prey stocked in the enclosures, as well as the scale of the enclosures, effectively equalized the vulnerability of prey across treatments.

Key words: *foraging, prey availability, Everglades, foraging-habitat selection, foraging success.*

Efectos de la Profundidad del Agua y de la Vegetación Acuática Sumergida sobre la Selección de Ambientes de Alimentación y el Éxito de Forrajeo de Aves Vadeadoras

Resumen. El forrajeo exitoso de las aves depredadoras es influenciado de forma importante por la disponibilidad de presas, la cual no sólo comprende la densidad de las presas sino también su vulnerabilidad a ser capturadas. Se cree que ciertas características del hábitat como la profundidad del agua y la densidad de la vegetación afectan la vulnerabilidad de las presas acuáticas de las aves vadeadoras (Ciconiiformes). Para determinar sus efectos sobre la selección del hábitat de alimentación y el éxito de forrajeo de las aves vadeadoras, manipulamos experimentalmente la profundidad del agua y la densidad de la vegetación acuática sumergida (VAS) en áreas cercadas (10 × 10 m) con densidades iguales de peces en enero y abril de 2007. Nuestros análisis de los resultados con el índice de selección de Manly mostraron que las aves vadeadoras prefirieron ambientes con aguas someras y VAS. Sin embargo, los dos componentes del hábitat tuvieron efectos débiles sobre el éxito de forrajeo de las aves, pues la tasa de captura no varió con la profundidad ni con la densidad de la VAS. La eficiencia de captura no varió con respecto a la densidad de la VAS y, de hecho, fue menor en aguas someras, un resultado contrario a lo que esperábamos. Nuestros resultados sugieren que las aves seleccionaron el hábitat con base en señales ambientales como la profundidad del agua y la VAS, pero esos factores no afectaron al éxito de forrajeo fuertemente. Planteamos la hipótesis de que las aves vadeadoras estaban seleccionando ambientes con aguas someras y VAS debido a que anticipaban un beneficio relacionado con el forrajeo mediante niveles mayores de densidad y vulnerabilidad de las presas. Sin embargo, la densidad relativamente alta y uniforme de las presas ubicadas en las áreas cercadas, así como la escala de estas áreas, efectivamente condujeron a igualar la vulnerabilidad de las presas entre los tratamientos.

INTRODUCTION

Food availability can be a major factor limiting avian populations (Skutch 1949, Lack 1954, 1966). The availability of food depends on both its density and accessibility. For organisms that forage by capturing mobile prey, the potential of prey

escape is an additional factor that emphasizes the importance of prey vulnerability. Prey availability is thus a composite variable consisting of both prey density and the vulnerability of that prey to capture, the latter being affected by various characteristics of the predator, prey, and environment (Wiens 1984, Sutherland 1996, Gawlik 2002).

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For predatory birds, prey vulnerability is an important but sometimes underappreciated component of prey availability. An example of a characteristic of avian predators that can influence prey vulnerability is the bill length of shorebirds, which may constrain the depth at which prey can be extracted from sediments. Prey items below a threshold depth in the sediment or water column are not available to these avian predators.

For wading birds (Ciconiiformes), multiple environmental characteristics contribute to prey vulnerability. Water depth can strongly influence wading birds' selection of foraging habitat (Smith et al. 1995, Strong et al. 1997, Arengo and Baldassarre 1999, Ntiamoa-Baidu et al. 1998, Gawlik 2002, Master et al. 2005, Gawlik and Crozier 2007). The length of wading birds' legs can determine the maximum depth at which they can forage and so limit the habitat suitable for their foraging. Master et al. (2005) observed that Snowy Egrets (*Egretta thula*) prefer shallow rather than deep pools in tidally influenced salt marsh. Because they found that water depth was not related to prey density, they suggested that Snowy Egrets selected the shallower pools because of greater access to prey (i.e., prey more vulnerable to capture). Thus water depth can affect both accessibility of foraging habitat and the vulnerability of prey to wading birds.

Submerged aquatic vegetation (SAV) also has great potential to influence the vulnerability of wading birds' prey, yet few studies have examined the relationships between SAV and wading birds' decisions in foraging. Many previous studies (e.g., Hoffman et al. 1994, Smith et al. 1995, Bancroft et al. 2002) used aerial sampling that could not assess SAV. Vegetation adds structural complexity to the water column, which increases the prey use of these areas in the presence of predators (Werner et al. 1983), and the density of prey is often higher in vegetated than in nonvegetated areas (Dvorac and Best 1982, Diehl 1988, Rozas and Odum 1988). In areas of structural complexity, prey may alter their behavior through microhabitat depression to lower their risk of attack (i.e., by using substrates such as SAV for cover; Charnov et al. 1976). Thus, although prey densities may often be higher in vegetated habitat, the relative changes to vulnerability will ultimately determine whether these prey are more available to predators.

Studies have shown that prey availability within a habitat is important in determining wading birds' selection of a site for foraging (Ntiamoa-Baidu et al. 1998, Laubhan and Gammonley 2000, Safran et al. 2000, Gawlik 2002). In seasonally fluctuating wetlands such as the Florida Everglades, habitat conditions change as water recedes through the dry season, so to select productive patches, wading birds must reassess potential foraging habitat continuously. Although the specifics of patch selection are unclear, wading birds evaluate prey availability by environmental and social cues, including visual cues indicating the presence of fish (Kushlan 1976a, Master 1992, Master et al. 2005, Gawlik and Crozier 2007). To nest successfully, wading birds must locate these areas of high

prey availability (Powell and Powell 1986, Frederick and Spalding 1994). The idea that prey availability limits populations of wading birds is termed the "prey-availability hypothesis" (Gawlik 2002). Decreased prey availability is thought to constrain avian populations in the Florida Everglades (Gawlik 2002) and in other wetlands around the world (Butler 1994, Hafner 1997). The decline in wading bird populations in the Everglades appears to be a response to major changes in hydrology (Kushlan et al. 1975, Ogden 1994). Man-made hydrologic changes, including construction of canals and levees in combination with draining, have drastically altered the natural water flow across the Everglades (Light and Dineen 1994). A key objective of the Everglades restoration is to re-establish a more natural hydrologic regime, and wading birds are useful bioindicators of ecosystem health and restoration.

Understanding the mechanisms by which habitat features like water depth and vegetation structure affect the availability of prey, and ultimately the quality of sites where wading birds feed, is a precursor for predicting how future habitat changes will affect wading bird populations. Currently, there are no models of how structural complexity may reduce the vulnerability of prey to avian predation or how vegetation density may affect wading birds' foraging success. Our objectives in this study were to experimentally test the effects of water depth and SAV density on the availability of prey to foraging wading birds, measured quantitatively through foraging-site selection and foraging success. We hypothesized that wading birds should preferentially select foraging habitat with shallow water and lower densities of SAV because of increased prey availability. In addition, we hypothesized that wading birds' foraging success within the selected habitats should be higher.

METHODS

STUDY AREA

To quantify the effects of SAV and water depth on wading birds' foraging-habitat selection and foraging success, we conducted one experiment in January 2007 and then repeated the experiment in April 2007. Both experiments were done at the Loxahatchee Impoundment Landscape Assessment in the Arthur R. Marshall Loxahatchee National Wildlife Refuge, Boynton Beach, Florida (see van der Valk et al. 2008). The complex consists of four 7-ha impoundments with a system that recirculates water and allows control over water depths. The impoundments ("macrocosms") were designed to mimic the physical features of the Everglades and consist of sloughs of deep and shallow open water separated by vegetated ridges.

EXPERIMENTAL DESIGN

Three 10- × 10-m enclosures were constructed in both the deep and shallow sloughs of two macrocosms. This size of enclosure is large enough to accommodate a flock of birds with their social behaviors but small enough for vegetation densities

and prey communities to be controlled. Enclosures were surrounded by a square floating curtain of black knotless nylon, mesh 3 mm. A weighted line was sewn around the bottom of the curtain and pushed into the sediment. Buoyant strips of closed-cell foam were affixed to the top of the curtain to create a continuous floating barrier to fish. Floats protruded approximately 1 cm out of the water so as to be inconspicuous to foraging birds.

We used two treatments of water depth to evaluate effects on wading birds' foraging, 10 cm in the shallow slough and 25 cm in the deep slough (shallow and deep, respectively). Depths were chosen on the basis of the maximum depths at which the target species wading birds forage. The shallow treatment was less than all species' maximum foraging depth, while the deeper treatment was readily available to the longer-legged Great Egret (*Ardea alba*), Great Blue Heron (*A. herodias*), and Wood Stork (*Mycteria americana*) and at the maximum depth threshold of smaller species (Powell 1987, Gawlik 2002).

The structural complexity of vegetation within the enclosures varied from no vegetation to high density. To ensure that enclosures were cleared of vegetation initially, we gathered the enclosure walls in the center of the study plot, then expanded them outward, removing any remaining vegetation by hand. We collected SAV from nearby marshes within the refuge and stocked each enclosure with 0, 2, or 5 L m⁻² of bladderwort (*Utricularia* sp.; "0," "light," and "heavy" densities, respectively). We chose this species because it is native to and characteristic of the Florida Everglades (Loveless 1959, Gunderson 1994).

We placed minnow traps in the enclosures 2 days prior to the experiment to remove existing prey. Enclosures were then stocked with 20 m⁻² eastern mosquitofish (*Gambusia holbrooki*), which is one of the most numerous native fish in the Everglades (Jenni 1969, Trexler et al. 2002) and common in the diet of many wading birds (Smith 1997). The density at which we stocked prey-sized fish would be considered high for the Everglades in the wet season (Trexler et al. 2002) but only one-third the average densities measured in concentrated pools during the dry season by Gawlik and Botson (2008). Fish were purchased from a commercial fish farm or caught locally by a combination of seining and minnow trapping. Their average standard length (excludes tail) was 2.56 ± 0.42 cm.

Every morning of the experiment, we placed white plastic decoys mimicking wading birds in each enclosure (Crozier and Gawlik 2003). These decoys served to attract wading birds to the macrocosms to forage and to ensure that birds were aware of each of our treatments. Sociality contributes significantly to wading birds' selection of foraging habitat (Caldwell 1981, Master 1992, Master et al. 1993, Gawlik and Crozier 2007). Krebs (1974) showed that decoys may attract wading birds to a specific area. In the January experiment, we placed two decoys in each enclosure (modified plastic lawn flamingos; see Crozier and Gawlik 2003). During the second experiment, when the foraging in surrounding areas was

excellent and wading birds were less attracted to small numbers of decoys, we increased the number of these decoys to five and added two Great Egret decoys to each enclosure. We removed decoys at the completion of observations each day.

On foot or from a vehicle, we observed the macrocosm from the surrounding levee. The presence of an observer or vehicle on the levee did not appear to change the birds' behavior. In January, the experiment ran 7 alternate days between 19 and 31 January. The second experiment ran from 3 to 17 April. Days on which fewer than 10 birds foraged in the macrocosms were eliminated from analysis, leaving a total of 5 days of observations in April. We assumed days to be independent because birds reassess patches within a general area (hundreds of square meters) each morning (Gawlik 2002, Master et al. 2005). Because foraging birds depleted enclosures of fish we restocked them with the appropriate number of fish each morning to restore the initial density. In this way, the density of fish in enclosures at the start of each morning of observation remained constant, and birds were required to assess foraging conditions daily.

To ensure the densities of fish were constant, we used mark-recapture methods to restock enclosures daily. Each day of the experiment, we marked batches of fish with Visible Implant Elastomer (Northwest Marine Technology, Shaw Island, WA) in one of six colors (red, orange, yellow, green, blue, and pink) unique to the day. This technique has been used successfully in fish as small as 8 mm (Frederick 1997). Prior to marking, we anesthetized fish with 50 parts per million of tricaine methanesulfonate (MS-222). Using 28-gauge insulin needles, we marked the fish above the lateral line and anterior to the caudal peduncle by injection with a small line of elastic polymer. By injecting the polymer into the fish while pulling the needle out, we created a lateral mark 1–2 mm long that terminated while the needle was still under the skin. Visible Implant Elastomer is made of surgical-quality plastic, with nontoxic dyes, and is not expected to affect the health of wading birds ingesting tagged fish (Northwest Marine Technology biological support, pers. comm.).

At the end of each day of observations, we placed bird netting over each enclosure to close the population of fish. A subsample of 200 marked fish (10% of the initial stock) was released into each enclosure and allowed to disperse for at least 2 hr. We then recaptured fish with minnow traps baited with pellets of fish food, which were allowed to soak for a minimum of 6 hr. We used Lincoln–Peterson population estimates (Williams et al. 2002) to assess the populations and added fish to restore the original density at which they were stocked.

FORAGING-HABITAT SELECTION

We quantified wading birds' selection of foraging habitat by identifying and counting birds foraging in each enclosure and comparing habitat use to availability. We recorded the numbers and arrival times of all birds foraging in the enclosures and their departure times and movements between enclosures.

Observers recorded the number of wading birds in each enclosure every 15 min for the entire observation period, which began at dawn and lasted approximately 3 hr. Because of the potential influence of sociality once birds began foraging within the enclosures, we scored enclosures as either used (1) or unused (0) for each of these 15-min intervals then averaged these scores over the entire morning to get a snapshot of use of the enclosures every day. Thus an enclosure with birds present for the entire duration would be given a score of 1, and an enclosure with birds present during half of the scans would be given a score of 0.5. We assumed that censuses within a day were not independent because birds often foraged within multiple enclosures or returned to enclosures where they had previously fed, so we averaged censuses throughout the morning to generate a single value representing bird use of an enclosure on that day. To evaluate selection of foraging habitat, we used Manly's selection index (Manly et al. 2004) to compare wading birds' use of the enclosures to availability of the enclosures, which was equal for all treatments. We analyzed the January and April experiments separately because in April birds avoided the deep-water treatment altogether, suggesting that pressures for habitat selection in the two months differed. Therefore, we compared wading birds' presence in association with vegetation density and water depth to availability across days for a total of 7 days in January and 5 days in April.

FORAGING SUCCESS

We videotaped birds foraging in the enclosures, then quantified foraging success by analyzing the videotapes and constructing time–activity budgets. We analyzed each individual bird separately to determine its rate and efficiency of capture. To minimize observer bias, one observer devised all time–activity budgets.

We analyzed videos with EthoLog 2.2, a tool for recording behavioral observations and their timing (Ottoni 2000). We recorded foraging techniques as state events and activities as instant events. All techniques and activities not given key codes in EthoLog were keyed in as “other,” and these behaviors were subsequently described. We defined foraging techniques as stand and wait, walking, probing, groping, or other, an umbrella term encompassing the remainder of feeding strategies as described by Kushlan (1976b) and Kelly et al. (2003). We measured foraging activity by recording the number of successful and unsuccessful strikes. We defined capture rate as the number of prey captured per minute and capture efficiency as the number of prey captured divided by the total number of attempts (successful strikes/total strikes). Both capture rate and capture efficiency were analyzed for all species pooled and for the Great Egret and Snowy Egret separately. For the White Ibis (*Eudocimus albus*) we analyzed only capture rate because we could not calculate the capture efficiencies of probing species.

Data were tested for normality prior to analyses. We used a square-root transformation of capture rate based on the slopes of the linear regression of \ln variance vs. \ln mean (Box et al. 1978). No transformation was necessary for capture efficiency. We analyzed January foraging-success data with a two-way analysis of variance (ANOVA) with water depth and SAV density as treatment variables (type III general linear model, PROC GLM, SAS version 9.1). Because in April birds selected the shallow-water enclosure exclusively (see Results), for that month we analyzed the effects of vegetation on foraging success with a one-way ANOVA with SAV density as the treatment variable. We compared the differences between experiments in capture rates and efficiencies in shallow water for all species pooled with a two-way ANOVA with terms for experiment, SAV density, and experiment \times SAV density.

RESULTS

FORAGING-HABITAT SELECTION

Great Blue Herons, Great Egrets, Glossy Ibises (*Plegadis falcinellus*), Little Blue Herons (*Egretta caerulea*), Snowy Egrets, Tricolored Herons (*E. tricolor*), White Ibises, and Wood Storks were all observed foraging within the experimental enclosures. At any given time, wading bird use ranged from 0 to 31 birds per enclosure and from 0 to 78 birds summed throughout the enclosures.

The comparison of wading birds' presence in the enclosures to availability by Manly's selection index showed that wading birds generally preferred the water 10 cm deep over that 25 cm deep (Table 1). The strength of this relationship appeared to be affected by the timing of the experiment. In April, wading birds selected only the enclosures with shallow water ($B_{\text{shallow}} = 1.0$, $B_{\text{deep}} = 0.0$). In January, they used all treatment combinations, tending to select the shallow water over the deep ($B_{\text{shallow}} = 0.581$, $B_{\text{deep}} = 0.419$), but confidence intervals for the two depth treatments overlapped slightly. Selection of vegetation treatments in the two months varied somewhat, although generally the birds preferred vegetated habitats. In January, the birds' strongest preference was for the “heavy” treatment, followed by the “light” treatment (Table 1). In the April experiment, however, birds selected the “light” and “0” treatments over the “heavy” treatment (Table 1).

FORAGING SUCCESS

We recorded 576 time–activity budgets totaling 3504 min. Durations of foraging ranged from 1 to 18 min ($n = 576$; mean \pm SE, 6.07 ± 4.32 min). The capture rate for all species pooled varied significantly by experiment ($P < 0.001$; Table 2), with most species' capture rates being higher in April (Table 3). In January, neither water depth, SAV density, nor the interaction between the two had a significant effect on capture rate for all species pooled ($P = 0.897$, $P = 0.743$, $P = 818$, respectively;

TABLE 1. Manly's selection index foraging-habitat selection for wading birds in January ($n = 7$ days) and April ($n = 5$ days). Use by wading birds was compared to availability across six enclosures at the Arthur R. Marshall Loxahatchee National Wildlife Refuge.

Month	Water depth (cm)	SAV ^a density	Population proportion	Used sample proportion	Confidence limits	
					Lower	Upper
January	10	0	0.167	0.143	0.079	0.207
	10	2	0.167	0.186	0.115	0.257
	10	5	0.167	0.252	0.173	0.332
	25	0	0.167	0.048	0.009	0.086
	25	2	0.167	0.176	0.107	0.246
	25	5	0.167	0.195	0.123	0.267
April	10	0	0.167	0.318	0.187	0.449
	10	2	0.167	0.477	0.337	0.618
	10	5	0.167	0.205	0.091	0.318
	25	0	0.167	0	0	0
	25	2	0.167	0	0	0
	25	5	0.167	0	0	0

^aSAV, submerged aquatic vegetation.

Table 4). The Great Egret had a significantly higher capture rate in the deep water ($P = 0.004$; Table 4), but the capture rate of the Snowy Egret and White Ibis were not affected by water depth or SAV (Table 4). In April, SAV density did not

TABLE 2. Analysis of variance by type III general linear model for effects of experiment on the capture rates and capture efficiencies of foraging wading birds were compared in shallow water for all species pooled with terms for experiment, density of submerged aquatic vegetation (SAV), and experiment \times SAV density.

Source	Error df	df	MS	<i>F</i>	<i>P</i>
Capture rate					
Experiment	529	1	28.285	101.37	<0.0001
SAV density	529	2	0.718	2.57	0.077
Experiment \times SAV density	529	2	0.014	0.05	0.951
Capture efficiency					
Experiment	263	1	0.038	0.53	0.469
SAV density	263	2	0.121	1.68	0.188
Experiment \times SAV density	263	2	0.082	1.14	0.322

significantly affect capture efficiencies of all species pooled or any of the species tested individually (Table 4).

Capture efficiency did not vary significantly by experiment ($P = 0.469$; Table 2). In January, none of the treatment variables had an effect on capture rates of all species pooled or of the species tested individually (Table 5). In April, foraging efficiency was not affected by SAV density for all species pooled or for the Snowy Egret but was weakly significant for the Great Egret ($P = 0.045$; Table 5).

TABLE 3. Capture rates (CR) and capture efficiencies (CE) of the Great Egret, Little Blue Heron, Snowy Egret, Tricolored Heron, Glossy Ibis, and White Ibis in January and April 2007. For all species except the Great Egret results are for the shallow-water treatment only. Only for the Great Egret were both water-depth treatments analyzed; results for deep water and shallow water are presented separately. Results are presented as mean captures $\text{min}^{-1} \pm \text{SE}$.

Species	SAV density	January				April			
		CR \pm SE	<i>n</i>	CE \pm SE	<i>n</i>	CR \pm SE	<i>n</i>	CE \pm SE	<i>n</i>
Great Egret (shallow water)	0	0.29 \pm 0.55	13	0.30 \pm 0.36	12	0.73 \pm 1.04	2	0.75	1
	light	0.19 \pm 0.34	9	0.60 \pm 0.55	5	0.75 \pm 0.67	9	0.33 \pm 0.13	9
	heavy	0.21 \pm 0.31	13	0.38 \pm 0.43	12	0.23	1	0.33	1
Great Egret (deep water)	0	1.58	1	1.00	1	—	—	—	—
	light	0.68 \pm 0.85	9	0.56 \pm 0.31	8	—	—	—	—
	heavy	0.26 \pm 0.18	9	0.68 \pm 0.30	7	—	—	—	—
Little Blue Heron	0	0.06 \pm 0.14	5	0.25 \pm 0.25	3	1.23 \pm 0.78	14	0.52 \pm 0.22	14
	light	0.28 \pm 0.23	12	0.57 \pm 0.33	7	1.21 \pm 0.77	17	0.51 \pm 0.20	17
	heavy	0.58 \pm 0.41	15	0.51 \pm 0.36	16	1.60 \pm 1.59	5	0.70 \pm 0.26	4
Snowy Egret	0	0.29 \pm 0.34	10	0.26 \pm 0.34	9	0.90 \pm 0.79	42	0.23 \pm 0.13	42
	light	0.53 \pm 0.66	15	0.30 \pm 0.31	14	1.17 \pm 1.11	67	0.27 \pm 0.16	66
	heavy	0.28 \pm 0.33	10	0.14 \pm 0.14	10	1.49 \pm 1.36	15	0.30 \pm 0.22	15
Tricolored Heron	0	0.54 \pm 0.70	6	0.39 \pm 0.22	5	0.99	1	0.40	1
	light	0.23 \pm 0.24	3	0.39 \pm 0.54	3	0.88	1	0.50	1
	heavy	1.31 \pm 0.22	2	0.49 \pm 0.01	2	—	0	—	0
Glossy Ibis	0	1.75	1	—	—	1.51 \pm 0.49	4	—	—
	light	—	0	—	—	1.51 \pm 1.22	18	—	—
	heavy	1.11 \pm 0.41	7	—	—	1.06 \pm 0.92	12	—	—
White Ibis	0	0.98 \pm 1.13	19	—	—	1.78 \pm 1.45	53	—	—
	light	0.79 \pm 0.71	25	—	—	1.9 \pm 1.44	44	—	—
	heavy	1.02 \pm 0.85	27	—	—	2.24 \pm 2.07	38	—	—

TABLE 4. Type III general linear model analysis of variance for capture rates of wading birds for all species pooled and for the Great Egret, Snowy Egret, and White Ibis in relation to water depth and density of submerged aquatic vegetation (SAV) in January and SAV density in April.

Source	Error df	df	MS	F	P
January					
All species	227				
Water depth		1	0.004	0.02	0.897
SAV density		2	0.068	0.30	0.743
Depth \times SAV		2	0.046	0.20	0.818
Great Egret	48				
Water depth		1	1.397	9.23	0.004
SAV density		2	0.310	2.05	0.140
Depth \times SAV		2	0.265	1.75	0.185
Snowy Egret	43				
SAV density		2	0.297	1.72	0.191
White Ibis	68				
SAV density		2	0.071	0.29	0.753
April					
All species	339				
SAV density		2	0.296	0.97	0.380
Great Egret	9				
SAV density		2	0.066	0.33	0.726
Snowy Egret	121				
SAV density		2	0.399	1.64	0.197
White Ibis	132				
SAV density		2	0.039	0.10	0.902

DISCUSSION

This experiment indicated that water depth and SAV density are important environmental cues in determining wading birds' selection of foraging habitat. The preference for shallow water habitat we observed is consistent with other studies that have examined the relationship between wading birds' foraging and water depth (Kushlan 1976a, Frederick and Collopy 1989, Dimalexis and Pyrovetsi 1997, Strong et al. 1997, Bancroft et al. 2002, Gawlik 2002).

The preference for vegetated habitat is contrary to some studies that show that species tend to forage in open water. Dimalexis and Pyrovetsi (1997) reported that long-legged waders prefer foraging in open water, presumably because the lack of SAV allows them to locate prey more effectively. Kersten et al. (1991) found that Little Egrets (*Egretta garzetta*) tend to form dense aggregations for foraging in areas of open water during early morning hours, when overnight respiration by SAV had severely depleted the water of oxygen and forced fish to the surface of open areas to breathe. Other studies, however, provide evidence that birds may choose to forage in or near vegetated areas because of elevated prey densities. Safran et al. (2000) found that White-faced Ibis (*Plegadis chihi*) are more likely to forage in areas close to vegetation, which they presumed to be because of higher prey abundance.

TABLE 5. Type III general linear model analysis of variance for capture efficiencies of wading birds for all species pooled and for the Great Egret and Snowy Egret in relation to water depth and density of submerged aquatic vegetation (SAV) in January and SAV density in April.

Source	Error df	df	MS	F	P
January					
All species	124				
Water depth		1	0.263	2.11	0.149
SAV density		2	0.059	0.47	0.625
Depth \times SAV		2	0.136	1.09	0.340
Great Egret	39				
Water depth		1	0.555	3.68	0.062
SAV density		2	0.023	0.15	0.857
Depth \times SAV		2	0.228	1.51	0.233
Snowy Egret	41				
Water depth		1	0.000	0.01	0.939
SAV density		2	0.036	0.53	0.595
Depth \times SAV		2	0.166	2.42	0.101
April					
All species	168				
SAV density		2	0.037	0.88	0.418
Great Egret	8				
SAV density		2	0.079	4.71	0.045
Snowy Egret	120				
SAV density		2	0.033	1.29	0.279

The shift in preference from higher to lower densities of SAV suggests that SAV density may be an environmental cue that varied seasonally between January and April. Cold weather may affect prey availability through prey behavior (Kushlan 1978, Frederick and Loftus 1993). In the Everglades, some species of fish, including mosquitofish, are less active in colder weather (8–11 °C air temperature) than in warmer weather (19–23 °C; Frederick and Loftus 1993). These authors sighted significantly fewer fish within study plots on cold mornings than on warm mornings, suggest the behavior of the fish changed with temperature, possibly affecting their availability as prey. Frederick and Loftus (1993) also found fish to be more likely to hide in vegetation when temperatures were cooler. Stolen (2006) suggested that densities of prey within vegetation may vary seasonally. Minimum daily temperatures during the January experiment ranged from 8.6 to 18.4 °C; average temperatures were 12.3–21.9 °C (DBHYDRO database, <http://www.sfwmd.gov/org/ema/dbhydro/>, South Florida Water Management District, West Palm Beach, FL). Therefore, during the cooler weather in January, the behavior of the fish relating to temperature and vegetation may have affected the birds' selection of foraging habitat. Moreover, seasonal variation in the foraging behavior and energetic demands of the birds may result in a shift of preferences for foraging habitat. The January experiment preceded these birds' breeding season, while the April experiment fell during the breeding season, when most birds were provisioning chicks. It is possible

that the changing needs of these breeding birds could result in a change in foraging activity. Campos and Lekuona (1997) and Matsunaga (2000) showed that herons vary their foraging strategies seasonally in relation to stage of breeding. The former authors found breeding birds to be more likely to forage in shallow water, in parallel to the increased selection for shallow water we found. Erwin (1985), Kazantzidis and Goutner (1996), and Matsunaga (2000) all found foraging success to be highest during breeding, in agreement with our study. The significantly higher capture rate in April, when capture efficiency was not significantly different from that in January, indicates that birds had increased foraging effort but were not necessarily more efficient in their foraging (i.e., higher number of capture attempts without higher efficiency).

For the Great Egret, capture rate but not capture efficiency was significantly affected by water depth, but not in the direction expected. This species' foraging success was actually higher in the deep water than in the shallow. Moreno et al. (2005) showed that Great Egrets foraging in a lagoon in Brazil most frequently chose a foraging depth of 25 cm. Gawlik (2002) found that Great Egrets have a "giving-up density" lower than that of other species and are more likely than other species to exploit deeper water. "Giving-up density" of prey is the density of prey remaining in a patch at the time that a predator stops foraging within it (Brown 1988). Although Great Egrets forage preferentially in shallow water, this "exploiter" (a species with a low giving-up density that stays in one patch until all prey is exploited) is more likely to forage in suboptimal conditions than "searcher" species (species with high giving-up densities that switch foraging patches more frequently; Gawlik 2002).

One of the more surprising findings of this study was that SAV did not significantly inhibit the foraging success of avian predators. Previous studies show that increased structural complexity limits the foraging success of predatory fish despite higher densities of prey (Vince et al. 1976, Diehl 1988), possibly by inhibiting the predators' swimming speed (Anderson 1984, Winfield 1986) or creating visual obstructions that inhibit foraging (Stoner 1982). On the basis of our finding that vegetation in enclosures did not significantly reduce the foraging success of wading birds, the aspects of SAV that impair the foraging success of predatory fish do not seem to have the same effect on predatory wading birds.

A general finding of this study was that water depth and vegetation density had a stronger effect on wading birds' habitat selection than on foraging success. This pattern may be more generalized for wading birds than previously thought. Gawlik (2002) showed strong patterns of habitat selection by wading birds in response to water depth and prey-density experiments but has found little change in foraging success (DEG, unpubl. data). Similarly, Moreno et al. (2005) did not find a relationship between water depth and foraging efficiency of the Great and Snowy Egrets, and Kent (1987) found that the habitat in which herons' capture efficiency was highest

was not always the habitat that the birds used most frequently. We offer three nonexclusive hypotheses that could explain why habitat features addressed in this study affected foraging habitat selection more than foraging success.

First, birds may have selected for environmental features that generally indicate productive habitat. We found shallow water and habitat with SAV to be more attractive to wading birds than were alternative sites. Because we maintained the density of prey constant, however, these habitats did not provide the birds additional energy (measured by foraging success). Birds may have been attracted to habitat features such as shallow water and SAV because they anticipated elevated densities of prey. Densities of aquatic prey are higher in vegetated areas than in unvegetated areas (Dvorac and Best 1982, Diehl 1988, Rozas and Odum 1988, Stolen 2006). If wading birds cued in on the shallow water and SAV in the enclosures as an indication of higher prey density, then the standardized prey densities maintained in the experiment could effectively equalize foraging success across treatments. Uniform foraging success indicates that, given the scale and relative densities of prey used in these experiments, the treatment variables did not greatly influence prey vulnerability. Seasonal variation in foraging success may be more affected by the breeding season than by environmental variables.

Next, prey vulnerability may be a function of prey density. Draulans (1987) found that the foraging success of the Gray Heron (*A. cinerea*) followed a type 2 functional response, leveling off when prey densities reached a threshold of 0.45 fish m^{-2} (Holling 1959). While his study took place at a different scale, the threshold prey density found by Draulans was significantly lower than the 20 m^{-2} fish we used. It is possible that the prey density we used was too high to reveal subtle differences in foraging success based on water depth and vegetation. A study specifically examining threshold energy-intake rates or capture rates may help to determine if there is a threshold prey density that may affect either foraging success or the decision to switch foraging patches.

An alternative hypothesis is that wading birds used environmental cues as an indication of patch quality, but, when they located and chose a patch, their foraging success varied greatly because of intrinsic inter- and intra-specific differences (e.g., age of bird, relative satiation, metabolic state, physiological differences). For example, other studies have shown that the mean capture efficiencies of Snowy Egrets foraging in a variety of habitats and regions varies greatly: 0.50 (Rodgers 1983), 0.42–0.64 (Master et al. 1993), 0.07–0.47 (Kent 1986), and 0.43 (Kent 1987). The capture efficiency of the Snowy Egrets we observed ranged from 0 to 1, and their capture rate ranged from 0 to 7 fish min^{-1} . This high variability indicates that although vegetation density and water depth do not affect foraging success strongly, additional factors may be influencing foraging success at some level. A study with individually marked birds may be able to discern differences among individuals in foraging success under different treatments.

The purpose of this study was to begin quantifying the linkages among hydrology, vegetation, and wading birds' foraging. Because both routine wetland management and large-scale ecological-restoration projects often concentrate on hydrologic manipulations with little understanding of their implications across the ecosystem, there is a need for understanding of the effects of hydrologic manipulation of wetland systems on the response by animals at upper trophic levels (Gawlik 2006). The chances of success of attempts to restore wetland ecosystems can be increased if wildlife is incorporated, but only if there is a clear understanding of the linkage with the processes being restored. The findings of our study suggest that changes in water and vegetation affect the attractiveness of foraging habitat to wading birds, but it is not yet clear how this may affect the birds' foraging and subsequent reproductive success. Declining habitat quality has been linked to declines in wading bird populations (Bancroft 1989, Frederick and Spalding 1994, Ogden 1994, USFWS 1996), and habitat manipulations clearly produce strong patterns of habitat selection (Gawlik 2002, Master et al. 2005, Gawlik and Crozier 2007), which are thought to be adaptive (Smith and Dawkins 1971, Smith and Sweatman 1974). However, if these habitat manipulations produce no benefit in terms of foraging success, then more work is needed to clarify how birds benefit from improved foraging habitat. Such work will be a key precursor to the use of wading birds as indicators of ecological restoration or routine wetland management.

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