HABITAT USE BY WADING BIRDS IN A SUBTROPICAL ESTUARY: IMPLICATIONS OF HYDROGRAPHY

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ABSTRACT.—The dynamics of foraging habitat use by long-legged wading birds was analyzed with respect to water-level fluctuation patterns in Florida Bay. Wading-bird presence at four sites situated to sample the heterogeneity of the bay was quantified by repeated surveys collected throughout the day and year. Models for habitat availability were generated using water-level data collected from continuous recorders, staff gauges, and habitat profile maps. These models were tested against the survey data.

Roseate Spoonbills (*Ajaia ajaja*) foraged on the study areas primarily at night. Great Blue Herons (*Ardea herodias*) fed both day and night, but primarily at night where the tidal range was small. Great Egrets (*Casmerodius albus*), Snowy (*Egretta thula*) and Reddish (*E. rufescens*) egrets, Little Blue (*E. caerulea*) and Tricolored (*E. tricolor*) herons, and White Ibis (*Eudocimus albus*) fed during daylight. Where tidal range was small (<5 cm) diurnal species fed throughout the day.

Florida Bay has a pronounced annual water-level cycle that causes monthly mean water levels to vary by as much as 30 cm between October (high) and May (low). Models derived from hydrology data predicted that this seasonal variation in water level would have a major impact on habitat availability, particularly where tidal flux was small. The predictions were supported by survey data. At sites with minor tides, most wading-bird species had a cycle in seasonal abundance that correlated with seasonal changes in water level; only the tallest species, *Ardea herodias*, was uniformly present throughout the year. The large daily range in tide ($\bar{x} = 80$ cm) afforded year-round access to foraging habitat, and these abundance patterns did not exist. The seasonal variability in habitat availability has major management implications because the maintenance of stable wading-bird populations depends on the availability of alternative foraging sites when water levels are high. Historically, these sites have tended to be targeted for human development. *Received 20 October 1986, accepted 11 June 1987.*

THE dynamics of foraging habitat use by wading birds have been well studied for short-legged waders (Charadriiformes; Goss-Custard 1970, Holmes 1970, Burger et al. 1977, Goss-Custard et al. 1977, Silliman et al. 1977, Myers 1980, Connors et al. 1981, Fleischer 1983) but are poorly known for long-legged species (Ciconiiformes). This is especially true for marine systems, where studies have focused on major environmental cycles (see Kushlan 1981 for review). Ciconiiformes (hereafter "wading birds") are known to alter their feeding-site selection in relation to major seasonal climatic changes (Ryder 1967, 1978; Henny 1972) and the lunar tidal cycle (Krebs 1974, Brandman 1976, Bayer 1978, Custer and Osborn 1978a, Pratt 1980). Beyond the patterns imposed by these major cycles, little is known about the dynamics of habitat use by wading birds.

In marine and estuarine ecosystems of southern Florida, where seasonal variations in the annual temperature cycle are relatively minor and the lunar tidal range tends to be small (NOAA tide tables 1986), habitat use by wading-bird populations is potentially independent of these factors. Therefore, an analysis of habitat-use patterns may identify other factors that function as determinants of habitat use. By combining data on habitat use by wading birds at a series of locations in Florida Bay in conjunction with an analysis of habitat topography and hydrography, I tested two null hypotheses. First, in the absence of restrictions imposed by a tidal cycle, foraging habitat use would be independent of time. And second, in the absence of a strong annual climatic cycle (temperature), habitat use by wading birds would be constant throughout the year.

METHODS

Study area.—Florida Bay is a large, shallow, lagoonal estuary situated between the southern coast of the

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Florida mainland and the island chain of the Florida Keys. A complex network of anastomosing, shallow mud banks runs throughout the bay (Fig. 1; Schomer and Drew 1982) and provides extensive foraging habitat for wading birds.

To provide a representative sample of habitat heterogeneity in Florida Bay, a study site was selected in each of four major regions of the bay (Fig. 1). These areas are recognized by general differences in vegetation (Zieman and Fourqurean 1986), which in turn reflect major differences in salinity and tidal cycle (Powell et al. 1987). The Northeastern habitat (Fig. 1, NE) was represented by a 6-km section of bank running from the mainland at Little Madiera Bay southeast through the Park Keys. The East Central habitat (EC) was represented by a bank (Cross Bank) running from Plantation Key, 8 km west toward Captain Key. The Atlantic habitat (At) was represented by a 4-km section of bank extending from the boundary of Everglades National Park at Bow-Legs Channel to the westernmost Buchanan Key. Finally, the Gulf habitat (Gu) was represented by a triangular area (4 × 2.3 km at its base) of shallow bank bounded by Frank Key on the east, Flamingo Channel on the north, and Conchie Channel on the south. Each study site consisted of shallow seagrass meadows interspersed with mangrove islands. The Northeast, East Central, and Atlantic areas were largely linear, with a maximum width of 300 m but typically less than 200 m in width. The Gulf site in western Florida Bay was a wide bank up to 2.3 km in width. The physical and floral characteristics of these sites were described in detail by Powell et al. (1987).

Wading-bird surveys.—Censuses of wading-bird use of the different study sites were made from a 5.1-m open skiff that was run along the edges of the study area. Because all of the study sites were located in Everglades National Park, the wading birds were accustomed to boat traffic and were undisturbed by relatively close approach. The narrow width of the sites coupled with the absence of obstructing vegetation permitted exact counts of the wading birds present. The survey was restricted to individuals that were foraging on the seagrass-covered banks. No attempt was made to quantify wading-bird usage of mangrove islands within the transect areas. Nighttime data were collected with the aid of a 300,000 candlepower spotlight. The birds were exposed to the light for less than 1 s, which did not cause them to flush. Repeated observations of recognizable individuals (either tagged or distinct blue-colored subspecies) during sequential nighttime surveys confirmed that birds did not leave in response to exposure to light. At the East Central site, where there were no natural landmarks on the bank, transect markers (numbered PVC stakes) were set at 100-m intervals. These markers made it possible to plot bird locations to the nearest 25 m. During the first year of the study, one site (East Central) was censused semimonthly at 3-h intervals for a continuous period of 72 h (24 censuses/survey period). These data were log transformed and analyzed by ANOVA and Student-Neuman-Keuls multiple range test. The first-year results indicated that a reduced censusing frequency would accurately measure wading-bird use of the study sites. Thus, during the second year, when all sites were surveyed, 221 surveys were run on randomly selected days during each of three 2-month periods ($\bar{x} = 13.7$ daylight and 6.2 nighttime surveys). The periods, which were selected to represent the major ecological periods in Florida Bay (Powell et al. 1987), included the dry season (March–April) when mean water level, water temperature, and salinity were low; the first half of the wet season (July–August) when water level was still low but water temperature and salinity were high; and the second half of the wet season (October–November) when water level and temperatures were high and salinity low. A nonparametric test (Kruskal-Wallis) was used to analyze these data because log transformation did not sufficiently reduce variance heterogeneity.

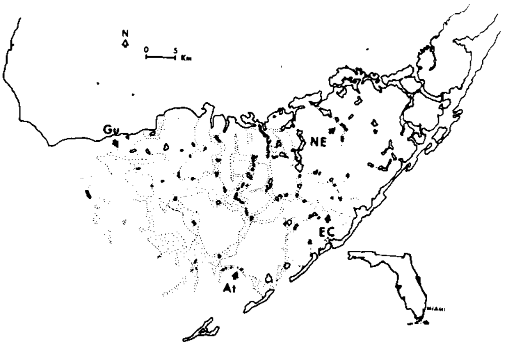

Fig. 1. Study sites in Florida Bay. Stippled areas represent shallow banks used by wading birds as foraging habitat. One study site is situated in each of 4 subsections of the Bay: Northeast (NE), East Central (EC), Atlantic (At), and Gulf (Gu).

Under the reduced survey schedule data were combined as either daylight or darkness. Darkness surveys were collected between 0.5 h after darkness and midnight, when nocturnal species were most abundant. At the Gulf site, where tidal range restricted wading-bird presence to periods of low tide, censuses were made at all tide levels, but semimonthly bird use profiles were generated from data collected during low tide.

Hydrographic data.—To develop a hydrographic model for the study sites, it was necessary to map the topography of each site. Mapping was accomplished by measuring the distance between the sediment surface and the water surface at slack high tide (at that time the water surface was assumed to be level). Measurements were made at 20-m intervals along cross-sections that ran perpendicular to the long axis of the study sites. At least 6 transects were measured on each

Table 1. Maximum foraging depth of Florida Bay wading-bird species as determined by leg length. Leg lengths were determined from study skins made available by the University of Miami.

	Abbreviation	Maximum foraging depth (cm)
Small species		
Tricolored Heron	TH	18 ± 0.7
Little Blue Heron	LB	17 ± 1.3
Snowy Egret	SE	17 ± 1.2
White Ibis	WI	16 ± 1.0
Medium species		
Reddish Egret	RE	26 ± 1.1
Great Egret	GE	28 ± 1.6
Roseate Spoonbill	RS	20 ± 0.9
Large species		
Great Blue/White Heron	*Ardea*	39 ± 2.1

of the 3 eastern sites where the banks were narrow. The Gulf site had greater topographic relief along its long axis, which necessitated a depth profile for that axis in addition to two cross-sectional profiles. To correlate the topographic maps with tidal fluctuations, a continuous water-level recorder (Leupold & Stevens Type F recorder) was placed in deep water (<2 m) at each of the study sites. Water-level data were collected between 1981 and 1985 for different time intervals at each site (NE: December 1983 to December 1984, EC: April 1981–1985, At: November 1983 to October 1985, Gu: April 1984 to October 1985). In conjunction with each recorder, 3–5 staff gauges were used on each study-site bank.

The translation of water-level changes registered on the continuous recorder into water depths on the feeding banks was accomplished by correlating water levels at the continuous recorder with water levels at its associated staff gauges. For the eastern half of the bay where tidal change was small, water-level changes on the shallow banks were equivalent to changes at the recorders. At the Gulf site in the western part of the bay, the water-depth relationship between bank top and the recorder was more complex and required separate equations for rising and falling stages (Powell et al. 1987). Equations, derived from these data, made it possible to predict water depth accurately at the staff gauges as a function of water level at the continuous recorders. Water level at the staff gauges was translated to depth on the bank through the topographic maps. Predictions of habitat availability for a particular wading-bird species at a given study site were generated by solving the bank-depth equations for times when levels were below maximum foraging depth of that species. Custer and Osborn (1978b) demonstrated that the water depth used by wading birds was dependent on leg length. To allow for maximum foraging access to the study sites by the various wading-bird species, I used total leg length as the maximum foraging depth (Table 1). In addition, the model was adjusted for species that fed only during daylight or darkness.

RESULTS

Eight wading-bird species were present on the study sites in sufficient numbers to be analyzed (see Table 1 for species list and abbreviations). One species, the Great Blue Heron (*Ardea herodias;* hereafter "*Ardea*"), resides in Florida Bay as two distinct color forms. A blue form (including Great Blue and Wurdemann's herons) has migratory and nonmigratory components, and a white form (Great White Heron) is nonmigratory (Robertson and Kushlan 1978). Because of the complexity of *Ardea* population structure, the two color forms were treated separately.

The first year of study at the East Central site demonstrated that most species were restricted to diurnal foraging. Two species, however, fed in either daylight or darkness (Roseate Spoonbill, *Ajaia ajaja;* and both *Ardea* color phases; Table 2). At this site, where tidal range was limited to a few centimeters, wading-bird presence during daylight hours was independent of time of day (Table 2). *Ardea* was present in slightly greater numbers between nightfall and 0330 than during the remainder of the night (Table 2).

The presence of all species, except white *Ardea,* varied significantly with time of year (Table 3). Blue *Ardea* showed a significant change only at the Northeast site, where numbers were higher during the October–November observation period. Roseate Spoonbills were present in such small numbers during most of the year that analysis of trends was possible at only two sites. Spoonbills were present at night in large numbers at the Northeast site during October–November and in small numbers at the East Central site during March–April (Table 3). Seasonal changes in populations of the other wading-bird species were more pronounced and at 3 of the 4 sites followed a trend of greater abundance in the dry season (March–April) than during the latter part of the wet season (October–November; $P < 0.05$; Table 3). The greatest fluctuations occurred in populations of the smaller species. At the 3 eastern sites, Little Blue (*Egretta caerulea*) and Tricolored (*E. tricolor*) herons, Snowy Egrets (*E. thula*), and White Ibis (*Eudocimus albus*) tended to be present in relatively large numbers only during March–April and to decline through the rest of the year (Table 3). The intermediate-size Great Egret (*Casmerodius albus*) and Reddish Egret (*Egretta rufescens*) tended to follow this same trend at the eastern sites, but relative changes in populations were less pronounced (Table 3).

At the Gulf site seasonal trends in wading-bird abundance differed from the eastern sites. Of the 4 small species, only the Tricolored Heron was present in lower numbers during the third sampling period. The 3 remaining species were most abundant on the banks during that period (Table 3). Once again, both color morphs of the largest species, *Ardea*, were uniformly present throughout the year.

Water-depth patterns.—The three narrow banks on the eastern side of the bay (Northeast, East Central, and Atlantic) are largely flat surfaces with relatively steep sides (Fig. 2). At these sites the availability of foraging substrate for wading birds simulated a step-function. When water levels were sufficiently low for a species to feed, the entire bank top area tended to be available. When the water level was higher than the maximum foraging depth for a given species, most of the bank area was unavailable. The Gulf study site, which is over 2 km wide, has a greater topographical range (Fig. 3). Therefore, at this site the amount of foraging substrate available to wading birds varied depending on the water level.

The 4 study sites showed a complex, heterogeneous pattern of water-level fluctuation in Florida Bay. Three cycles with different periods were apparent. Water levels exhibited a pronounced annual cycle that occurred uniformly throughout the bay. Mean daily water levels between September and November averaged up to 30 cm deeper than between February and June (Fig. 4). The pattern of this annual cycle, high summer and low spring water levels, is consistent with patterns described for the Atlantic Ocean (Marmer 1954). A daily fluctuation in water level was recorded at each site, though the range differed by an order of magnitude among sites. Daily tides ranged from a highly irregular cycle of just a few centimeters at the Northeast site ($\bar{x}$ = 3.3 cm) to a regular, semidiurnal tide of up to 1 m at the Gulf site ($\bar{x}$ = 61 cm). The East Central site had a daily tidal range similar to, but somewhat more regular

TABLE 2. Temporal distribution of wading birds (mean number present during survey ± SD) foraging on East Central study site. Species abbreviations are given in Table 1. Diurnal samples showed no significant differences in daytime presence of species (ANOVA, $P > 0.05$). Primarily nocturnal, *Ardea* (at this site, about 95% were the white form) was present in greater numbers during the first two darkness periods (ANOVA, $P < 0.05$).

		GE		SE		RE		LB		TH		WI		RS		*Ardea*	
	n	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Dawn	33	8.4	6.5	1.6	2.3	4.2	3.5	11.9	13.1	7.6	8.9	24.5	30.7	1.6	2.5	22.4	17.6
Postdawn–1100	25	6.6	5.8	1.3	2.2	3.8	3.0	8.1	10.1	5.4	5.2	12.6	20.6	0.7	1.4	17.9	19.8
1100–1300	16	5.5	4.6	0.3	1.0	3.9	2.6	6.8	8.9	6.5	7.5	8.1	12.0	0.5	1.2	22.6	21.7
1300–1530	17	6.7	6.4	3.0	4.9	4.7	3.9	14.3	16.2	9.5	8.7	20.0	30.3	0.4	1.0	19.8	19.1
1530–predusk	29	8.0	6.2	2.3	4.2	4.5	3.2	11.7	12.3	6.6	5.9	20.4	30.3	1.0	1.9	16.1	11.1
Dusk	12	8.4	5.8	0.6	0.7	3.7	2.8	8.7	7.0	6.6	7.6	27.5	31.5	2.9	3.3	31.5	15.4
1850–2230	29	0.9	2.7	0.1	0.7	0.2	0.9	0.6	2.4	0.3	1.8	1.2	6.1	3.1	5.3	81.4	27.9
2230–0330	12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	4.1	83.0	13.5
0330–0615	21	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	2.5	4.8	58.0	22.7

TABLE 3. Mean number of wading birds foraging on 4 survey transects in Florida Bay. See Fig. 1 for transect locations.

	Mean no. of birds		
Area[a]	March–April	July–Aug.	Oct.–Nov.
Great Egret			
NE	2.7	4.9	2.2
EC**	10.5	6.9	2.6
At**	5.0	6.3	1.0
Gu**	99.5	40.7	74.5
Reddish Egret			
NE**	6.7	1.9	1.0
EC**	3.2	1.1	0.1
At**	4.4	1.0	0.0
Gu[b]	0.0	0.0	0.0
Snowy Egret			
NE[b]	0.0	0.0	0.0
EC**	5.5	0.5	0.0
At**	0.9	0.0	0.1
Gu*	1.0	0.1	9.7
Little Blue Heron			
NE	0.9	0.1	0.2
EC**	10.7	3.8	0.3
At**	18.7	1.0	0.2
Gu**	41.0	55.4	105.0
Tricolored Heron			
NE**	9.7	0.5	0.0
EC**	8.4	1.1	0.0
At**	8.0	0.8	0.0
Gu**	24.4	15.9	5.5
White Ibis			
NE**	6.4	0.5	3.2
EC**	25.1	12.0	1.8
At**	18.0	0.2	0.0
Gu**	33.0	4.0	68.0
Roseate Spoonbill			
NE*	4.3	0.0	24.8
EC**	9.8	0.0	0.0
At**	1.7	0.0	0.0
Gu[b]	0.0	0.0	0.0
Great Blue Heron			
NE**	0.7	0.0	3.3
EC	2.8	1.9	2.9
At	1.0	1.1	0.5
Gu	13.8	12.0	10.6
Great White Heron			
NE	17.0	13.9	13.3
EC	43.7	27.3	35.4
At	14.0	10.3	5.7
Gu	57.3	43.5	34.3

[a] * = $P < 0.05$, ** = $P < 0.01$.

[b] Insufficient numbers to test for significant seasonal differences.

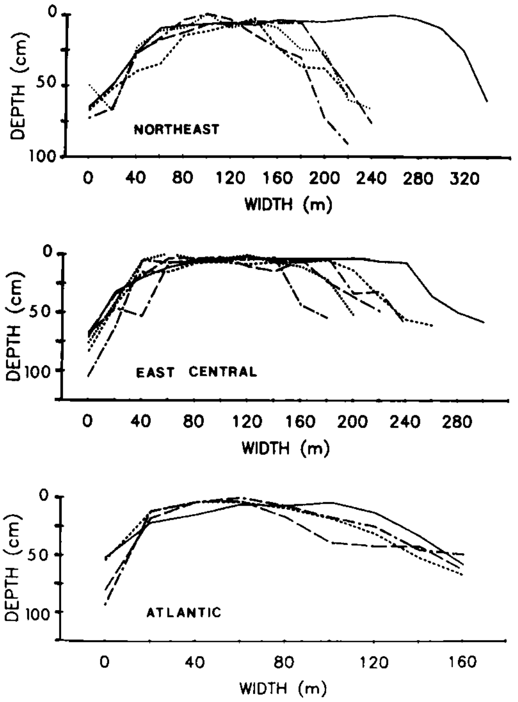

Fig. 2. Bank profile data from 3 study sites in eastern Florida Bay. Each line is a cross-sectional transect run perpendicular to the long axis of the bank.

than, that of the Northeastern site. The Atlantic site had a regular, semidiurnal cycle of 12 cm. The third cycle in water-level fluctuations was irregular, with a period of 3–7 days and a mean amplitude of 21 cm ($n = 15$ in 1984; Fig. 5). These cycles, which occurred infrequently and irregularly, appear to be an effect of wind on the shallow bay. Strong winds, particularly those associated with frontal activity, produce asymmetrical tidal movements (Allen 1942, Ginsburg 1956, Gorsline 1963, Enos and Perkins 1979). In association with cold fronts, wind direction shifts clockwise from the fair-weather east through southeast, when water levels rise for one to several days, through northwest, when there is a net loss of water from the bay, again for several days, before ultimately returning to the easterly tradewind and normal water levels (Table 4).

The availability of foraging habitat for wading birds, calculated on the basis of water-level data, follows a marked seasonal cycle. At the 3 eastern sites (Fig. 6) water levels are predicted to be sufficiently low to allow all species of wading birds to forage daily during the dry

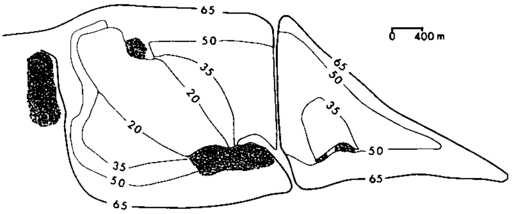

Fig. 3. Topographic map of Gulf study site in western Florida Bay. Contour lines (cm) were generated from 3 cross-sectional transects, 1 run down the long axis of the bank and 2 perpendicular to the long axis.

season and into the beginning of the wet season (the large species represents *Ardea*, which may feed both day and night; its access to foraging sites is predicted on the basis of 24 h as opposed to 12 h for the remaining species). By the latter part of the wet season, however, water levels are consistently too deep for foraging by all species except *Ardea*, which, by virtue of its size, is largely immune to seasonal water-level changes (Fig. 6). The situation for western Florida Bay, as exemplified by the Gulf site, differs from that of the east. At the Gulf site predicted habitat availability is far less variable, and all species are expected to have access to sufficiently shallow water on the banks throughout the year (Fig. 6).

DISCUSSION

Diurnal species of wading birds in an area with little lunar tide were uniformly active on the foraging sites throughout daylight hours. This habitat-use pattern is consistent with the null hypothesis and therefore does not allow its rejection. Two species, *Ardea* and the Roseate Spoonbill, were present on the study areas primarily at night. The Roseate Spoonbill feeds actively in daylight as well, but primarily in mangrove habitats adjacent to Florida Bay (Allen 1942). At the eastern sites most *Ardea* rested on nearby mangrove islands during daylight and flew onto the flats at or just after dusk to forage. Nocturnal foraging by *Ardea* has been noted for other environments (Willard 1975, Bayer 1978, Pratt 1980), but only Black and Collopy (1982) quantified diurnal and nocturnal occurrences. They found that *Ardea* presence was dependent on tidal cycle but independent of time (day or night). The preponderance of nocturnal foraging in Florida Bay probably was related to diel patterns of forage-fish abundance at the study sites (Powell et al. 1987) as substantially larger numbers of fish were present

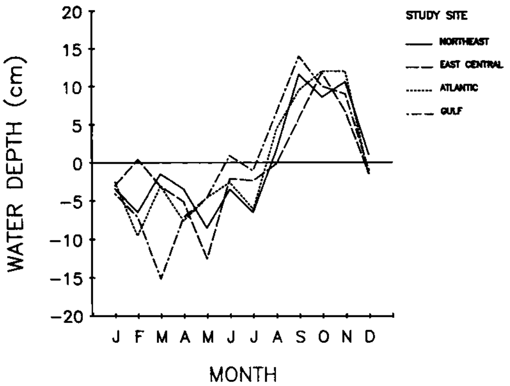

Fig. 4. Variation in mean monthly water level at 4 study sites in Florida Bay. Zero is annual mean water level for each site.

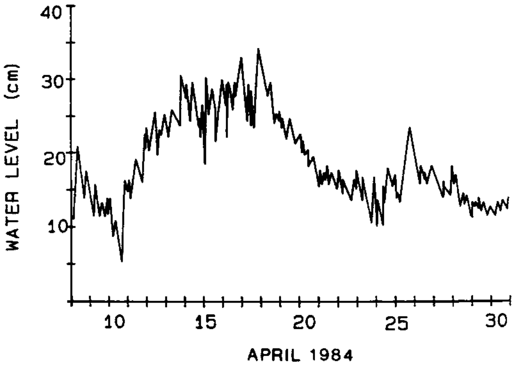

Fig. 5. Continuous water-level trace from Northeast study site showing wind-related water-level fluctuation during April 1984.

TABLE 4. Wind direction and water-level changes at the East Central site.

Wind direction	Tide	Mean daily change (cm)	*n* (days)
NNE–E	Falling	3.59	192
	Rising	3.45	185
SSE–E[a]	Falling	3.06	87
	Rising	5.17	88
SSW–W	Falling	4.53	27
	Rising	5.12	32
WNW–N[a]	Falling	5.26	85
	Rising	3.76	69

[a] Rising and falling tides significantly different (ANOVA, $P < 0.01$).

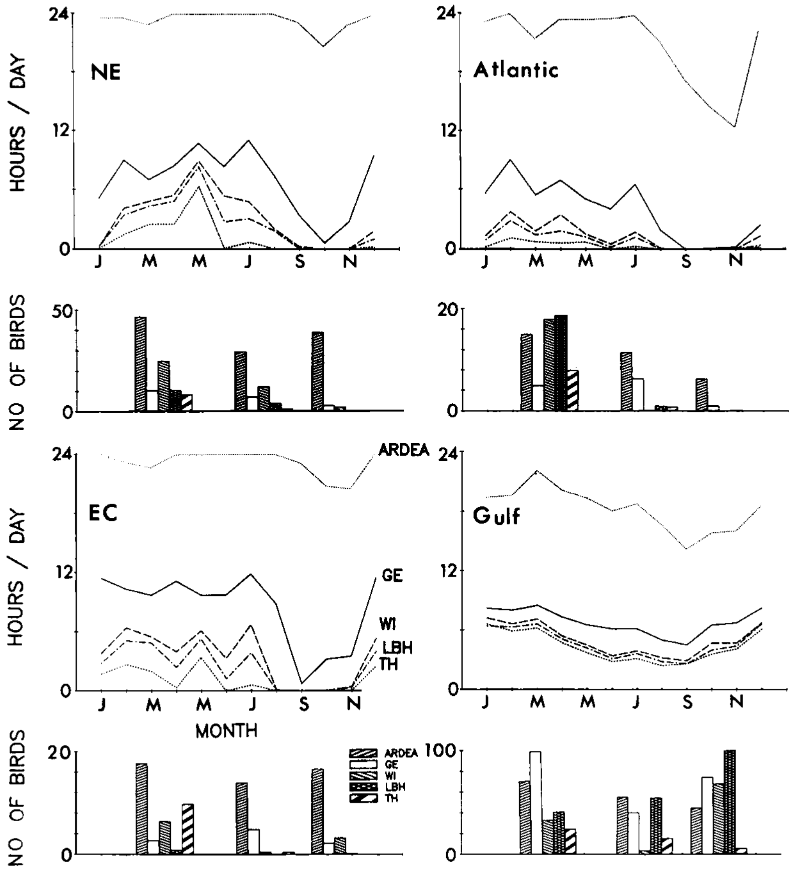

Fig. 6. Relationships between seasonal variation in habitat availability and wading-bird presence at 4 locations in Florida Bay (see Table 1 for species abbreviations). The large species, *Ardea* (which can feed 24 h/day), has relatively constant access to all habitats and is uniformly present year-round. Smaller species have marked seasonal variation in access at 3 sites, which is reflected in population fluctuations.

on the flats during darkness. The greater presence of *Ardea* from darkness through about 0330 indicates that additional, but undetermined, factors influence nocturnal activity patterns. In western Florida Bay, at the Gulf site, *Ardea* activity was correlated with tidal cycle and independent of the diel cycle, as reported in other ecosystems with large lunar tides (Brandman 1976, Black and Collopy 1982).

The observed seasonal variations in wading-bird habitat use on the study sites were largely inconsistent with the predictions of the null hypothesis that, in the absence of a pronounced winter season and associated freezing of shallow-water habitats, wading-bird presence would be constant throughout the year. Wading-bird use of available habitat was consistent, however, with predictions of the hydrology model. In the eastern bay, where the model predicts seasonality in habitat availability, most species had a strong seasonal component to their presence, with greatest abundances coinciding with periods of greatest predicted habitat availability (Fig. 6). Only the Great White Heron was uniformly present in eastern Florida Bay. This species is large and may feed any time (day or night) independent of seasonal water-level fluctuations. The seasonal variation in Great Blue Herons probably reflected seasonal migration because numbers were highest during fall months when migrating birds or winter residents were present. Seasonal distributions of wading birds were also consistent with habitat predictions for western Florida Bay. In conjunction with year-round habitat availability, all species were present throughout the year

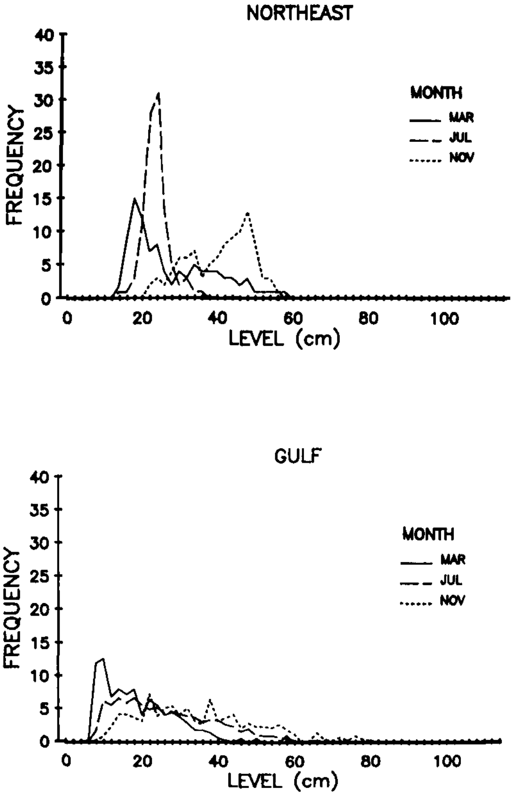

Fig. 7. Frequency distributions in hourly water levels at an eastern (Northeast) and western (Gulf) study site during 3 months. When the mean water level is low (May) wading birds have access to both feeding sites. When the mean water level is high (October), however, the tidal range at the eastern site is insufficient to permit access by most wading-bird species to the foraging site at low tide.

TABLE 5. Number of days (greatest number of consecutive days) that water remained too deep for 3 species to feed at the Northeast site.

	Great Egret	Tricolored Heron	White Ibis
January	0	11 (4)	7 (4)
February	0	6 (5)	1 (1)
March	2 (2)	0	11 (6)
April	0	8 (8)	7 (7)
May	0	5 (2)	1 (1)
June	0	6 (6)	5 (5)
July	0	0	0
August	0	20 (14)	8 (6)
September	11 (4)	30 (30)	30 (30)
October	9 (4)	26 (22)	22 (20)
November	11 (7)	24 (12)	19 (7)
December	0	4 (4)	1 (1)

(Fig. 6). Most species demonstrated significant seasonal trends, but there was no consistency in these trends among species.

Although eastern and western Florida Bay have the same annual cycle in mean water level (Fig. 4), the predicted and observed impacts of this cycle on habitat availability differed markedly. The divergent habitat-use patterns result from differences in the magnitudes of lunar tides at the two locations. In eastern Florida Bay, where daily tides amount to only a few centimeters, a seasonally induced change in the mean water level has a greater impact on habitat availability than at the western site, where the semidiurnal tide may be greater than 1 m. In September through November the water level in the bay reaches its maximum levels, and the lunar tidal range in the western bay is sufficient to lower water levels below maximum foraging depth for all species on a daily basis (Fig. 7). In contrast, the tidal range in eastern Florida Bay is so small that water levels may remain too deep for foraging during entire tidal cycles (Fig. 7). The component of water-level variability induced by wind also exerts a greater impact on habitat availability in the eastern bay. Here again, because of the small daily tides, a relatively minor rise in daily mean water level can result in water that is too deep for wading birds to forage even at low tide (Fig. 6). Thus, during storms the foraging habitat in the eastern bay typically is unavailable, particularly to the small wading birds, for several days at a time, even during the months of low mean water level (Table 5).

The occurrence of extended periods in eastern Florida Bay when water levels are too deep for most wading birds to feed has major implications. When access to foraging sites is prevented by high water levels, the birds either must shift to alternative foraging habitats in the area or must disperse. This loss of habitat occurs predictably between September and December when the annual water-level cycle is at its peak. Periods of deep water may also occur unpredictably because of wind-induced changes in water level in April and May, when water levels are typically low and most small wading-bird species are breeding (Nesbitt et al. 1982).

The Roseate Spoonbill migrates from Florida Bay during the months when water levels are highest. Spoonbills breed in Florida Bay during winter, though they feed primarily in the mangrove areas adjacent to the bay (Robertson pers. comm.). The remaining seven species (excluding *Ardea*) either feed in small open areas of higher elevation located on the islands in Florida Bay and the bay's eastern fringe or, possibly, shift to the western side of the bay (a distance of 40–50 km). Two of the 4 smaller species that declined in numbers in eastern Florida Bay during periods of high water were present in greater numbers on the western side of the bay at that time (Table 3). This suggests that the response of some birds is to shift to the western sites. While this strategy may be an option for birds during the nonbreeding season, the western foraging areas are probably too far away for breeding birds nesting in the eastern bay. Feeding flights by these species are generally less than 5 km, and maximum flights are less than 30 km (Bateman 1970, Custer and Osborn 1978a, Erwin 1983, Hafner and Britton 1983). The largest known flight distance is for coastal colonies of White Ibis (Bildstein and Fredericks pers. comm.) that regularly fly up to 20 km, and rarely 40 km, to food-rich inland foraging sites. A further deterrent to long flights to the western bay is that the western area also experiences high water levels (Fig. 4) and reduced foraging habitat availability (Fig. 6) when eastern-bay areas are flooded. Suitable alternative foraging habitat in the vicinity of eastern Florida Bay consists of seasonally flooded areas that are kept open by high soil salinity, hurricane destruction of mangrove vegetation, or both (Craighead and Gilbert 1962). These high marsh habitats, located on the mangrove islands in Florida Bay and along the bay's fringes, amount to a small fraction of the extensive bank habitat in Florida Bay.

Periods of high water, particularly during the breeding season, are undoubtedly stress periods for birds, and the availability of alternative habitats during these periods limits the size of wading-bird populations. The distribution of alternative foraging habitats also may explain the distribution of breeding colonies in eastern Florida Bay. The major colonies are situated in a ring along the eastern fringe of the bay (Nesbitt et al. 1982, Powell and Bjork unpubl. data). These colonies are close to alternative foraging sites along the margins of the bay.

The dependence of wading birds on alternative, higher-elevation breeding sites has major management implications. Although Florida Bay is within Everglades National Park, most of the alternative foraging sites that fringe the eastern bay are privately owned and in the past have been heavily affected by human development. The stability of the publicly owned northeastern fringe is potentially threatened by water-management plans that are being formulated without adequate consideration of potential consequences on downstream habitat. The destruction of fringe habitats presumably has reduced the carrying capacity of the Florida Bay ecosystem, and future maintenance of viable wading-bird populations in eastern Florida Bay will depend on preventing further loss of these areas.

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