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Foraging Microhabitat Selection by Wading Birds in a Tidal Estuary, with Implications for Conservation

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Abstract.—The importance of the lower Rahway River, New Jersey, to wading birds was investigated, and foraging patterns and interspecific differences in wading bird microhabitat use are described. Foraging decisions by wading birds are complex and occur at several levels. In order to examine foraging decisions at the habitat and microhabitat levels, 79 censuses were conducted by boat along a 5-km tidal section of this river in 1988, 1998, 1999, and 2002. The locations of 1,148 birds were recorded on maps, and patterns of microhabitat use were determined. Overall, year, date, and tide level were important predictors for the numbers of wading birds that were recorded. However, each species responded to a different combination of variables: for Great Egret it was year and date; for Snowy Egret date and tide level; and for Glossy Ibis year, date, and tide level. Tide flow direction was not important for any species. For all three species, spatial distributions long the river were clumped rather than uniform, which were associated with physical characteristics along this section of the river. All three species used the mouths of narrow tidal creeks more frequently than expected, but species differed in the use of mudflats and areas of slow-moving water. There was little overlap among species in spatial distribution along the river, but the overall use of microhabitats was broadly similar. This study suggests that the lower Rahway River estuary in New Jersey is valuable to local wildlife and should be considered in future development plans. *Received 29 May 2004, accepted 10 May 2005.*

Key words.—egrets, estuary, foraging habitat, ibises, river, salt marsh conservation, wading birds.

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Foraging decisions are complex, and often involve many different considerations that may be influenced by both biological and physical factors. For example, foraging decisions may reflect prey dispersion, the likelihood of prey detection and capture, and the energetic and nutritional values of different types of prey (Krebs and Cowie 1976; Iwasa *et al.* 1981; Sherry and McDade 1982; Safina and Burger 1985; Wanless *et al.* 1998; Gawlik 2002). Competition and the threat of predation also affect some foraging decisions (Lima and Dill 1990; Houtman and Dill 1998; Cristol and Switzer 1999).

Many species of long-legged wading birds (Ciconiiformes) breed in colonies, from which they fly to find food for themselves and their young. Such colonies are often surrounded by a constellation of foraging habitat types of unequal quality and at varying distances. Thus, egrets, herons, and ibises lend themselves to studies of foraging decisions. Erwin (1983) identified three levels, or scales, of wading bird foraging decisions. These begin with the bearing that a bird takes as it flies from the colony. Finer levels involve, first, the choice of a habitat patch and, finally, the actual foraging microhabitat within that patch. Patch choice and microhabitat selection by wading birds is influenced by many factors, including aspects of social foraging (Caldwell 1981; Erwin 1983); water level (Strong *et al.* 1997; Bancroft *et al.* 2002); proximity and height of vegetation (Safran *et al.* 2000; Bancroft *et al.* 2002); the stage of the breeding season (DeSanto *et al.* 1997), and prey availability (Safran *et al.* 2000; Gawlik 2002).

Prey availability is a complex component of habitat selection, and might involve prey density and distribution (Arengo and Baldassarre 1999), the probability of prey detection and capture (Kent 1987), and competition (Maccarone and Parsons 1994; Gawlik 2002). In turn, the densities and distributions of small fish and invertebrates eaten by wading birds are themselves dependent on habitat quality and nutrient availability, both of which are affected by small-scale variations in the physical environment (Christensen *et al.* 1997; Safran *et al.* 1997; Yozzo and Smith 1997). In the lower

Rahway River in New Jersey, these might include salinity, turbidity, water level, vegetation and shoreline slope.

Here, two levels of foraging decisions made by wading birds during the breeding season are examined. A pattern of habitat use is first described, namely, factors affecting overall wading bird abundance in the lower Rahway River. This is followed by an analysis of microhabitat selection. Finally, the ecological value of the lower Rahway River is considered. As top carnivores in this ecosystem, egrets and herons feed on many of the same prey as Blue Crab (*Callinectes sapidus*), Striped Bass (*Morone saxatilis*), White Bass (*M. chysops*), and Bluefish (*Pomatomus saltatrix*).

METHODS

Study Area

This study examined the lower 5-km section of the Rahway River (Fig. 1). This section of the river is tidally influenced and estuarine. There are extensive mud flats exposed at low tide along both shores, which are lined with salt-tolerant marsh vegetation (*Spartina alterniflora* and *S. patens*). This dredged river is navigable at all tide levels and is representative of the many tidal estuaries in this area. The river bottom slopes steeply toward its center channel. Because of this topography, little foraging habitat is available during high tides. This site is seldom used by wading birds at high tide when water inundates the dense shoreline vegetation. Shoreline and bottom sediment is composed of silt, so water clarity and visibility vary in response to current velocity. The use of this estuary by wading birds was first documented in 1988 (Maccarone and Parsons 1988).

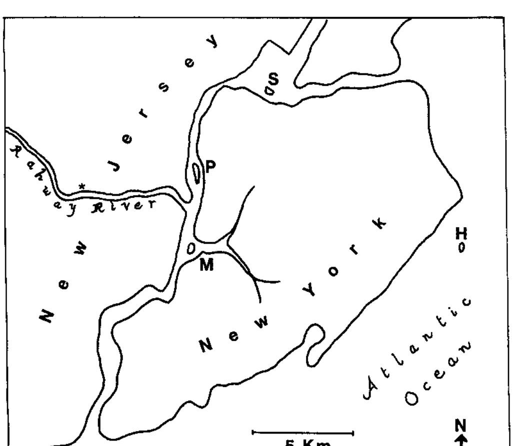

Figure 1. Map of the New Jersey-New York City (Staten Island) study area. Censuses were made by boat along a 5-km section of the Rahway River between its mouth and a point indicated by the asterisk. Also shown are three former breeding colonies at Shooter's Island (S), Prall's Island (P), and Isle of Meadows (M), and the only active colony at Hoffman Island (H).

Methods and Analyses

A total of 79 censuses were conducted between late May and early August during four years: 32 censuses in 1988, seven in 1998, nine in 1999, and 31 in 2002. Most censuses were made during low and medium tide in the Arthur Kill, the narrow tidal strait into which the Rahway River empties. Censuses were made at random times between 07.00 h and 18.00 h. At the start of each census, time, tide level (using a tide gauge) and tide direction (ebb or flood) were recorded. A small boat with two observers followed the center of the river, and each observer searched for foraging birds along one shore, including at the mouths of five narrow tidal creeks that flow into the Rahway River. The species and exact locations of all birds were recorded on maps.

Multiple regression analysis with forward selection was first used to examine patterns of wading bird abundance in the lower Rahway River. The independent variables used in the regression were year, Julian date, time of day, tide level, and tide direction. The dependent variables were numbers of the three major species: Great Egret (*Ardea alba*), Snowy Egret (*Egretta thula*), and Glossy Ibis (*Plegadis falcinellus*), and total wading birds. Total wading birds also included Great Blue Heron (*Ardea herodias*), Little Blue Heron (*Egretta caerulea*), Black-crowned Night Heron (*Nycticorax nycticorax*), and Yellow-crowned Night Heron (*N. violaceus*). Great Blue Heron were the only species among the seven observed that do not breed in the area. Linear correlations were used examine pair-wise associations in the numbers of wading birds observed during the 79 censuses.

The 5-km census route was divided into 100-m sections, beginning at an abandoned railroad bridge located at the mouth of the river. This produced 50 sections along both the north and south shores of the river, which allowed the examination of finer patterns in foraging microhabitat selection. Topographic maps and direct observation were used to determine the microhabitat for each section. From this, areas of high and low bird abundance could be correlated with physical characteristics in this section of the river. Each section of the shore was classified into one of three microhabitat types: (1) areas of slow-moving water caused by natural bends in the river or by manmade obstructions such as concrete footings; (2) shallows and mud flats exposed during medium and low tides; and (3) the mouths of tidal creeks. When the mouth of a tidal creek was flanked by a mud flat, we considered the microhabitat to be the creek mouth. All birds were assigned to one of these three microhabitat types.

The numbers of wading birds observed within the 100-m sections were used to test three null hypotheses: (1) That wading birds along the lower Rahway River followed a uniform spatial distribution. To test this, the number of birds observed within each section was compared to expected values, which were determined by dividing the total number of birds by the 100 sections. (2) That wading birds used foraging microhabitats in proportion to their availability in the study area. To test this, the number of birds observed in each of the three microhabitats was compared with expected values. The expected values for each microhabitat were determined by multiplying the total number of wading birds by the number of sections of each microhabitat. (3) That the spatial distributions of the three major species of wading birds were similar. To test this, pair-wise comparisons were performed of the three major wading bird species by examining the total number of birds observed within each of the 100 sections of shoreline.

Chi-square tests were used to compare numbers of observed and expected birds based on foraging microhabitat availability. All three microhabitats were first included in the analysis. The microhabitat with the largest significant effect was then removed from further analysis. New expected values for the two remaining microhabitats were then determined, which were compared with the observed values. A one-way Kolmogorov-Smirnov goodness-of-fit test was used to compare the spatial distributions of the three major species against a hypothesized uniform distribution (Unistat 1984). Two-way Kolmogorov-Smirnov tests were used to compare pairs of species against hypothesized identical spatial distributions (Unistat 1984). For each pairing, the numbers of birds observed within each 100-m section were compared. The entire sample of 79 censuses was used for Kolmogorov-Smirnov tests. Means and one standard error are reported.

RESULTS

A total of 1,146 wading birds were observed during the 79 censuses, a mean of 14.5 ± 1.4 birds/census. Snowy Egret (N = 407; x = 5.2 ± 0.7), Glossy Ibis (N = 315; $\overline{x}$ = 4.0 ± 0.6) and Great Egret (N = 306; $\overline{x}$ = 3.9 ± 0.7) together comprised 90% of all birds. The remaining 118 birds of other wading bird species were not used in further analyses. Multiple regression analysis of the biological and physical data collected during each census enabled a significant proportion of the overall variation in the numbers of foraging wading birds to be explained (Table 1). Tide direction was not an important variable for any species, but wading birds were most abundant during medium and low tides (Fig. 2). High tides were under represented by censuses, but the small numbers of birds present during high water was consistent. Based on census data across all four years, the numbers of Snowy Egret observed along the census route correlated with those of Great Egret (r_{77} = 0.51, $P < 0.001$) and Glossy Ibis (r_{77} = 0.24, $P < 0.05$), but the numbers of Great Egret correlated inversely with those of Glossy Ibis (r_{77} = -0.23, $P < 0.05$).

Of the total of 100 sections of shoreline, 70 consisted of mudflats and shallows that were uncovered during medium and low tides, 24 were areas of slow-moving water, and six contained tidal creek mouths (Fig. 3).

Based on the one-way Kolmogorov-Smirnov tests, all three species showed a non-uniform spatial distribution (K-S statistics: Snowy Egret = 7.16, Glossy Ibis = 7.93, Great Egret = 2.79; all $P < 0.001$). Individuals

Table 1. Results of multiple regression analysis that examined variation in the numbers of three wading bird species observed foraging during 79 censuses of the lower Rahway River. Significant predictor variables are shown after each species. There were no significant correlations between the independent variables used in the final model.

Snowy Egret: Julian date, tide level; R^2 = 0.30				
Variables	Coefficient	S. E.	t-statistic	Significance
Constant	-8.49			
Date	0.11	0.02	4.61	<0.001
Tide level	-2.47	0.99	2.50	<0.02
Glossy Ibis: Year, Julian date, tide level; R^2 = 0.32				
Variables	Coefficient	S. E.	t-statistic	Significance
Constant	630.90			
Year	-0.31	0.08	3.73	<0.001
Date	-0.06	0.02	2.84	<0.01
Tide level	-2.12	0.82	2.59	<0.01
Great Egret: Julian date, year; R^2 = 0.72				
Variables	Coefficient	S. E.	t-statistic	Significance
Constant	-572.99			
Date	0.17	0.01	11.07	<0.0001
Year	0.28	0.06	4.55	<0.0001

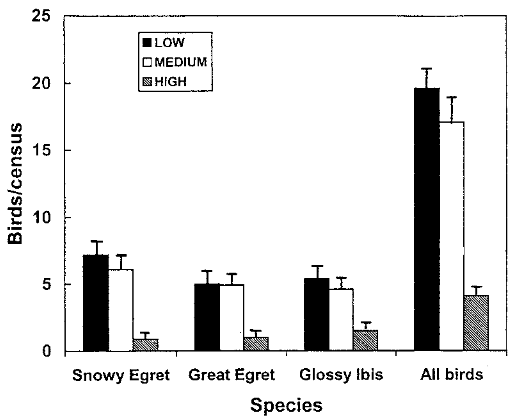

Figure 2. Mean numbers (+1 S. E.) of three major species and total wading birds observed foraging along the lower 5-km section of Rahway River during low, medium, and high tides. Each phase of the tide cycle lasts for two hours. Tidal amplitude = 1.8 m. Based on 79 censuses along the river conducted over four years.

tended to congregate within a relatively small number of sections: 75% of all Glossy Ibis were found in twelve sections; 72% of the Great Egrets were found in 18 sections, and 73% of all Snowy Egrets were found in 17 sections. Many sections were used very little, and birds were never observed in 53 (Snowy Egret and Great Egret) and 64 (Glossy Ibis) of the 100 sections (Fig. 4).

All three species showed a highly significant ($P < 0.001$) heterogeneous distribution among the three microhabitats, and all showed a marked preference for creek mouths ($P < 0.001$ in all cases) (Table 2, primary analysis). Although creek mouths comprised only 6% of the total study area, they accounted for 18% of Glossy Ibis and 21% of both Great and Snowy egret. This was also true for four of the five tidal creeks in the study area: Deep Creek (65 birds), Marshes Creek (44 birds), Cross Creek (53 birds), and Rolph's Creek (30 birds) (χ^2 tests, all $P < 0.001$). The eight birds observed at a narrower, unnamed creek at the western end of the study area did not differ from expected. Glossy Ibis showed no preference between slow-moving water and mudflats. In relation to the available habitats, the Snowy Egret and Great Egret both occurred significantly less on mud flats compared with their occurrence on slow-moving water ($P < 0.01$), although because of the greater extent of the mud flats, more individuals of all three species actually fed on the mud flats than at either of the other two microhabitats (Table 2, secondary analysis).

Although the χ^2 goodness-of-fit test determined that the overall proportionate use of three foraging microhabitats by the three

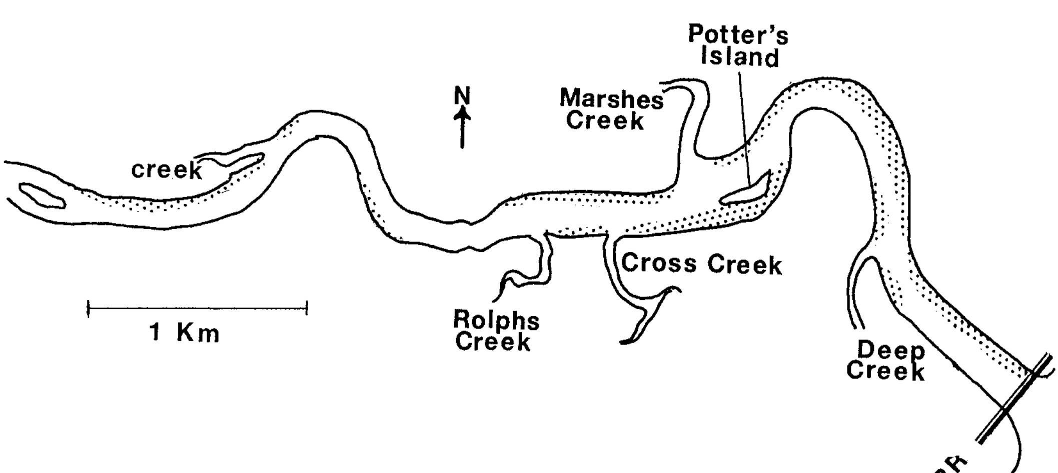

Figure 3. Detailed map of the lower Rahway River study area at low tide, showing the spatial distributions of three microhabitats, which were determined by direct observation and topographic maps. Each 5-km shoreline was divided into 50 100-m sections, beginning at an abandoned railroad bridge (RR) located at the mouth of the river. Mud flats (70% of shoreline) are stippled, five tidal creek mouths (6%) are labeled, and the remaining areas (24%) are stretches of slow-moving water.

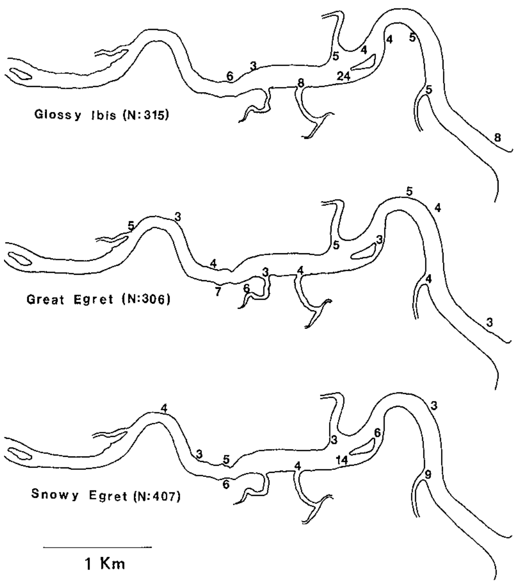

Figure 4. Major foraging locations of three species of wading birds. Numbers are the percentages of all foraging birds of each major species observed within each of 100 sections, each of which covered 100 m of shoreline. Percentages <2% are not shown. Based on 79 censuses along the 5-km census route over four years.

major species was broadly similar ($\chi^2_4 = 8.5$, n.s.), the two-way Kolmogorov-Smirnov tests showed that the actual spatial distribution of each wading bird species differed significantly from those of the other two (Table 3). Thus, each species used the three available microhabitats in similar proportions, but the actual locations of these microhabitats along the census route differed among species.

DISCUSSION

The positions of 1,148 wading birds were recorded along a 5-km section of the lower Rahway River in four years. For the Glossy Ibis and Great Egret, year of census was a significant factor, in that the number of birds increased over the course of our study. This increase was unexpected, given the history of colony occupation in this estuary. In the first year of this study (1988), all birds nested on three small dredge-spoil islands, two of which (Prall's Island and Isle of Meadows) were located only 1 and 2 km, respectively, from the mouth of the Rahway River. The third island (Shooter's) was 7 km away. By the time of our later censuses, wading birds had abandoned all three islands, and a new colony had been established on Hoffman Island, located off the SE shore of Staten Island and >12 km away from the mouth of the Rahway River (Maccarone and Brzorad 2000) (Fig. 1). Welty and Baptista (1988) estimated that avian flight demands between 6-20 times more energy than resting metabolism, and that slow, powered flight, like that used by egrets, is the most costly. Thus, the higher energetic costs associated with flying this much greater distance suggests that this estuary is import to breeding wading birds. Prey were not sampled each year and therefore it cannot be determined whether the increase in wading birds over time occurred with prey availability.

The increased use of the Rahway River may have also marked an ecological recovery from a series of oil spills in 1990, when both prey densities and wading bird use of this estuary plummeted (Burger 1994; Maccarone and Brzorad 2000). The number of wading birds on the lower Rahway River also grew between May and August, which suggests that this estuary increased in importance later in the wading bird reproductive cycle. Periodic sampling for fish and invertebrates in the Rahway River 1990, 1991, and 2002 has shown that total prey biomass may increase by 100 times between May and August (Brzorad and Burger 1994; Brzorad *et al.* 2004).

The number of birds counted during each census ranged from 0 to 50, but the presence or absence of birds, as well as the types of microhabitats that they used, was not random. Rather, wading birds seemed to respond to two types of cues. At one level, tide height may have signaled the availability of preferred foraging locations. Medium and low tides exposed the mouths of tidal creeks, broad, low-relief mud flats, and shallows, all of which greatly increased the total amount of surface area available for foraging. Tide direction was not an important factor for any species, which suggests that birds did not make a distinction between rising or falling tides, but only the actual water level. Water level has been shown to affect wading bird habitat selection (Strong *et al.* 1997; Bancroft *et al.* 2002).

Table 2. The use of three foraging microhabitats by three species of wading birds in relation to their availability. Numbers of birds were determined from 79 censuses along a 5-km section of the lower Rahway River. Each shore was divided into fifty 100-m sections, giving a total of 100 sections. Microhabitat type was determined by direct observation and topographic maps. An initial χ^2 test was used to compare overall observed and expected values. The most significant departure from expected for all three species was creek mouths (Primary analysis). With creek mouths removed, the two remaining microhabitats were then reanalyzed using new expected values (Secondary analysis). Numbers of four less common wading bird species are not included.

Primary analysis: Comparison of birds among all three microhabitat types

		Number of foraging individuals					
		Snowy Egret		Glossy Ibis		Great Egret	
Type of microhabitat	N. 100- m sections	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Creek mouth	6	86	24	57	19	64	18
χ^2			160		76.0		117
Slow-moving water	24	105	98	66	76	92	73
χ^2			0.5		1.3		4.9
Mud flat/ shallow	70	216	285	192	220	150	214
χ^2			16.7		3.6		27.3
Total	100	407		315		306	
Total χ^2_3			177		80.9		

Secondary analysis: Comparison of birds using slow-moving water and mudflats/shallows

		Number of foraging individuals					
		Snowy Egret		Glossy Ibis		Great Egret	
Type of microhabitat	N 100- m sections	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Slow-moving water	24	105	82	66	66	92	62
χ^2			6.5		0.0		14.5
Mud flat/ shallow	70	216	239	192	192	150	180
χ^2			2.2		0.0		5.0
Total	94	321		258		242	
Total χ^2_2			8.7		0.0		19.5

However, this broad characterization overlooks large interspecific differences that were apparent at both levels. For example, numbers of Snowy Egret and Glossy Ibis were highly correlated with each other, and both species used the Rahway River only during low and medium tides. Numbers of Glossy Ibis were inversely correlated with those of Great Egret, the only species which used this section of the river independent of water level. This same pattern was documented previously in the Rahway River, as well as in other nearby estuarine foraging sites (Maccarone and Parsons 1994). The two smaller species may be more restricted in the use of certain foraging patches than are the taller Great Egret because of the water depth.

Although this section of the river attracted numbers of all three species of wading birds, differences in microhabitat preferenc-

Table 3. The results of two-way Kolmogorov-Smirnov tests that compared the spatial distributions of three species of wading birds within 100 sections of the lower Rahway River in New Jersey. Each section covered 100 m of shoreline. A significant K-S value rejects the null hypothesis that two different wading bird species had the same spatial distribution. Thus, there was little overlap in the locations of foraging wading birds observed during 79 censuses in four years.

Pair-wise Comparison	K-S Statistic	P-value
Snowy Egret-Glossy Ibis	4.53	<0.001
Great Egret-Snowy Egret	3.68	<0.001
Great Egret-Glossy Ibis	4.53	<0.001

es also were apparent. At a finer level, once a bird decided to forage along this river, it may select or avoid specific types of microhabitats. The spatial distributions of all three species departed significantly from uniform, but a more clustered distribution was evident for the Snowy Egret and the Glossy Ibis. The Great Egret was somewhat more evenly distributed, again possibly because height afforded them better access to different microhabitats. Their sit-and-wait foraging strategy also might be suitable in a greater variety of settings than the ambulatory strategies used by Snowy Egret and Glossy Ibis (Maccarone and Brzorad 2000).

Wading birds used four of the five creek mouths in numbers significantly higher than expected, with each species concentrating its foraging efforts at different creeks (Fig. 4). There are several possible explanations for this pattern. For example, water moves through these narrow creeks at all times except during slack high tide, and carries nutrients and small fish from more elevated parts of the estuary. As such, this microhabitat may be attractive to wading birds because of: (1) the higher predictability of prey drawn to these nutrients, (2) the higher prey density created by the narrow channels, or (3) the greater ease of prey capture because fish have few options for escape. Some of the marshes drained by these tidal creeks provide extensive habitat used by Atlantic Silverside (*Menidia menidia*) and Mummichog (*Fundulus heteroclitus*), and by Grass Shrimp (*Palaeomonetes* spp.) and other invertebrates. Many of these small organisms leave the marsh when the tide ebbs, and the creek mouths carry them into the Rahway River and past waiting egrets.

The fact that the Great Egret was more evenly distributed than the Snowy Egret may also be due to differences in anatomy and strike velocity. Maccarone and Brzorad (2002) and Brzorad *et al.* (2004) showed that the Great Egret had a higher strike success and greater foraging efficiency than the Snowy Egret. This may be linked to differences in strike velocity between the species, since the Great Egret strikes almost twice as fast as the Snowy Egret (Brzorad *et al.* 2004). To compensate for their lower success, Snowy Egret may prefer microhabitats, such as creek mouths, where fish move past them. Better at catching prey (Maccarone and Brzorad 2002), the Great Egret appears to be less tied to specific locations. In addition, the aggressive defense of foraging patches has been observed, especially by Snowy Egret against conspecifics (Maccarone and Parsons 1994; Brzorad *et al.* 2004), and Great Egret have been observed to relocate from one patch to another so as to remain close to a foraging Snowy Egret (Maccarone and Parsons 1994). Egrets seldom interfere with or follow Glossy Ibis, but the Glossy Ibis does capture fish and also may be attracted to Snowy Egrets. Thus, because of local enhancement and other social behavior occurring in wading birds (Caldwell 1981; Erwin 1983), the large aggregations at the mouths of tidal creeks may form, in part, because of social attraction.

Both Great Egret and Snowy Egret eat mostly fish in this estuary (Maccarone and Brzorad 2002) and used areas of slow-moving water in numbers higher than expected based on their availability (24% of the study area). It is possible that the low turbulence in these areas increased water clarity and improved prey visibility. Although Snowy Egret used mudflats in proportion to their availability (70% of the study area), the Great Egret was significantly under represented in this microhabitat. Shallow waters near the shore often have poor visibility, especially when moving water increases the sediment load. Thus, mudflats and shallows, while very abundant, were not very attractive to these visual hunters. However, both egret species eat invertebrates associated with mudflats, such as shrimp (Maccarone and Brzorad 2002), which might account for their presence on the vast mudflats exposed at low tides. Glossy Ibis used both areas of slow-moving water and mudflats in proportion to their availability, possibly because they forage tactilely, eat more invertebrates (DeSanto *et al.* 1997; Safran *et al.* 1997, 2000) and their foraging success would not be as affected by poor water clarity.

The regression analysis was able to account for relatively little of the total variation in the numbers of the Snowy Egret ($R^2 = 0.30$)

and the Glossy Ibis ($R^2 = 0.32$) that foraged in this tidal estuary. The independent variables identified in the regression analysis were strong predictors only for the Great Egret ($R^2 = 0.72$), but neither of the two variables in the final regression model (year of census, Julian date) seems directly related to the river itself. Clearly, there are other, more important factors associated with the decision to use this site. This study quantifies the use of the lower Rahway River estuary, and indicated its importance as a feeding area for breeding wading birds. Despite a much longer commute from the more distant Hoffman Island colony, a mean of 15 birds were observed per census, and as many as 50 birds were counted during some censuses. There are approximately 7 km^2 of tidal wetlands and other foraging habitat in the study area. This undeveloped estuary is a valuable fish and shellfish nursery amid a highly industrialized urban area (Brzorad and Burger 1994; Brzorad *et al.* 2004), and this study also suggests the broader value of this estuary in providing different microhabitats to various species. Although all three species preferred tidal creek mouths to capture prey, Glossy Ibis congregate around Potter's Island, and Great Egret do not appear to be linked to any particular section of the river and may benefit from the estuary as a whole. However, the area adjacent to Potter's Island and other sections along the lower Rahway River are being considered for commercial development. We believe that the disruption or change of any portion of this river estuary would be detrimental to both the fish fauna and to other species at higher tropic levels, such as wading birds.

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LITERATURE CITED

Arengo, F. and G. A. Baldassarre. 1999. Resource variability and conservation of American flamingos in coastal wetlands of Yucatan, Mexico. Journal of Wildlife Management 63: 1201-1212.

Bancroft, G. T., D. E. Gawlik and K. Rutchey. 2002. Distribution of wading birds relative to vegetation and water depths in the northern Everglades of Florida, USA. Waterbirds 25: 265-277.

Burger, J. 1994. Before and After an Oil Spill: The Arthur Kill (J. Burger, Ed.). Rutgers University Press, New Brunswick, New Jersey.

Brzorad, J. N., A. D. Maccarone and K. Conley. 2004. Foraging energetics of Great Egrets and Snowy Egrets. Journal of Field Ornithology 75: 266-280.

Brzorad, J. N. and J. Burger. 1994. Fish and shrimp populations in the Arthur Kill. Pages 178-200 *in* Before and After an Oil Spill: The Arthur Kill (J. Burger, Ed.). Rutgers University Press, New Brunswick, New Jersey.

Caldwell, G. S. 1981. Attraction to tropical mixed-species flocks: Proximate mechanisms and consequences. Behavioral Ecology and Sociobiology 8: 99-103.

Christensen, J. D., M. E. Monaco and T. A. Lowery. 1997. An index to assess the sensitivity of Gulf of Mexico species to changes in estuarine salinity regimes. Gulf Research Reports 9: 219-229.

Cristol, D. A. and P. V. Switzer. 1999. Avian prey-dropping behavior II: American crows and walnuts. Behavioral Ecology 10: 220-226.

DeSanto, T. L., J. W. Johnston and K. L. Bildstein. 1997. Wetland feeding site use by white ibises (*Eudocimus albus*) breeding in coastal South Carolina. Colonial Waterbirds 20: 167-176.

Erwin, R. M. 1983. Feeding habits of nesting wading birds: Spatial use and socia influences. Auk 100: 960-970.

Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72: 329-346.

Houtman, R. and L. M. Dill. 1998. The influence of predation risk on diet selectivity: A theoretical analysis. Evolutionary Ecology 12: 251-262.

Iwasa, Y., M. Higashi and N. Yamamura. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. American Naturalist 117: 710-723.

Kent, D. M. 1987. Effects of varying behavior and habitat on the striking efficiency of egrets. Colonial Waterbirds 10: 115-119.

Krebs, J. R. and R. J. Cowie. 1976. Foraging strategies in birds. Ardea 98: 104-116

Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology 68: 19-40

Maccarone, A. D. and J, N. Brzorad. 2002. Foraging patterns of breeding egrets at coastal and interior locations. Waterbirds 25: 1-7.

Maccarone, A. D. and J. N. Brzorad. 2000. Wading bird foraging: Response and recovery from an oil spill. Waterbirds 23: 246-257.

Maccarone, A. D. and K. C. Parsons. 1994. Factors affecting the use of freshwater and estuarine foraging habitats by breeding wading birds in New York City. Colonial Waterbirds 17: 60-68.

Maccarone, A. D. and K. C. Parsons. 1988. Differences in flight patterns among nesting ibises and egrets. Colonial Waterbirds 11: 67-71.

Safina, C. and J. Burger. 1985. Common tern foraging: seasonal trends in prey fish densities and competition with bluefish. Ecology 66: 1457-1463.

Safran, R. J., M. A. Colwell, C. R. Isola and O. E. Taft. 2000. Foraging site selection by non-breeding White-faced Ibis. Condor 102: 211-215

Safran, R. J., C. R. Isola, M. A. Colwell, and O. E. Williams. 1997. Benthic invertebrates at foraging locations of nine waterbird species in managed wetlands of the northern San Joaquin Valley, California. Wetlands 17: 407-415.

Sherry, T. W. and L. A. McDade. 1982. Prey selection and handling in two neotropical hover-gleaning birds. Ecology 63: 1016-1028.

Strong, A. M., G. T. Bancroft and S. D. Jewell. 1997. Hydrological constraints on Tricolored Heron and Snowy Egret resource use. Condor 99: 894-905.

Unistat. 1984. Users Guide for Statistical Package for Windows. London: Unistat, Ltd.

Wanless, S., D. Gremillet and M. P. Harris. 1998. Foraging activity and performance of Shags *Phalacrocorax aristotelis* in relation to environmental characteristics. Journal of Avian Biology 29: 49-54.

Welty, J. C. and L. Baptista. 1988. The life of birds. Saunders College Publishing, New York.

Yozzo, D. J. and D. E. Smith. 1997. Composition and abundance of resident marsh—surface nekton: Comparison between tidal freshwater and salt marshes in Virginia, USA. Hydrobiologia 362: 9-19.