

Effects of Tide Stage on the Use of Salt Marshes by Wading Birds in Rhode Island

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Abstract - Salt marshes provide important foraging habitats for wading birds (Ardeidae), and it has been suggested that the lack of suitable marsh habitats can limit the size of wading bird populations. It is therefore important to be able to accurately assess wading bird use of salt marshes over multiple spatial and temporal scales. The goal of this study was to determine how wading bird utilization of Narragansett Bay, RI salt marshes is affected by changing tide levels. Bird surveys were conducted across the tidal range at three different marshes. Wading birds foraged over much of the tidal cycle, but reverted to increased loafing during mid-tides when shallow foraging habitats were limited. Birds foraged in increasingly deeper water at higher tide stages rather than seeking out consistently shallow water over the tidal period. At Round Marsh, the primary study site, bird abundances were significantly related to tidal stages, but different patterns were observed at two additional sites. Wading bird abundance appears to depend on the availability of habitats that provide shallow foraging areas across tidal stages. Results from this study can be used to improve wading bird monitoring protocols and field studies on wading birds in salt marshes by ensuring that tidal stage is accounted for.

Introduction

Wading birds are conspicuous predators of nekton (fishes and decapod crustaceans) in salt marshes and other shallow estuarine habitats (Custer and Osborn 1978, Kushlan 1976). In southern New England, common wading birds found in salt marshes include *Ardea alba* L. (Great Egret), *Egretta thula* Molina (Snowy Egret), *Ardea herodias* L. (Great Blue Heron), *Egretta caerulea* L. (Little Blue Heron), *Plegadis falcinellus* L. (Glossy Ibis), and *Butorides virescens* L. (Green Heron) (Reinert and Mello 1995, Trocki 2003). Wading birds primarily use these marshes for foraging, but the dynamic hydrology of shallow estuarine habitats may result in considerable changes in the distributions and abundances of wading birds over multiple spatial and temporal scales. These patterns must be quantified in order to fully understand the value of marshes for wading birds and develop quantitative wading bird monitoring and survey protocols.

Wading bird use and abundance in fresh and estuarine marshes can vary according to season (Hom 1983, Willard 1977), time of day (Hom 1983),

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water level or tidal stage (Custer and Osborn 1978, Maccarone and Brzorad 2005, Strong et al. 1997), and meteorological conditions (Kushlan 1981). These local patterns can also be superimposed over inter-annual and decadal changes in abundance (Ferren and Myers 1998). Temporal changes in wading bird use of tidal marshes can be associated with concurrent changes in microhabitat selection. For example, Custer and Osborn (1978) observed that wading birds foraged on shallow tidal flats during periods of low tidal water, but switched to foraging on the vegetated salt marsh surface when it flooded. Similarly, Matsunaga (2000) found that *Ardea cinerea* L. (Grey Heron) foraged in shallow eelgrass beds during extreme low spring tides, but were relegated to foraging less efficiently in mud flats during low neap tides. The foraging ecology of wading birds has been studied along the Gulf and Atlantic coasts of the southeastern United States, but relatively few studies have been conducted in New England, which represents the northern limit of the range of many wading bird species.

Although research from other regions can be used as a general guide for predicting wading bird patterns in New England salt marshes, enough fundamental differences exist between this region and more southern areas to warrant further study in New England. The warm season when prey resources are most productive is shorter than in more southern marshes. Tidal ranges are generally higher in New England than along the southeast coastal plain (Roman et al. 2000). Tides in New England are also more predominantly driven by astronomical forces and therefore may be more predictable than in the Gulf of Mexico, where astronomical tidal patterns are often overridden by meteorological conditions (Rozas 1995). Water clarity is generally higher in New England (Roman et al. 2000), making it potentially easier for birds to locate prey. Salt marshes are much smaller and less extensive in New England (particularly in southern New England), than along the mid-Atlantic, southeast, and Gulf coasts (Roman et al. 2000). Smaller patch sizes may lead to relatively greater effects from surrounding land-use patterns (e.g., inhibited foraging from excessive plant growth due to elevated nutrient inputs). Finally, marsh pools and pannes are valuable foraging habitats, but they are uncommon throughout much of southern New England due to historic ditching and tidal restrictions (Adamowicz and Roman 2005). Taken in aggregate, these differences in geomorphology, habitats, and hydrology can potentially affect patterns in wading bird use and abundances in New England salt marshes. This potential variability highlights the need to quantitatively assess basic temporal and spatial patterns of wading bird use of New England salt marshes.

The purpose of this study is to quantify patterns in wading bird use of salt marshes in Narragansett Bay, RI in relation to tidal levels. Specifically, this study will determine how bird abundances, habitat use, behavior, and foraging are affected by the tides. Most of the data were collected from a single salt marsh in Narragansett Bay, RI, although additional data were collected from two nearby marshes for comparative purposes. This study will add to

the relatively depauperate body of research on wading bird ecology in New England and ultimately allow for the development of more accurate monitoring and survey protocols in this region.

Methods

Study sites

This study was primarily conducted in the Audubon Society of Rhode Island's Round Marsh salt marsh complex in Jamestown, RI (Fig. 1). This 21.7-ha marsh is comprised of 17.2 ha of vegetated salt marsh (79%),

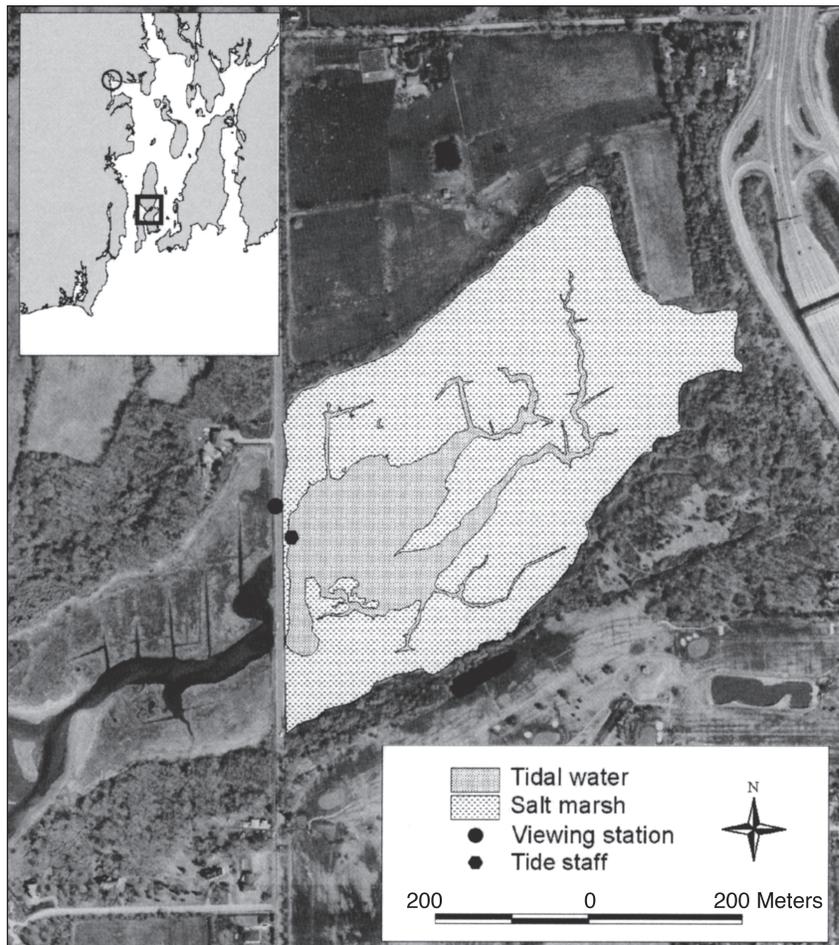


Figure 1. Map of the Round Marsh study site, located in Jamestown, RI in lower Narragansett Bay. The map shows vegetated salt marsh habitats, adjacent tidal water habitats (i.e., tidal flats, creeks, and ditches), as well as the locations of the viewing station and tide staff. The map is placed over an aerial photograph of the surrounding landscape for context. The open circle in the locus map denotes the location of the Apponaug Cove and Thatch Marsh study sites in Greenwich Bay, RI.

interspersed with a small number of tidal creeks and narrow ditches, with a relatively large expanse of mud flats (in this study, the terms mud flat and tidal flat are used interchangeably and are defined as unvegetated soft-bottom habitats that are either exposed to the air or covered by shallow water at low tide). The marsh contains a mix of plant species typical of New England salt marshes, including *Spartina alterniflora* Loisel. (Smooth Cordgrass), *Spartina patens* (Ait.) Muhl. (Salt Hay Grass), *Distichlis spicata* (L.) Greene (Spikegrass), and *Juncus gerardii* Loisel. (Black Grass), while the upland edge consists primarily of *Iva frutescens* L. (Hightide Bush), *Panicum virgatum* L. (Switchgrass), and *Phragmites australis* (Cav.) Trin. ex Steud. (Common Reed). Only a few salt marsh pools and pannes are present in Round Marsh due to historic mosquito ditching. The marsh is surrounded by a mix of residential and agricultural lands, is abutted by a two-lane highway to the west of the marsh, and is connected to Narragansett Bay through a single tidal creek flowing through a culvert under the road. Tides are semi-diurnal and averaged 0.89 m during the study period. Freshwater inputs to the marsh are minimal and are primarily from precipitation and groundwater flow, resulting in a mean salinity of 21 ppt. At low tide, a portion of the tidal flats become exposed, and a small area of deep water remains directly upstream of the culvert.

Supplemental data were collected from two additional sites in nearby Greenwich Bay, RI (Fig. 1). Thatch Marsh is a 9.9-ha meadow marsh and is generally similar in habitat composition to Round Marsh (i.e., a relatively large area of vegetated salt marsh with a smaller area of creeks and tidal flats). Apponaug Cove (6.1 ha; hereafter referred to as Apponaug) differed from Thatch and Round Marshes in that it is primarily an intertidal, unvegetated cove that supported only a small amount of fringing marsh vegetation. Apponaug was specifically chosen in order to collect data from a site that differed in the relative amount of tidal flat and salt marsh surface habitats, since it was hypothesized that the amount of these habitats in a site would strongly affect patterns in wading bird abundances observed throughout the tidal cycle.

Field methods

Wading birds were surveyed at Round Marsh on July 10, 12, 13, 17, 19, and 20, 2006. Surveys were conducted over an approximately six-hour period during the course of one-half of a tidal cycle (e.g., from slack high tide to slack low tide). All surveys were conducted during daylight hours between 0730 and 1700 EST. Even though direction of tidal flow has been shown to be an ineffective determinant of wading bird abundances (Maccarone and Brzorad 2005), birds were sampled from high to low tide on July 10, 12, and 13, and from low to high tide on July 17, 19, and 20, 2006. On each date, wading birds were surveyed from a fixed site on the embankment off the road adjacent to the marsh (Fig. 1). Observations were made of all visible portions of the marsh every 10 minutes over the entire six-hour period using a 32 x 60 spotting scope or 10 x 50 binoculars. Every 10 minutes, all wading birds observed in the marsh were identified

to species, counted, and their location in the marsh marked on a map. Additional data recorded included the habitat where each bird was located and its activity (derived from a list originally compiled by Kushlan [1976] and later modified by Kelly et al. [2003]), and tidal depth (from a fixed tide staff placed directly in front of the viewing station).

Water depths on the mud flats where birds foraged were determined after all surveys were completed. This follow-up data collection was accomplished by returning to the locations of each bird sighting using a handheld Garmin GPS with coordinates derived in GIS from digital copies of field maps. Once on location, the water depth at each location was measured, as was the water depth at the original tidal staff. These data were used to indirectly calculate the water depth in which each bird was originally foraging by solving the equation:

$$B_1 = (TS_1 - TS_2) + B_2,$$

where B represents the water depth at the location of each bird, TS represents the water depth on the tide staff, and subscripts 1 and 2 represent the first and second recording times, respectively.

Wading bird abundance in the entire marsh, expressed as the mean number of birds observed during a single observation period, was averaged for 5-cm tide-height intervals (e.g., from 66–70 cm, 71–75 cm, etc.) over the six survey dates. Wading bird abundances were also determined using the same approach for the two major habitat types (mud flat and vegetated salt marsh surface) at Round Marsh. A best-fit nonlinear regression model was applied to the data to determine the relationship between bird abundance and tide level. Patterns in mean foraging depths in mud flats and bird behaviors were also examined in relation to tidal water levels.

Wading bird surveys were conducted at Thatch Marsh on September 12, 14, and 21, and at Apponaug on September 26 and 30, 2007. On each date, surveys were conducted over one-half of a tidal cycle as described above for Round Marsh. At Apponaug, bird surveys were conducted every 10 minutes. At Thatch Marsh, surveys were conducted every 20 minutes due to the need to view birds from multiple locations at this site. At both sites during each survey, data that were collected included wading bird species, the number of individuals, habitat used, and water depths (i.e., tide staff height). Bird behaviors, locations, and foraging water depths were not assessed at these sites.

The availability of foraging habitats at each site was determined using a combination of field- and computer-mapping techniques. The area of intertidal vegetated marsh surface habitats was digitized from 2006 color orthophotographs (1:12,000 scale). The area of intertidal mud flat habitats was determined by walking the perimeter of this habitat at low tide with a handheld GPS. The area of shallow subtidal habitats (defined as subtidal areas covered by less than approximately 28 cm of water) was determined by measuring water depths throughout subtidal areas at low tide and then interpolating these depths in GIS to determine the 28-cm contour.

Error estimation

At Round Marsh, every effort was made to record the location of each bird on the maps as accurately as possible using prominent geographic features (e.g., creeks and pools, marsh edges, etc.) in the marsh. To quantify the error associated with mapping bird locations, one person was sent out into the marsh to 30 randomly predetermined locations. At each location, the person in the field crouched down, recorded their location using the handheld GPS unit, and waited for an observer at the original viewing station (the same observer who collected all the original data) to record their location on a map. The GPS coordinates determined in the field were then compared to GPS points derived from the point located on the map. This procedure provided an error estimate that could be examined by habitat (mud flat and marsh surface) and by distance from the viewer. The error associated with determining locations was then used to assess the error associated with determining wading bird foraging water depths in mud flat habitats. For 10 randomly selected points in the mud flats, eight haphazard water depths were measured within a circle (with a radius based on the pre-determined distance error) around each point.

Results

Round Marsh

Over the six-day sampling period, six wading bird species were observed in Round Marsh. The Great Egret comprised 72% of all bird observations, followed by Snowy Egret (18%), Great Blue Heron (5%), *Nycticorax violaceus* L. (Yellow-crowned Night-heron, 3%), Little Blue Heron (1%), and *Nycticorax nycticorax* L. (Black-crowned Night-heron, 1%). In general, wading birds were found throughout much of Round Marsh in a variety of habitat types, including flooded mud flats, marsh vegetation, creeks, pools, and pannes.

Overall wading bird abundance (all species and all behaviors combined) was closely related to tide stage in Round Marsh and was best explained with a third-degree polynomial nonlinear regression ($R^2 = 0.85$, $F = 32.44$, $P < 0.0001$; Fig. 2). At the lowest tide levels, when water was concentrated in shallow areas on the mud flats, wading bird abundance was relatively high. As tide levels increased, bird abundance quickly dropped until water levels became high enough to flood the vegetated marsh surface, at which time bird abundance once again increased. At the highest tide levels, bird abundances dropped off again.

In mud flat habitats, bird abundance was only high during the lowest tide levels (Fig. 3). As water levels increased, bird abundance exhibited a significant exponential decay ($R^2 = 0.67$, $F = 36.43$, $P < 0.0001$) on the mud flats and remained low throughout the high-tide period. In contrast, bird abundance on the vegetated marsh surface was best explained with a second-order Gaussian model ($R^2 = 0.76$, $F = 33.39$, $P < 0.0001$), with lowest bird abundances occurring at low tide levels (when most birds were on the flats),

followed by a peak at mid-tide levels and a drop again at the highest tide levels (Fig. 3).

Water depths in which Great and Snowy Egrets foraged on the mud flats increased concomitantly with increasing tide levels (Fig. 4). Both species continued foraging in the mud flats in deeper water as the tide levels increased. However, the maximum foraging depth for Snowy Egrets was approximately half the maximum depth for Great Egrets; consequently, on incoming tides Snowy Egrets ceased foraging in the flats much earlier than Great Egrets. Overall, Snowy Egrets were found foraging in water depths that ranged from 3–23 cm, with an overall mean foraging depth of approximately 13 cm (Fig. 4). Great Egrets foraged in waters ranging from 3–44 cm in depth, with an overall mean foraging depth of 14 cm.

Great and Snowy Egrets each exhibited seven distinct behaviors in Round Marsh. Differences in behaviors were observed between the two species and among the different stages of the tide. Overall, Snowy Egrets spent considerable time actively foraging for food, displaying behaviors such as stalking, walking slowly, and walking quickly (these three behaviors accounted for 71% of all observations. Conversely, Great Egrets were much less active

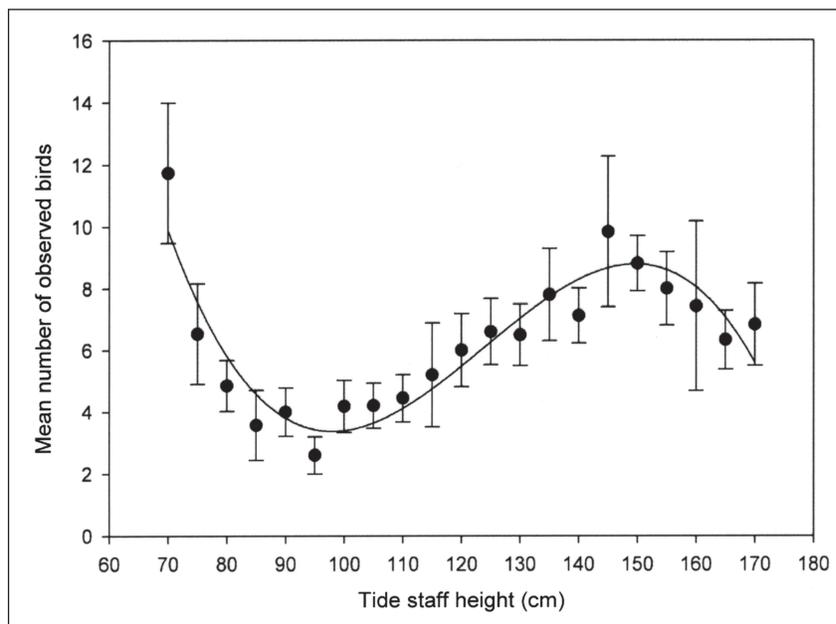


Figure 2. Mean (± 1 S.E.) numbers of wading birds observed (all habitats, species, and behaviors combined) in relation to tide level in Round Marsh. Mean values were derived by averaging all observations from July 10, 12, 13, 17, 19, and 20, 2006, within 5-cm tide-height intervals (e.g., from 66–70 cm, from 71–75 cm etc.). Tide elevations were read from a fixed tide staff near the mouth of the marsh. The elevation of the staff was not surveyed, so tide heights are relative (e.g., the tidal pattern from low to high tide runs from the left to right on the x axis).

and generally spent more time preening, standing and waiting, and looking around (66% of all observations for all three behaviors combined). In general, both species spent more time displaying foraging behaviors during the low and high tide levels, when shallow water was present on mud flat and marsh surface habitats, respectively. Conversely, during mid-tide levels, individuals of both species that remained in the marsh spent relatively less time foraging and more time preening.

Error estimation

The measurement error associated with mapping bird locations and then returning to those same locations to measure water depths increased with increasing distance from the viewing station. The amount of measurement error averaged 4.5 m for distances within 100 m of the viewing station. This error increased to an average of 9.9 m for distances between 100–200 m, and to 32.5 m for distances between 200–300 m. However, all locations where water depths were measured were in the shallow mudflat tidal basin (Fig. 1), which was within 200 m of the viewing station. The mean error for distances between 0–200 m was 8.9 m. Water depths varied very little within this 8.9-m radius around 10 randomly selected points on the shallow tidal

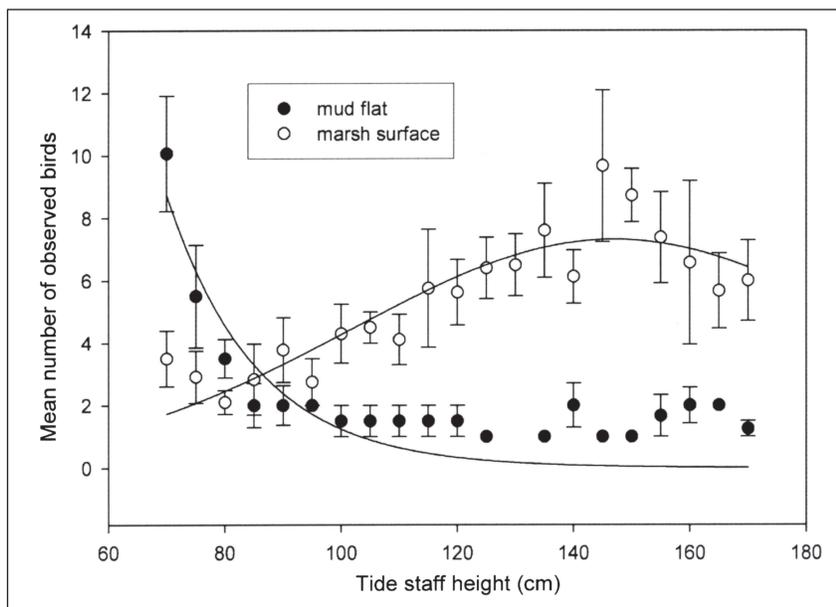


Figure 3. Mean (± 1 S.E.) numbers of birds in mud flat and marsh surface habitats in relation to tide level in Round Marsh. Mean values for each habitat were derived by averaging all observations from July 10, 12, 13, 17, 19, and 20, 2006, within 5-cm tide height intervals (e.g., from 66–70 cm, from 71–75 cm etc.). Tide elevations were read from a fixed tide staff near the mouth of the marsh. Since the elevation of the staff was not surveyed, the tide heights are relative; the tidal pattern from low to high tide runs from left to right on the x axis.

flats. Mean error in water depths within this zone was only 1.8 cm due to the uniform mud flat bottom, illustrating the relative accuracy of the depth measurements estimated in this study.

Inter-marsh comparisons

Patterns in wading bird abundances differed at both Thatch Marsh and Apponaug compared to Round Marsh (Fig. 5). Bird abundance at Thatch Marsh exhibited two distinct peaks, but these occurred at somewhat different stages of the tide than at Round Marsh. At Thatch Marsh, bird abundance peaked at the highest tide levels and a secondary peak occurred at water levels slightly above slack low tide. Unlike the pattern at Round Marsh, bird abundance fell during slack low tide. Bird abundance at Thatch Marsh was best explained with a third-degree polynomial non-linear regression ($R^2 = 0.66$, $F = 10.24$, $P = 0.0005$). At Apponaug, bird abundance was highest at slack low tide, quickly dropped off at higher tide levels, and was best explained with a logarithmic regression ($R^2 = 0.69$, $F = 61.65$, $P < 0.0001$).

The area of foraging habitats that was available at different tide stages also differed among the three study sites (Fig. 6). Shallow subtidal areas (mud flats at low tide that are covered by less than 28 cm of water) were common at both Round Marsh and Apponaug, but relatively scarce at Thatch

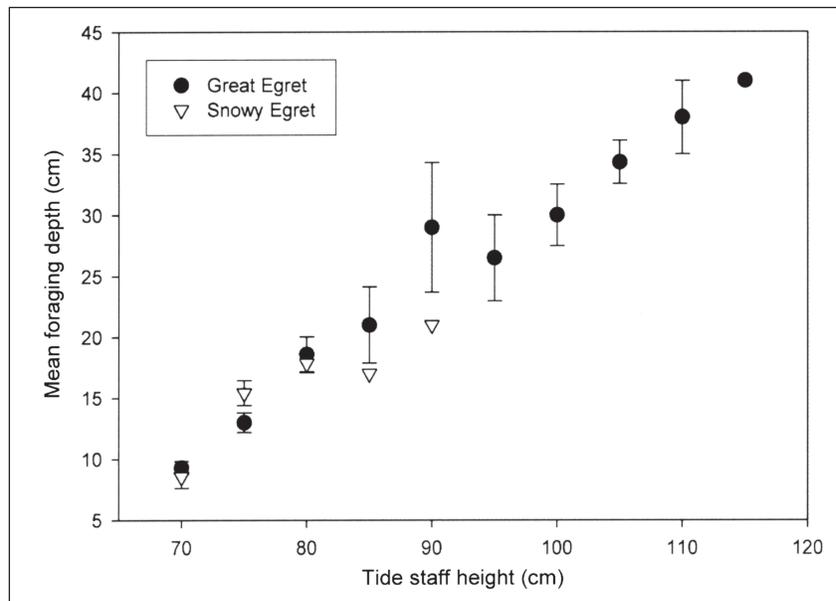


Figure 4. Mean (± 1 S.E.) water depths in which Great and Snowy Egrets were actively foraging at varying tide levels in Round Marsh tidal flat habitats. Mean numbers for each species were derived by averaging all observations from July 10, 12, 13, 17, 19, and 20, 2006 within 5-cm tide height intervals (e.g., from 66–70 cm, from 71–75 cm etc.).

Marsh. Intertidal mud flats were present at all three sites, but were most common at Apponaug. In contrast, vegetated salt marsh habitats were common at both Round and Thatch Marshes, but were virtually absent from Apponaug.

Discussion

Six species of wading birds were found in salt marshes in this study and, except for the absence of Glossy Ibis, the composition of the wading bird community was similar to those reported from other southern New England marshes (Clark et al. 1984, Reinert and Mello 1995, Trocki 2003). However, there were typically fewer than a dozen birds in each of the three marshes in this study at any given time. After adjusting for the area of each site, the maximum densities observed were 2.6 birds ha⁻¹ at Apponaug, 1.0 birds ha⁻¹ at Thatch Marsh, and 0.6 birds ha⁻¹ at Round Marsh. These maximum densities are smaller than those reported in other studies at lower latitudes (e.g., Gawlik 2002, Velasquez 1992). Because wading bird densities in New England can be so small, it is important to understand how marsh use varies over small-scale time periods since a difference in only a small number of birds can disproportionately alter the perceived value of a marsh for wading birds.

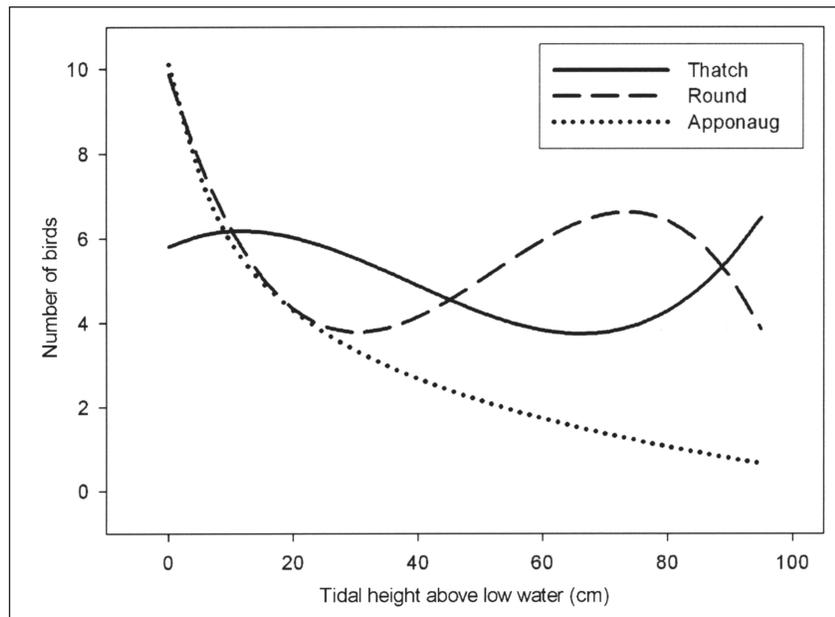


Figure 5. Modeled bird abundances from the three study sites. Models were derived using best-fit regressions to actual bird abundances over tidal cycles at each site. To account for differences in relative tide staff levels at each site, modeled data were normalized according to the height above the low-tide staff level at each site. Bird numbers were not adjusted for site area (e.g., not converted to density) to ensure that models overlaid each other to facilitate visual comparisons.

Wading birds in Round Marsh exhibited patterns in abundances, behaviors, and foraging that were related to water depths associated with the diurnal tidal cycle. The behaviors displayed by Great and Snowy Egrets in this study were similar to those observed in other marshes in Narragansett Bay, RI (Trocki 2003). The observation that Snowy Egrets spent relatively more time actively foraging compared to Great Egrets was also consistent with studies from other regions (e.g., DuBowy 1996, Kushlan 1976). In this study, both egret species spent the majority of their time utilizing various foraging behaviors while using Round Marsh. The exception occurred during intermediate tidal stages (i.e., mid-tide) when tidal water levels were relatively deep over the unvegetated flats but had not yet flooded the emergent marsh surface. During this period, shallow-water foraging habitat was not readily available and birds either left the marsh completely or remained behind and displayed loafing behaviors (e.g., preening or standing and waiting). Similar results were observed by both Austin (1996) and Sawara et al. (1990), who found that the feeding activities of Great Blue and Grey Herons were restricted by the level of the tide.

The water depths in which egrets foraged in this study fall within the general range documented for both species in other areas (Gawlik 2002, Hom 1983, Powell 1987, Willard 1977). Surprisingly, neither Great nor Snowy Egrets appeared to actively seek out the shallowest areas for foraging as

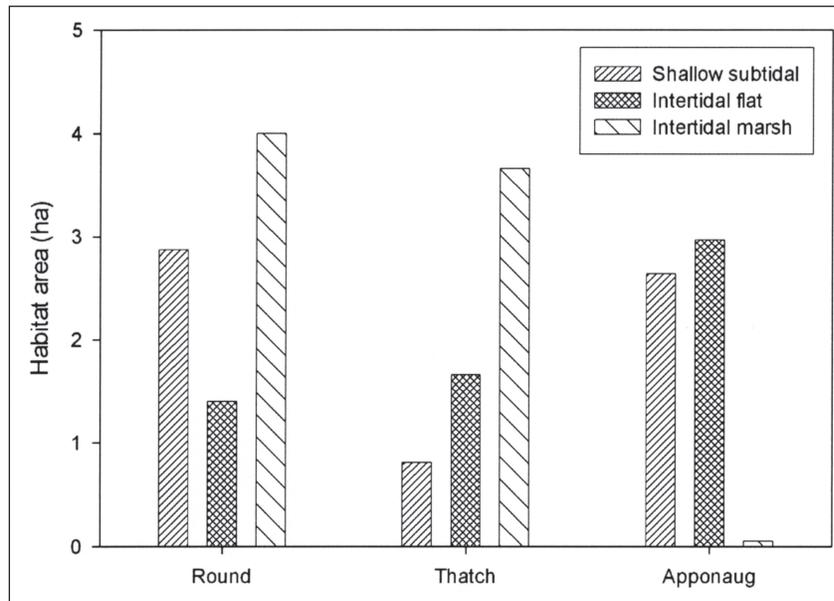


Figure 6. Total area of three foraging habitat types at the three study sites. Shallow subtidal habitats are areas at low tide covered by less than 28 cm of water. Intertidal marsh habitats are areas on the marsh surface that are covered by rooted emergent vegetation. Intertidal flat habitats are areas without rooted emergent vegetation that are located vertically between the other two habitats.

has been reported elsewhere (Gawlik 2002). Instead, both species foraged in water that became continually deeper as tide levels rose in Round Marsh. This pattern makes sense for Great Egrets, which generally limit their movements while foraging and can forage more successfully in deeper water than smaller species (Powell 1987). Conversely, Snowy Egrets spent relatively more time walking while foraging, but this was apparently not in an attempt to find the shallowest areas in which to forage.

At any given time in Round Marsh, birds may simply have had limited choices in terms of foraging water depths because of the uniform topography of the tidal flats (as evidenced by the small variability in water depth across the flats). Coupled with the presence of steep-sided, erosional marsh banks, birds were largely relegated to foraging in deeper water on the flats as tide levels rose. In other marshes that have gradually sloping substrates that grade into depositional marsh banks, birds have the choice of following the shallowest leading edges of the water as it floods or ebbs across the flats. At these sites, birds can therefore forage in consistently shallow water even as tidal levels change. Ultimately, the pattern of increasing foraging depth with rising tide levels observed in this study may not be generically applied to all marshes; patterns may vary depending on marsh geomorphology, slope, and habitat configuration. The pattern observed at Round Marsh exemplifies the “step-function” scenario described by Powell (1987), where foraging habitat is accessible during low tide on shallow flats and at high tide on the flooded marsh surface, but not necessarily during mid-tides when waters are deep on the flats and the marsh is dry.

Patterns in overall bird abundances in Round Marsh mirrored those observed for behavior and were again related to the amount of shallow habitats that were available to birds at any given point in time due to tidal changes. Higher bird abundances occurred when shallow water covered either the mud flats (during slack low water) or the marsh surface; bird abundances dropped when the water was too deep to forage on the flats or the marsh surface (during slack high water). Other research has consistently found a link between water levels and wading bird abundances. For example, Matsunaga (2000) found that the numbers of herons increased at lower tide levels and differed between spring and neap tide levels. Abundances were higher during spring low tides when water levels were lower and prey densities were presumably higher. Maccarone and Brzorad (2005) found that tide level was a significant predictor for abundances of Snowy Egret, Great Egret, and Glossy Ibis. In the Everglades, water level had the greatest effect on wading bird abundances and distribution (Bancroft et al. 2002). At multiple marshes in Narragansett Bay, Trocki and Paton (2006) found that bird abundances did not significantly differ between low and high tides. Surveys at Round Marsh support this conclusion but also illustrate that this is a simplified picture; abundance patterns are much more complex over the course of the tides and are clearly a reflection of differences in the availability of shallow foraging habitats. High-resolution

temporal data from this study provide a picture of the variability of wading bird abundances in New England salt marshes in relation to rapidly changing water levels associated with the diurnal tides.

Results from Thatch Marsh and Apponaug indicate that the temporal pattern in bird abundances observed at Round Marsh is not generic, thus suggesting that the relationship between bird abundances and tide stage are to some degree site-specific depending on the foraging habitats available to birds at a site. The two additional sites in this study were specifically chosen to illustrate two different extremes in the relative amounts of different types of foraging habitats available to wading birds. For example, the only time birds were abundant at Apponaug was near slack low tide when relatively large areas of shallow subtidal habitats were available for foraging. A second peak in abundance did not occur at Apponaug due to the virtual absence of higher-elevation vegetated salt marsh habitat. Consequently, bird abundances decreased rapidly as tide levels increased above slack low and remained at or near zero throughout the mid- and high-tide stages. The same pattern did not occur at Thatch or Round Marsh, both of which contained sizable areas of vegetated salt marsh where birds could forage at higher tides.

Abundance patterns at Thatch Marsh were similar to those at Round Marsh, although there was a shift in the timing of bird abundance peaks between the two sites. At Thatch Marsh, there was a dip in bird abundance at slack low tide and a subsequent peak when water levels rose slightly. This was probably due to a minimal amount of shallow subtidal habitat in which birds could forage at slack low tide in contrast to Round Marsh. It is possible that some birds left Thatch Marsh at slack low tide and moved to nearby Apponaug (only 0.8 km away) to forage on the newly available shallow subtidal flats at that site. The overall inverse pattern in bird abundances seen at Thatch compared to Round Marsh is difficult to explain with such limited data and, in general, could be due to differences in tide heights among survey days or differences in the relative elevations/topography of mud flat and marsh habitats. For example, if mud flats in Thatch Marsh sit at a higher elevation than at Round Marsh, then the flats will flood relatively later at Thatch. Prohibitively deep water over the flats and the consequent dip in bird abundance would therefore also occur later in the tidal cycle and result in the pattern shown in Figure 5. However, this explanation remains speculative, and the phase-shift in abundance could be due to many interrelated factors. Regardless of the factors responsible, the main point is that the tidal pattern in bird abundance differed between Thatch and Round Marshes.

The fact that patterns in wading bird abundances can vary among different sites has important ramifications for monitoring programs and study design. For example, it may not be appropriate to sample all sites at the same tide stage if the project goal is to quantitatively compare birds among multiple sites. Hypothetically, if birds had been surveyed at the

three sites in this study only at slack low tide, the data would suggest that Apponaug and Round Marsh were relatively more valuable than Thatch Marsh for wading birds. However, if all available data were averaged across the entire tidal cycle, a different conclusion emerges. Mean bird abundances over the tidal range at Round and Thatch Marshes were 5.5 and 5.0 birds respectively, while at Apponaug it was 3.1 birds, indicating that conclusions drawn from sampling only at slack low water would be misleading. A further problem is that tidal water level, and therefore wading bird abundances, can change rapidly. Based on data from this study, a 10-cm change in water depth can occur in as little as one hour in Narragansett Bay, and substantial changes in bird abundances were observed over this same period. Therefore, a bird survey conducted at a marsh at slack low tide might yield substantially different results than if the same survey was conducted only an hour earlier or later.

An alternate method to surveying birds at only one tide stage would involve conducting frequent surveys of birds in a marsh over the entire tidal cycle and then replicating these tidal surveys over time to account for other factors such as weather and tidal phases (i.e., spring vs. neap). This approach would obviously entail much more work on a given day (e.g., over six hours compared to a brief survey at a single tide level). However, it is also possible that sampling could be conducted over fewer days since much more data would be collected within each tidal survey. If birds are to be surveyed at a single time stage, preliminary tidal surveys could also be conducted to identify the timing of abundance peaks in order to help guide further sampling. The tidal-survey approach should provide more meaningful data than sampling at a single tidal stage, but the sampling methodologies employed will depend on the specific goals of each research or monitoring program.

The results of this study provide a better understanding of how wading birds use New England salt marshes over the tidal cycle. However, this study is limited in that data were only collected from three sites and only comprehensively from Round Marsh. To corroborate the results found here, similar sampling should be conducted at additional marshes with a variety of habitat configurations to better understand how different patterns in wading bird abundances across the tides are related to specific habitat mosaics in a marsh. The three marshes in this study were purposefully chosen to reflect differences in the ratios of only three general habitat types: shallow subtidal flats, intertidal flats, and vegetated marshes. The relative effects of additional habitat types, such as marsh pools that can provide shallow foraging habitat during all tidal stages, should also be investigated. This study provides time-series data of wading bird abundances over the tidal cycle and demonstrates that tide-related patterns in bird abundances can vary dramatically among marshes. The results provide a better understanding of how these birds use New England salt marshes for foraging and should lead to more accurate and efficient planning of survey and monitoring programs in this region.

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Literature Cited

- Adamowicz, S.C., and C.T. Roman. 2005. New England salt marsh pools: A quantitative analysis of geomorphic and geographic features. *Wetlands* 25:279–288.
- Austin, H.M. 1996. Observations on daylight feeding periodicities of wading birds (Ardeidae) in Sarah's Creek, York River, Virginia. *The Journal of the Elisha Mitchell Scientific Society* 111:137–145.
- 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* 25:265–391.
- Clark, J.A., B.A. Harrington, T. Hruby, and F.E. Wasserman. 1984. The effect of ditching for mosquito control on salt marsh use by birds in Rowley, Massachusetts. *Journal of Field Ornithology* 55:160–180.
- Custer, T.W., and R.G. Osborn. 1978. Feeding-habitat use by colonially breeding herons, egrets, and ibises in North Carolina. *The Auk* 95:733–743.
- DuBowy, P. 1996. Effects of water levels and weather on wintering herons and egrets. *The Southwestern Naturalist* 41:341–347.
- Ferren, R.L., and J.E. Myers. 1998. Rhode Island's Maritime Nesting Birds. Rhode Island Department of Environmental Management, Division of Fish and Wildlife, West Kingston, RI. 222 pp.
- Gawlik, D.E. 2002. The effects of prey availability on the numerical response of wading birds. *Ecological Monographs* 72:329–346.
- Hom, C.W. 1983. Foraging ecology of herons in a southern San Francisco Bay salt marsh. *Colonial Waterbirds* 6:37–44.
- Kelly, J.F., D.E. Gawlik, and D.K. Kieckbusch. 2003. An updated account of wading bird foraging behavior. *Wilson Bulletin* 115:105–107.
- Kushlan, J.A. 1976. Feeding behavior of North American herons. *Auk* 93:86–94.
- Kushlan, J.A. 1981. Resource-use strategies of wading birds. *Wilson Bulletin* 93:145–163.
- Maccarone, A.D., and J.N. Brzorad. 2005. Foraging microhabitat selection by wading birds in a tidal estuary, with implications for conservation. *Waterbirds* 28:383–391.
- Matsunaga, K. 2000. Effects of tidal cycle on the feeding activity and behavior of Grey Herons in a tidal flat in Notsuke Bay, northern Japan. *Waterbirds* 23:226–235.

- Powell, G.V.N. 1987. Habitat use by wading birds in a subtropical estuary: Implications of hydrography. *The Auk* 104:740–749.
- Reinert, S.E., and M.J. Mello. 1995. Avian community structure and habitat use in a southern New England estuary. *Wetlands* 15:9–19.
- Roman, C.T., N. Jaworski, F.T. Short, S. Findlay, and R.S. Warren. 2000. Estuaries of the northeastern United States: Habitat and land-use signatures. *Estuaries* 23:743–764.
- Rozas, L.P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: A pulsing ecosystem. *Estuaries* 18:579–590.
- Sawara, Y., N. Azuma, K. Hino, K. Fukui, G. Demachi, and M. Sakuyama. 1990. Feeding activity of Grey Heron *Ardea cinerea*, in tidal and non-tidal environments. *Japanese Journal of Ornithology* 39:45–52.
- Strong, A.M., G.T. Bancroft, and S.D. Jewell. 1997. Hydrological constraints on Tricolored Heron and Snowy Egret resource use. *The Condor* 99:894–905.
- Trocki, C.L. 2003. Patterns of salt marsh and farmland use by wading birds in southern Rhode Island. M.Sc. Thesis. University of Rhode Island, Kingston, RI. 97 pp.
- Trocki, C.L., and P.W.C. Paton. 2006. Assessing habitat selection by foraging egrets in salt marshes at multiple spatial scales. *Wetlands* 26:307–312.
- Velasquez, C.R. 1992. Managing artificial salt pans as a waterbird habitat: Species' responses to water-level manipulation. *Colonial Waterbirds* 15:43–55.
- Willard, D.E. 1977. The feeding ecology and behavior of five species of herons in southeastern New Jersey. *The Condor* 79:462–470.