Behavior, Habitat Use, and Food of Three Egrets in a Marine Habitat

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Abstract.—Behavior, habitat use, and prey were compared for Snowy Egrets (*Egretta thula*), Tricolored Herons (*E. tricolor*), and Little Blue Herons (*E. caerulea*) in a marine habitat to assess resource partitioning. All three species tended to use behaviors in different frequencies. Little Blue Herons used only Walking Slowly, Snowy Egrets used Walking Slowly and Foot Stirring most often, and Tricolored Herons used Walking Slowly and Disturb-and-Chase most often. Partitioning occurred through differences in prey type and prey size. Tricolored Herons and Little Blue Herons tended to eat different prey types as measured by frequency of prey captured and percent of diet by weight. Snowy Egrets and Tricolored Herons ate different prey types when prey as a percent of diet were compared. Snowy Egrets and Little Blue Herons broadly overlapped in prey type but ate fish of different sizes.

Key words.—Egrets, food, foraging behavior, Little Blue Heron, resource partitioning, Snowy Egret, Tricolored Heron.

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Several studies have considered partitioning mechanisms among coexisting heron species. Whitfield and Blaber (1979) found that segregation was achieved through a combination of prey size and wading depth among four different size herons in Lake St. Lucia, Natal, South Africa. Custer and Osborn (1978) found that Great Egrets (*Egretta alba*) fed in deeper water than did the smaller Snowy Egret (*Egretta thula*) and Tricolored Heron (*E. tricolor*). Willard (1977) working in fresh and salt water marshes in New Jersey found that larger herons ate larger fish and fed in deeper water than did smaller herons. Hom (1983) found differences in prey size among Snowy Egrets, Great Egrets, and Great Blue Herons (*Ardea herodias*) in a California salt marsh.

Evidence exists that similar size herons partition resources among themselves. Jenni (1969) found differences in food items, behavior, and foraging depth among four herons in freshwater in Florida. Willard (1977) found medium size herons ate similarly sized fish but used different behaviors and habitats. Rodgers (1983) study of heron foraging behavior in Tampa Bay suggested that Little Blue Herons (*E. caerulea*), Snowy Egrets, and Tricolored Herons foraged in a similar manner.

In this study, I compare the foraging behavior, habitat use, and food of three species of similarly sized herons, Snowy Egrets, Tricolored Herons, and Little Blue Herons in a marine habitat in Florida. These species are flexible in their use of habitats and food types, and they employ a variety of foraging behaviors (Hancock and Kushlan 1984). My objective was to quantify the resource use of each species, determine the extent of resource overlap, and identify potential partitioning mechanisms.

METHODS

The study was conducted in Old Tampa Bay and Safety Harbor, northern extensions of Tampa Bay, Hillsborough and Pinellas Counties, Florida. The study area was exposed once daily providing shallows, pools, and mudflats that are used as feeding areas by herons, shorebirds, gulls, pelicans, and others. The substrate is sandy with seagrass (*Halodule wrightii*) and marine algae (*Ulva* sp., *Gracilaria* sp., *Enteromorpha* sp.) present in some areas. Red Mangrove (*Rhizophora mangle*) and marsh grass (*Spartina alterniflora*, *Juncus roemenarius*) border the bay.

Foraging birds were observed on 234 occasions (Snowy Egret 73, Tricolored Heron = 98, Little Blue Heron = 63) on 103 days for approximately 65 hours (Snowy Egret = 1227 min, Tricolored Heron = 1527 min, Little Blue Heron = 1118 min). Observations were made approximately twice weekly from October 1981 through August 1982. Herons were observed with binoculars and spotting scope, and data were dictated into a tape recorder. Observations began immediately following a strike and continued until the bird ceased feeding, left the area, or I switched to another individual. Bias was minimized by sampling all species and individuals present within an area for approximately the same length of time. Foraging behavior, habitat, prey type, and prey size were recorded. Prey size was estimated by comparison with culmen measurements of Florida museum specimens (n = 60).

The terms for behaviors follow Hancock and Kushlan (1984) with the following exceptions. Disturb-and-Chase included Walking Quickly, Running, and Hopping. Stand-and-Chase was defined as a heron standing in shallow water along the shoreline,

its back to the shore, then Running or Hopping in an attempt to capture prey. Essentially a Standing-Running-Hopping sequence, the regularity of the pattern warranted designation as a distinct behavior in this study. I restricted behavioral categories to body movements, foot movements and aerial methods and did not distinguish postures, wing movements, and head and neck movements, which I view in this study as variations of more fundamental techniques.

The habitat was defined as the area in which prey were captured and was divided into five parts. The divisions were: 1) shore; 2) shoreline, in the water within 5 m of shore; 3) pool, a body of water separated or nearly separated from the main body of water; 4) open water, more than 5 m from shore; and 5) canal, an extended, narrow (1-3 m) body of water. Two canals were present in the study area.

Prey were identified to the lowest possible taxon. Many fusiform fish could not be regularly identified to species and are referred to only as "fish spp.". The study area was sampled with a quarter-inch mesh seine and the resulting prey lengths were converted to wet weight by constructing species length-weight curves. Wet weight of the fish that were combined was obtained from a curve constructed with fusiform fish found in the foraging area.

The size of prawns and fish, the most frequently eaten items in the diet of all three species was divided into five categories which correspond with bill lengths: 1) 18-30 mm, or ¼ bill lengt , 2) 31-52 mm, or ½ bill length; 3) 53-75 mm, or ¾ bill length; 4) 76-100 mm, or bill length, and; 5) 101-115 mm, or greater than bill length. Prey fewer than 18 mm long were not observed. Only pipefish (*Syngnathus* spp.) were longer than 115 mm and are included in the greater-than-bill-length category.

A comparison was made of the frequency each species used a foraging behavior, habitat, or prey item with χ^2 for 'k' independent samples. Chi-square contingency analysis was used to test the significance of associations between a species and a behavior, habitat, and prey item, and between behavior and prey (Siegel 1956).

Levin's (1968) diversity index $B = 1/\Sigma p_{ih}^2$, where p_i is the proportion of an h behavior or resource of an ith species, was used to estimate the extent of behavior and resource use. B varies from 1 to n where n is the number of categories. Horn's (1966) measure $\hat{C}_\lambda = 2\Sigma x_i y_i / \Sigma x_i^2 = \Sigma y_i^2$, where x_i is the frequency of a variable for one species and y_i the frequency of the variable for a second species, was used to determine the degree of overlap among species. A value of 1 indicates complete overlap and zero an absence of overlap.

RESULTS

Five foraging behaviors were identified among the three species (Table 1). Little Blue Herons used only Walking Slowly; Snowy Egrets used Walking Slowly and Foot Stirring most often ($\chi^2 = 47.4$, $p < 0.001$, df = 4); and Tricolored Herons used Walking Slowly and Disturb-and-Chase most often ($\chi^2 = 20.7$, $p < 0.001$, df = 3). Foot Stirring was unique to Snowy Egrets during this study. A significant association existed between heron species and foraging behavior ($\chi^2 = 1947.6$, $p < 0.001$, df = 8). Little Blue Herons were associated with Walking Slowly, Snowy Egrets with Foot Stirring, and Tricolored Herons with Standing, Disturb-and-Chase, and Stand-and-Chase.

A significant association existed between Snowy Egret behavior and prey type (polychaetes, prawns, fish) captured ($\chi^2 = 330.6$, $p < 0.001$, df = 6). Walking Slowly was associated with polychaetes, Disturb-and-Chase and Foot Stirring with prawns, and Standing with fish. A significant association existed between Tricolored Heron behavior and prey type (prawns, fish) captured ($\chi^2 = 69.8$, $p < 0.001$, df = 3). Walking Slowly was associated with prawns.

Little Blue Herons ($\chi^2 = 55.7$, $p < 0.001$, df = 4) and Snowy Egrets ($\chi^2 = 76.7$, $p < 0.001$, df = 4) foraged most often along the shoreline and in pools (Table 2). Tricolored Herons foraged most often along the shoreline ($\chi^2 = 28.0$, $p < 0.001$, df = 4). Tricolored Herons never foraged for prey located on shore but did occasionally stand on shore and attempt to capture prey in the water.

A significant association existed between two heron species and habitat (χ^2 =

Table 1. Foraging behavior (% total observation time) of Snowy Egrets (SE), Tricolored Herons (TH), and Little Blue Herons (LBH) in Old Tampa Bay and Safety Harbor, Florida.

Behavior	Species		
	SE	TH	LBH
Standing	9.7	17.0	
Walking Slowly	38.9	36.7	100
Foot Stirring	30.3		
Disturb-and-Chase	20.4	35.6	
Stand-and-Chase	0.6	10.7	

Table 2. Habitat use (% total observation time) by foraging Snowy Egrets (SE), Tricolored Herons (TH), and Little Blue Herons (LBH).

Habitat	Species		
	SE	TH	LBH
Shore	4.3		15.3
Shoreline	47.0	46.7	32.2
Pool	34.5	21.7	42.1
Open water	9.9	19.8	8.5
Canal	4.3	11.8	2.0

Table 3. Prey consumed by Snowy Egrets (SE), Tricolored Herons (TH), and Little Blue Herons (LBH).

Prey Item	SE n	SE % captured	SE % total wt	TH n	TH % captured	TH % total wt.	LBH n	LBH % captured	LBH % total wt.
Insects							4	1.0	0.3
Polychaetes									
Nereis sp.	57	12.9	3.3	1	0.3	0.03	122	30.3	3.0
Isopod									
Ligia exotica	24	5.4	3.3				51	12.7	4.2
Prawn									
Palaemonetes sp.	166	37.7	19.7	68	17.0	2.8	75	18.6	1.2
Fiddler Crab									
Uca sp.							4	1.0	2.1
Blue Crab									
Callinectes sp.	3	0.7	22.5				11	2.7	37.7
Crab spp.	5	1.1	5.7				1	0.3	0.9
Flounder spp.	6	1.4	13.7				12	3.0	16.8
Pipefish									
Syngnathus spp.	5	1.1	0.4	21	5.2	0.4	11	2.7	0.7
Needlefish									
Strongylura sp.	1	0.2	1.0	18	4.5	7.4	1	0.3	0.6
Red Drum									
Sciaenops sp.							7	1.7	2.5
Fish spp.	174	39.5	30.7	293	73.1	89.3	104	25.8	29.9
Total	441			401			403		

529.4, $p < 0.001$, df = 8). Little Blue Herons were associated with the shore and pools and Tricolored Herons were associated with open water and canals. Snowy Egrets could not be clearly associated with any particular part of the habitat.

Prey types were analyzed in two ways, first as frequency of prey captured and secondly as percentage of total weight of the diet (Table 3). When prey items were considered as percentage of prey captured Little Blue Herons ate many polychaetes (*Nereis sp*) and fish, Snowy Egrets ate many prawns (*Palaemonetes pugio*) and fish, and Tricolored Herons ate mostly fish. Tricolored Herons never ate crabs although on several occasions crabs were captured and released. A significant association exists between heron species and frequency of prey type (polychaetes, isopods, prawns, crabs, fish) in the diet ($\chi^2 = 316.3$, $p < 0.001$, df = 8). Little Blue Herons were associated with polychaetes, isopods and crabs, Snowy Egrets with prawns, and Tricolored Herons with fish.

When prey items were considered as percent of total weight of the diet Snowy Egrets' diet consisted primarily of prawns, crabs, and fish. Crabs, particularly blue crabs (*Callinectes sapidus*) became important to Little Blue Herons. Fish made up almost the entire diet of Tricolored Herons.

Most prawns eaten by the herons were 18-30 mm long (Table 4). A significant association existed between species of heron and size of fish eaten ($\chi^2 = 153.5$, $p < 0.001$, df = 8). Little Blue Herons ate 31-100 mm fish and Snowy Egrets 18-30 mm fish. Tricolored Herons ate fish of intermediate size but no association was detected (Table 5).

The diversity measurements indicate the variety of behaviors used by Snowy Egrets and Tricolored Herons (Table 6). There was no difference in the extent that the three species used the habitat. Tricolored Herons used the prey base less extensively than Little Blue Herons or Snowy Egrets. Tricolored Herons and Little Blue Herons used a wider range of prey sizes than did Snowy Egrets.

Table 4. Size of prawns consumed (% of total) by Snowy Egrets, Tricolored Herons, and Little Blue Herons.

Species	Prawn size (mm) 18-30	31-52
Snowy Egret	83.4	16.6
Tricolored Heron	69.5	29.5
Little Blue Heron	84.3	15.7

Table 5. Size of fish consumed (% of total) by Snowy Egrets (SE), Tricolored Herons (TH), and Little Blue Herons (LBH).

Species	Fish length (mm) 18-30	31-52	53-75	76-100	100-115
SE	79.0	9.7	7.1	0.8	0.5
TH	42.5	33.7	14.5	8.4	0.9
LBH	10.4	49.6	23.0	15.6	1.5

Table 6. Diversity (B)[1] of behavior and resources use by Snowy Egrets (SE), Tricolored Herons (TH), and Little Blue Herons (LBH).

	SE	TH	LBH
Behavior	3.34	3.31	1
Habitat	2.81	3.15	3.22
Prey			
% prey captured	3.15	1.76	4.72
% total wt. diet	4.81	1.24	3.79
Prey Size	1.49	2.84	3.26

[1]Levins 1968

Table 7. Resource overlap ($\hat{C}_\lambda$)[1] of Snowy Egrets (SE), Tricolored Herons (TH), and Little Blue Herons (LBH).

	SE-TH	SE-LBH	TH-LBH
Behavior	0.52	0.60	0.56
Habitat	0.95	0.94	0.83
Prey			
% total captured	0.80	0.82	0.59
% total wt. diet	0.55	0.87	0.50
Prey Size			
overall	0.84	0.72	0.98
ıish	0.79	0.31	0.79

[1]Horn 1966

Niche indices show moderate overlap for foraging behavior and considerable overlap for habitat use among the herons (Table 7). The greatest overlap in prey type was between Little Blue Herons and Snowy Egrets. The smallest overlap in prey type occurred between Little Blue Herons and Tricolored Herons. Generally, there was considerable overlap in prey size except for little overlap in fish size between Little Blue Herons and Snowy Egrets.

DISCUSSION

Behavior is commonly considered to be one mechanism of resource partitioning (Meyerriecks 1962 , Jenni 1969, Willard 1977, Recher and Recher 1980), presumably based on the idea that herons hunting in different ways are exposed to, or can capture, different prey. Indeed, the herons of this study used different behaviors, but they sometimes ate the same prey types. Whereas an association between behavior and type of prey captured was demonstrated for Snowy Egrets and Tricolored Herons, Little Blue Herons used only Walking Slowly but ate the widest variety of prey types. Further research should consider differences in the diet due to behavior and those due to selectivity on the part of the heron. I suggest that behavioral differences alone should not be considered to be the partitioning mechanism without also examining the effect of habitat, prey, and prey size.

Custer and Osborn (1978) found Snowy Egrets and Tricolored Herons used the same sites on the North Carolina coast. Recher and Recher (1980) found no habitat difference among Snowy Egrets, Tricolored Herons, and Little Blue Herons in Florida Bay. This study also found considerable overlap in habitat use.

Snowy Egrets and Little Blue Herons in this study had a smaller proportion of fish in their diet than did those observed by Recher and Recher (1980) in Florida or New Jersey. They also found that Little Blue Herons captured a greater proportion of crustaceans and bottom-dwelling fish than did Snowy Egrets or Tricolored Herons. In my study Snowy Egrets captured more prawns than did Tricolored Herons or Little Blue Herons, but Little Blue Herons captured more bottom-dwelling fish and crabs. Overall, the diets of Snowy Egrets and Little Blue Herons were considerably more diverse than was the diet of Tricolored Herons. Rodgers (1982) also found the diet of Little Blue Herons to be diverse on the west coast of Florida.

Snowy Egrets ate the smallest prey and used the narrowest range of prey lengths

of the species in my study, as was the case in Hom's (1983) study. Recher and Recher (1980) and Jenni (1969) found that Little Blue Herons ate larger fish did than Snowy Egrets or Tricolored Herons, as did the Little Blue Herons in my study. Conversely, Willard (1977) found that Tricolored Herons captured slightly larger fish than did Little Blue Herons or Snowy Egrets.

Pianka (1974) and Schoener (1974) have suggested that for groups where more than one niche dimension is important, separation should be complementary. For example, a significant overlap for one resource should be offset by a difference in use of a second resource. Indeed, though no differences occurred in habitat, Snowy Egrets and Tricolored Herons, and Tricolored Herons and Little Blue Herons appear to partition the resources via differences in diet. Snowy Egrets and Little Blue Herons have similar diets but eat different size fish.

It is useful to consider the extent of overall niche overlap (Pianka, 1974). If niche dimensions were independent (i.e. any behavior is possible in any part of the habitat and for any prey item) overall resource overlap can be considered the product of the individual resource overlaps. The overlap products for behavior, habitat, prey type as percentage of total weight, and prey size (prawns and fish), were Snowy Egret—Tricolored Heron 0.23, Snowy Egret—Little Blue Heron 0.35, and Tricolored Heron—Little Blue Heron 0.23. However, if the resources were dependent (i.e., a behavior occurs in only one part of the habitat and results in the capture of one prey type and size) then overall overlap can be considered the arithmetic mean. The mean values for Snowy Egret—Tricolored Heron were 0.72, Snowy Egret—Little Blue Heron 0.78, and Tricolored Heron—Little Blue Heron 0.72.

The relationship between niche dimensions in this study seem at least partially dependent. An association exists between foraging behavior and habitat (Kent, in prep.) and between behavior and prey type for Snowy Egrets and Tricolored Herons. By way of exception, Little Blue Herons used one behavior in all parts of the habitat and for all prey types. It seems that an appropriate measure of overall niche overlap lies between the product and sum estimates. Thus some overall partitioning occurred among these species in my study. Most likely, overlap among the species varies as their demand for resources relative to resource supply varies (Pianka 1972, Rusterholz 1981).

Why are these three species feeding in the same habitat, and presumably having similar nutritional requirements, using the food resources in different ways? Interspecific aggression may force a change in the foraging behavior of subordinate species, thus altering the type or size of prey the species is exposed to or is able to capture (Morse 1974). A subordinate species would be expected to have a lower rate of net energy intake. However, a mechanism of this nature requires a relatively constant dominance hierarchy. Caldwell (1979) has noted a linear hierarchy of Snowy Egret > Tricolored Heron > Little Blue Heron in Panama. But interspecific aggression was rare in my study (18 interactions in 65 hours) with no clear dominant-subordinate pattern.

Alternatively, species specific differences in foraging efficiency may exist, perhaps due to slight morphological or physiological differences (Kent 1986). Each species would then be viewed as eating a combination of prey that maximizes its net energy return. Comparable rates of net energy intake would be expected among the species.

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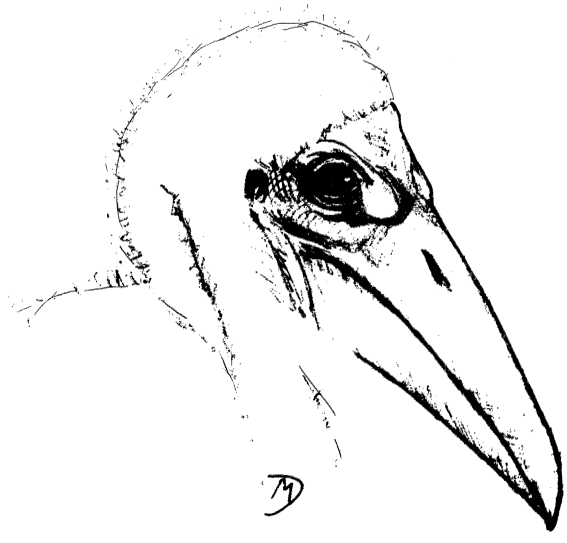

Wood Stork (*Mycteria americana*) by Dave Maehr