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BEHAVIOR, HABITAT USE, FOOD, AND FORAGING EFFICIENCY OF THREE SPECIES OF SYMPATRIC MERONS (EGRETTA)

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BEHAVIOR, HABITAT USE, FOOD, AND FORAGING EFFICIENCY OF THREE SPECIES OF SYMPATRIC HERONS (EGRETTA)

by

Donald M. Kent

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Arts in the
Department of Biology in the
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Major Professor: Andrew J. Meyerriecks

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CERTIFICATE OF APPROVAL

MASTER'S THESIS

This is to certify that the Master's Thesis of

Donald Michael Kent

with a major in Zoology has been approved by the
Examining Committee on April, 1983 as satisfactory
for the thesis requirement for the Master of Arts degree.

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BEHAVIOR, HABITAT USE, FOOD, AND FORAGING EFFICIENCY OF THREE SPECIES OF SYMPATRIC HERONS(EGRETTA)

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An Abstract

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ABSTRACT

The foraging ecology and behavior of Little Blue Herons (Egretta caerulea), Snowy Egrets (E. thula), and Tricolored Herons (E. tricolor) was studied from October 1981 to August 1982 in Old Tampa Bay and Safety Harbor, Hillsborough and Pinellas Counties, Florida. Little Blue Herons foraged exclusively by walk-slow and employed head sways or tilts during 75% of the observations. Snowy Egrets used stand, walk-slow, disturb-and-chase, and foot-stirring. Tricolored Herons used stand, walk-slow, disturb-and-chase, and stand-and-chase. Tricolored Herons using stand-and-chase stood near shore facing open water and when prey was spotted they ran or hopped in the direction of the prey and attempted capture. After an attempt the bird returned to its original location and posture. Open-wing and neck-tilt behaviors may be mechanisms for reducing glare.

Interspecific aggression was infrequent, but intraspecific aggression by Snowy Egrets was more frequent. Snowy Egrets occasionally initiated foraging associations with others species of birds but these associations did not appear to be immediately profitable for the Snowy Egrets.

Microhabitat use was similar for all three species. All three species spent more time along the shoreline than

would be expected from a random use of the habitat. Snowy Egrets and Little Blue Herons spent more time foraging in pools than would be expected from random use of the habitat. Tricolored Herons did not forage on shore. The overlap index indicated that all three species foraged at the same depth. Snowy Egrets used only walk-slow on shore, while pools were usually foot-stirred, and disturb-and-chase was most prevalent in open water. Tricolored Herons used walk-slow most often along the shoreline and in canals, and disturb-and-chase in open water.

Little Blue Herons and Snowy Egrets had the most diverse diets and showed significant overlap ($\hat{C}_\lambda = 0.82$) for prey type. Polychaetes (30.3%) and fish (33.6%) were the most frequent prey items of Little Blue Herons; prawns (37.6%) and fish (42.2%) of Snowy Egrets. There was significant dietary overlap ($\hat{C}_\lambda = 0.80$) between Snowy Egrets and Tricolored Herons. Fish (83.0%) was the most frequent item in the diet of Tricolored Herons. Fish made up the greatest percentage by weight of all prey species for all three heron species. All three heron species had high overlap ($\geq \hat{C}_\lambda = 0.97$) for size of prawns eaten. Fish-size overlap was low ($\hat{C}_\lambda = 0.31$) between Little Blue Herons and Snowy Egrets and significant between Little Blue Herons and Tricolored Herons ($\hat{C}_\lambda = 0.79$) and between Snowy Egrets and Tricolored Herons ($\hat{C}_\lambda = 0.79$). When the results of the three species are combined, prawns and polychaetes were

caught with the walk-slow behavior and fish with stand and walk-slow behaviors.

Little Blue Herons were more efficient than Snowy Egrets and Tricolored Herons, both for percentage successful strikes and grams per minute of food. Snowy Egrets were most successful using stand behavior, while Tricolored Herons were equally successful using all behaviors. Little Blue Herons were most successful on shore and Tricolored Herons along the shoreline. Snowy Egrets were equally successful in all microhabitats.

Little Blue Herons and Tricolored Herons differed in major food items and Snowy Egrets and Little Blue Herons differed by fish size. No obvious food differences were detected between Snowy Egrets and Tricolored Herons. Foraging behavior use differed among all three heron species while habitat use was very similar. Little Blue Herons used one behavior in all microhabitats to catch all prey items. Snowy Egrets and Tricolored Herons adjusted behaviors which sometimes were used to capture different prey items.

Abstract Approval: ~~Major Professor~~

Professor, Department of Biol

22 APRIL 83

Date of Approval

INTRODUCTION

The study of the ecology and behavior of herons began with the standardization of nomenclature for feeding behaviors (Meyerriecks, 1960, 1962; Kushlan, 1976, 1978). This was followed by studies of the adaptive significance of behaviors, e.g. head and neck movements (Krebs and Partridge, 1973), disturb-and-chase behaviors and the use of the feet and wings (Meyerriecks, 1959, 1962, 1966, 1971), and aerial feeding (Mock, 1974; Rodgers,1974). This provided the groundwork for studies of feeding ecology. Major questions asked next were: What habitats are the herons using, what are they eating, and is there resource overlap?

Mock and Mock (1980) found that the Goliath Heron (Ardea goliath) used a stand-and-wait behavior (Meyerriecks, 1960) to capture large food items. Whitfield and Blaber (1979) studied resource partitioning among four species of different-sized herons in the same lake and determined that segregation was achieved by a combination of prey size and wading depth. Williard (1977) arrived at the same conclusion for five species of different-sized North American herons. Similar-sized herons segregated by a combination of habitat and feeding behavior. This raises two questions; 1) what is the mechanism for resource partitioning, if it exists, within the confines of a single

habitat, and 2) does a difference in feeding behavior partition the available resources?

Jenni (1969) has, at least in part, addressed the first of these questions in a study of four species of herons in Florida during their breeding season. He concluded that within a freshwater habitat, primary segregation was achieved on the basis of major food items and that behavior and partitioning of the habitat played a role. Meyerriecks (1962) suggested that in a marine environment each species shows a preference for a part of the total foraging area. Behaviors developed to fit these foraging niches, and thus direct competition presumably is avoided. This suggests that either there is enough food for all species within an area and the primary consideration is avoiding interspecific interactions, or that each species is using a different food or food size.

The intent of this study is to compare the foraging behavior and ecology of three species of sympatric congeneric herons, Little Blue Herons (Egretta caerulea), Tricolored Herons (E. tricolor), and Snowy Egrets (E. thula), within the confines of a marine environment. All three species use a variety of habitats (Palmer, 1962) and food types (Table 1; Kushlan, 1978; Rodgers, 1982). A large, resident breeding population of Little Blue Herons, Snowy Egrets, and Tricolored Herons (Rodgers, 1980a, 1980b) is increased by a large winter influx of northern breeders. All three species are similar in weight and morphology (Table 2; citations within) and should thus have comparable abilities for capturing and

Table 1. Food of Little Blue Herons (LBH), Tricolored Herons (TH), and Snowy Egrets (SE) (Summarized from the literature).

Food	LBH	TH	SE
fish	x	x	x
frogs	x	x	x
tadpoles	x	x	x
salamanders		x	
lizards	x	x	x
snakes	x	x	x
turtles	x		
crayfish	x	x	
other crustaceans	x	x	x
insects	x	x	x
spiders	x	x	
worms			x
polychaetes	x		
snails		x	x
leeches		x	

Table 2. Weight and morphological measurements of Little Blue Herons (LBH), Tricolored Herons (TH), and Snowy Egrets (SE).

	LBH	TH	SE
weight (g)*	397	312	369
length (mm)**	558	558	507
wing (mm)*	272	255	255
bill (mm)***	75.7	90.5	79.7
± S.D.	±4.9	±8.6	±5.2
tarsus (mm)***	92.5	86.3	92.4
± S.D.	±6.5	±8.7	±8.5
feathers[1] (mm)***	145.5	132.9	148.0
± S.D.	±15.7	±19.5	±18.4

* Palmer, R.S. 1962

** Robbins, C.S., B. Brunn, and H.S. Zim. 1966

*** Measurements of Florida birds from the Florida State Museum (n=20).

1 measured from flat of foot to feathers on tibiotarsus

handling prey. Because of their similarities they should have comparable daily and long-term nutritional requirements. Kushlan (1978) suggested a linear relationship between bird size and daily food consumption on the order of log Y = 0.966 log X - 0.640, where X is gram wet body weight of the bird and Y is grams/day wet weight of the prey (Figure 1 and Table 3). Junor (1972) found the daily food intake of piscivorous birds to be approximately 16% of the wet body weight (Table 3). The three species should provide a strong foundation for the study of resource use.

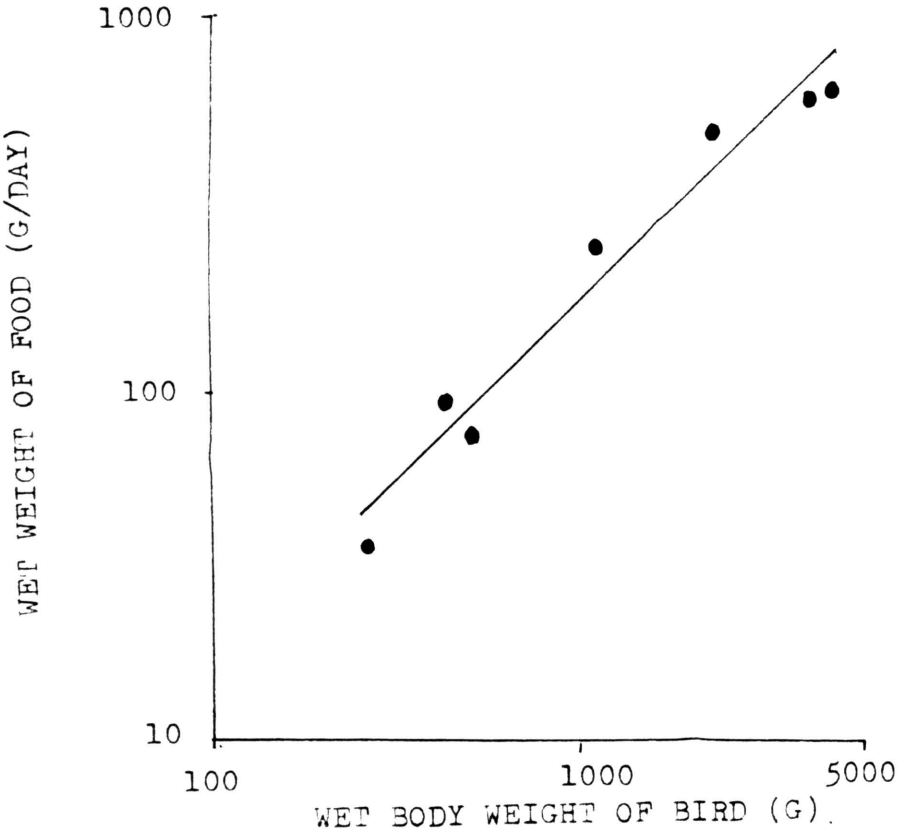

Figure 1. Relationship of daily food requirements of wading bird to size of bird, log Y = 0.966 log X - 0.640 (Kushlan, 1978).

Table 3. Estimated daily food requirement of Little Blue Herons (LBH), Snowy Egrets (SE), and Tricolored Herons (TH).

Species	Wet Wt. of Body (g)	Daily Food Requirement (Wet Weight g)	
		Junor (1972)	Kushlan (1978)
LBH	397	63.52	74.00
SE	369	59.04	69.14
TH	312	49.92	58.80

STUDY AREA AND METHODS

The behavior, habitat use, food, and efficiency of foraging Little Blue Herons, Tricolored Herons, and Snowy Egrets was studied from October 1981 to August 1982 in Old Tampa Bay and Safety Harbor, northern extensions of Tampa Bay, Hillsborough and Pinellas Counties, Florida. The study sites were exposed, on average, twice every twenty-four hours providing shallows, pools, and mudflats which were used as feeding grounds by the local herons, shore birds, gulls, pelicans, and others. The substrate is sandy with seagrass (Halodule wrightii) and marine algae (Ulva sp., Gracilaria sp., Enteromorpha sp.) in some areas. Red Mangrove (Rhizophora mangle) and marsh grass (Spartina alterniflora) border the bay. Salinity ranged from 16‰ to 24‰ over the course of the study and was uniform throughout the study area. Polychaetes and nematodes dominated the infauna.

Approximately 65 hours were spent in detailed observation using 8 X 40 binocular or 20X to 45X zoom spotting scope, and data were dictated directly into a tape recorder. The focal bird was chosen haphazardly and noted for behavior, prey, prey size, position within the habitat, depth, number of strikes and successful strikes, and interactions. Date, time, and weather conditions were noted for each ob-

servation. Prey size and wading depth were estimated from known bill lengths and leg measurements respectively (Table 2). Observations continued until the focal bird ceased feeding, left the area, or I observed another bird.

Terms for behaviors are those of Kushlan (1978) unless otherwise stated. The frequency with which the herons used a foraging behavior, ate a particular prey item, used a microhabitat, or foraged at a depth (percent of total observation time) was tested with χ^2 for 'k' independent samples (Siegel, 1956). The extent of the association between a heron species and a foraging behavior, prey item, prey size (prawn and fish), microhabitat, or foraging depth, and between prey type and foraging behavior, was determined with the contingency coefficient C (Siegel, 1956). Degree of overlap among species was determined for foraging behavior, prey type, prey size, foraging depth, and microhabitat use with Horn's (1966) modification of Morasita's 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 behavior, prey, prey size, depth, or microhabitat for one species and y_i the frequency of the same variable for a second species. Unity indicates complete overlap and zero, an absence of overlap.

Prey are identified to the lowest possible taxon. Fish which could not be identified to species because they were without distinctive morphological characteristics were combined. The study site was sampled with a quarter-inch mesh seine. Prey length was converted to wet weight by using

species length-weight curves. Wet weight of the fish which were combined was obtained from a curve constructed with the fish found in the foraging area (Table 8). Only a percentage of captured prey was identified (Little Blue Heron - 65%, Snowy Egret - 59%, Tricolored Heron - 51%) so it is assumed for the purposes of calculating grams wet weight of prey/min that the unidentified prey are comparable in weight and distribution to the identified prey. The striking efficiency of each species and the striking efficiency of each behavior within a species was tested with the Wilcoxon - Mann - Whitney Test (Steel and Torrie, 1980). The mean and standard deviation of the smaller sample were used to compute the statistic Z, which is approximately normally distributed, when the table was inadequate.

BEHAVIOR

Foraging Behavior

Little Blue Heron. Walk-slow was used by Little Blue Herons regardless of microhabitat, prey, depth of foraging, or weather (χ^2 = 3875.3, $p<0.001$). Typically a foraging bird walks slowly with neck extended at a 45° angle, stops when the prey is sighted, lowers its neck and head to a horizontal plane, places the tip of the bill at the surface, and then strikes. On 2 of 63 occasions the foraging birds employed neck sways from a horizontal position. Both instances were in open water on sunny days and the captured prey were fish. Individuals employed head sways, head tilts, or both during 47 of the 63 observations. Head movements were never employed when capturing polychaetes. Head sways and tilts were employed as the head and neck were lowered to horizontal in preparation for striking.

Gleaning was observed on 1 of 63 occasions. The individual walked slowly upright out of the water onto the shore and gleaned red mangroves at head level. This was observed for ten minutes, after which the bird was no longer seen. Spiders were found on the mangroves.

Little Blue Herons walked at a mean pace of 57 steps/min (range 6 - 72 steps/min). The slower pace was used

when capturing polychaetes and the faster pace was used when capturing prawns or fish.

Snowy Egret. Snowy Egrets used five behaviors (Figures 2 and 3). Stand was used during 13 of 71 observations (9.7% of total observation time). Their posture was typically upright with a slight "S" to the neck, with the bill held just below the horizontal plane. Walk-slow was used during 57.8% of the observations (38.9% of total observation time). Pace while walking averaged 84 steps/min (range 14 - 91 steps/min). The slower pace was used when capturing polychaetes. The posture for walk-slow behavior was similar to that used for stand behavior. The prey captured with walk-slow was captured with a quick striking motion.

Disturb-and-chase methods were used during 30 of the observations (20.4% of total observation time). Snowy Egrets walk quickly and run after the prey is spotted, often with open wings. Many times the process culminates with a Kushlan's Hop. The head and neck of Snowy Egrets walking quickly is held upright. An erect posture is typically assumed after a missed strike or after a series of hops. Foot-stirs and probes frequently followed missed strikes.

Foot-stirring was used during 31 of 71 observations (30.4% of total observation time). Foot-stirring is done while standing, but mostly while walking. An average of 64 foot-stirs/min was seen (range 51 - 73 foot-stirs/min). Usually a Snowy Egret alternates the foot with which it

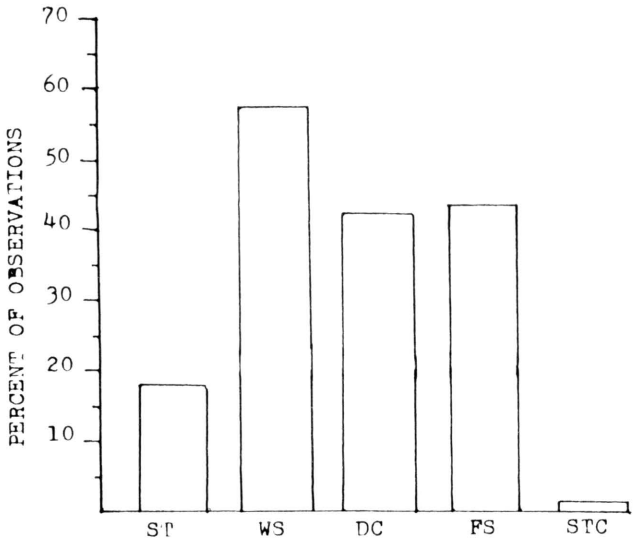

Figure 2. Snowy Egret foraging behavior. ST = stand, WS = walk-slow, DC = disturb-and-chase, FS = foot-stirring, STC = stand-and-chase.

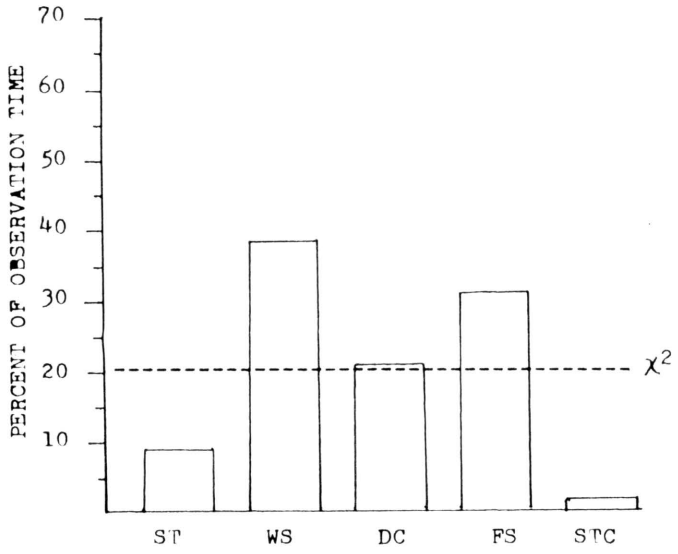

Figure 3. Snowy Egret foraging behavior. ST = stand, WS = walk-slow, DC = disturb-and-chase, FS = foot-stirring, STC = stand-and-chase.

stirs the water while walking through a foraging area. If prey are encountered the Snowy Egret might change to foot-stirring in a tight circle. This was particularly common in areas with aquatic vegetation. The posture while foot-stirring is upright, but the bill is held below the horizontal plane. When the bird foot-stirs in a tight circle the bill is lowered to nearly vertical and the neck is pulled in tight against the shoulders.

In one instance a Snowy Egret used a stand-and-chase behavior, described in the section describing Tricolored Herons. This behavior accounted for 0.6% of the total observation time. The use of behaviors by Snowy Egrets was tested against randomness and found to differ significantly ($\chi^2 = 437.77$, $p < 0.001$). Walk-slow and foot-stir behaviors were used more often than would be expected if behaviors were used at random, disturb-and-chase as expected if random, and stand and stand-and-chase less than expected.

Tricolored Herons. Tricolored Herons used four foraging behaviors (Figures 4 and 5). Stand was used during 24 of 96 observations (16.9% of total observation time). Upright or erect postures (15 of 24 observations) were used after prolonged periods of disturb-and-chase foraging, particularly after missed strikes. Standing in a crouch was used during 10 of 24 observations. Three of these were the typical stand-and-crouch (Williard, 1977), two of which occurred on cloudy days. Seven observations were made of a posture which I term the awkward-crouch. This posture

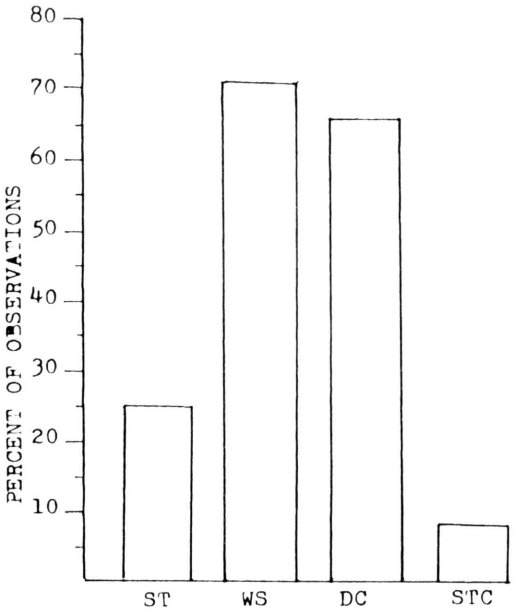

Figure 4. Tricolored Heron foraging behavior. ST = stand, WS = walk-slow, DC = disturb-and-chase, STC = stand-and-chase.

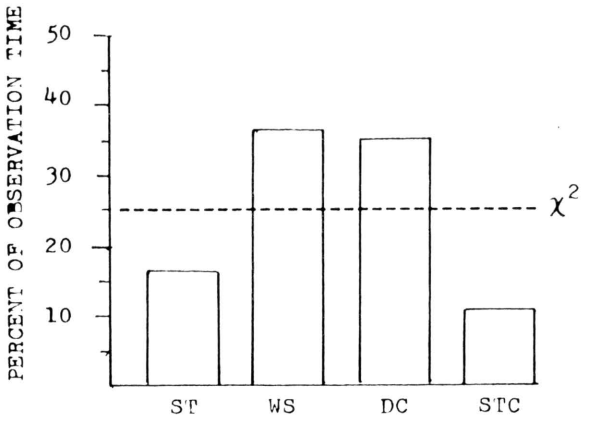

Figure 5. Tricolored Heron foraging behavior. ST = stand, WS = walk-slow, DC = disturb-and-chase, STC = stand-and-chase.

resembles a normal crouch but the neck is tilted far to one side of the body, at times nearly touching the water. All observations of the awkward-crouch were made on sunny days. The neck was held so that the line of vision was directed away from the sun. The neck was shifted as the bird changed its position to maintain this orientation.

Open-winged feeding was observed twice for brief periods (2 and 8 min). The first observation occurred in the middle of a stand-crouch period under cloudy skies. The second observation occurred on a sunny day. As the individual walked along the shoreline, it encountered a small, temporary pool with trapped fish. At first the left wing was held open blocking the sun and the bird struck in the shadow which was created. The individual then reversed direction, retracting the left wing and extending the right wing, again striking in the shadow. Finally the individual placed its back to the sun, opened both wings, and struck again. Seventeen strikes were attempted with five successful captures of small fish.

Walk-slow was used during 68 of 96 observations (36.7% of total observation time). The pace averaged 60 steps/min (range 49 - 73 steps/min) while walking slowly. An awkward crouch was used with the walk-slow behavior while individuals foraged on the shoreline or the edge of pools and canals (29 of 68 observations). With one exception, the sun was shining on all occasions. The one observation of a walk-slow with an awkward crouch without the sun shining

occurred during a thunderstorm when the wind was disturbing the surface of the water. Walk-slow behavior was accompanied by an upright posture when individuals foraged in the middle of canals, pools, or in open water, and when the weather was cloudy or rainy (39 of 68 observations). It was also used amidst disturb-and-chase periods. A neck-tilt was used in the upright position on three occasions, two of which were on sunny days. Foot-probes were observed on four occasions by individuals which had been walking slow. Each occurred after a missed strike. The individual peered down, extended one foot slightly forward, and pushed the substrate. Prawns were captured in all four instances.

Disturb-and-chase behavior was used during 63 of 96 observations (35.6% of total observations). Tricolored Herons searched an area by walk-quickly (average 105 steps/min, range 90 - 123 steps/min), ran with open wings and finished with a Kushlan's Hop. Wing-flicking frequently occurred during the walk-quickly phase of disturb-and-chase foraging. It was accompanied by darting movements of the head and neck, and pivoting of the body. Tricolored Herons stood upright or erect after an unsuccessful foraging period. Foot-probes occurred infrequently (21 probes during 546.5 min) after an unsuccessful strike and led to at least one more strike in 18 of 21 instances, none of which resulted in the capture of prey.

Some Tricolored Herons stood erect for long periods

of time with their backs to the shore and peered at the water in front of them. They ran/hopped to an area 4 - 8 m in front and then an extended chase would ensue. Following the chase the individual returned to the original position near the shore and resumed its erect posture. I term this behavior 'Stand-and-Chase'. It was used during 8 of 96 observations (10.7% of total observation time).

The frequency distribution of behavior use by Tricolored Herons differed significantly from random (χ^2 = 315.99, $p<0.001$). Walk-slow and disturb-and-chase were used more than would be expected if use of behaviors was random, while stand, and stand-and-chase were used less than would be expected. Species of heron was tested against behavior and the frequency distribution of behavior use was found to be significantly different than random (χ^2 = 1946.29, $p<0.001$, Table 4). A moderately high degree of association between species and behavior was determined ($\hat{C}_\lambda$ = .60), suggesting that at least at a very general level a species of heron can be associated with a particular behavior or behaviors. Each species exhibited a moderate amount of overlap with the other species with regard to foraging behavior use (Table 5).

Aggression

Herons were involved in inter- and intraspecific aggressive actions on 42 occasions, 40 of which involved

Table 4. Frequency of foraging behavior use as percent of total observation time for Snowy Egrets (SE), Tricolored Herons (TH), and Little Blue Herons (LBH) in Old Tampa Bay and Safety Harbor, Florida. ST = stand, WS = walk-slow, DC = disturb-and-chase, FS = foot-stir, and STC = stand-and-chase.

	Foraging Behavior				
Species	ST	WS	DC	FS	STC
LBH		100.0			
SE	9.68	38.94	20.46	30.36	0.55
TH	16.95	36.69	35.64		10.72

Table 5. Resource overlap among Little Blue Herons (LBH), Snowy Egrets (SE), and Tricolored Herons (TH) foraging in Old Tampa Bay and Safety Harbor, Florida.

Species	Foraging Behavior	Microhabitat	Foraging Depth	Food Type	Prey Size	
					Prawn	Fish
LBH X SE	.60	.94	.93	.82	.99	.31
LBH X TH	.56	.83	.94	.59	.97	.79
SE X TH	.52	.95	.98	.80	.98	.79

only the three species which are the object of this study (Table 6). Little Blue Herons displaced other Little Blue Herons 4 times by chasing them out of the foraging area. A foraging Little Blue Heron displaced a Snowy Egret on one occasion. Little Blue Herons displaced a Yellow-crowned Night Heron (Nycticorax violaceus), a Green-backed Heron (Butorides striatus), and a Boat-tailed Grackle (Quiscalus major). Aggressive actions by Little Blue Herons involved raising the neck and crest feathers and pointing the bill at the other bird.

Snowy Egrets were involved in 23 interactions, 21 with other Snowy Egrets. The Snowy Egret which was the aggressor ran with erect neck, raised crest, and opened wings at a Snowy Egret which had come into its immediate foraging area. This action resulted in the Snowy Egret which was the subject of the aggression being chased from the immediate vicinity. Snowy Egrets twice displaced Tricolored Herons after the Tricolored Herons had attempted to capture a prey item. There were no piracy attempts and the displacement did not result in the acquisition of food for the Snowy Egrets. The Tricolored Herons regained the foraging areas within seconds of being displaced. A Great Egret (Casmerodius albus) displaced a Snowy Egret on one occasion.

On one occasion each, Tricolored Herons displaced a Little Blue Heron and a Snowy Egret which were in the foraging path. Two Snowy Egrets which attempted to follow

Table 6. Aggression among foraging Little Blue Herons (LBH), Snowy Egrets (SE), Tricolored Herons (TH), and Great Egrets (GE) in Old Tampa Bay and Safety Harbor, Florida.

		NON-AGGRESSOR		
		LBH	SE	TH
AGGRESSOR	LBH	4	1	
	SE	2	21	2
	TH	1	3	6
	GE		1	

a Tricolored Heron were threatened with erect neck, raised crest, and a stab with the bill. On six occasions, Tricolored Herons with raised crests and hoarse croaks chased other Tricolored Herons from the foraging area before returning to feed.

Foraging Associations

Snowy Egrets followed foraging Little Blue Herons on four occasions and foraging Tricolored Herons on four occasions. On all occasions the association was brief (1 - 3 min) and did not result in strikes. Snowy Egrets followed White Ibises (Eudocimus albus) on six occasions for periods of 1 - 8 minutes. Snowy Egret - White Ibis foraging associations were uncommon at all times of the year. Snowy Egrets did not defend their White Ibis companions against conspecifics. While associated with White Ibises, Snowy Egrets made 31 strikes, four of which resulted in the capture of prey. This is a striking efficiency of 12.9%, well below the average efficiency for foraging Snowy Egrets (42.8%).

Snowy Egrets followed Red-breasted Mergansers (Mergus serrator) on two occasions and a Brown Pelican (Pelecanus occidentalis) on one occasion. No strikes were attempted. A Tricolored Heron followed a Brown Pelican swim-feeding in a canal for 7.5 minutes. The Tricolored Heron walked quickly one meter to the side and one meter behind the

pelican. Twenty-one strikes were attempted by the Tricolored Heron with six fish captured, an efficiency of 28.6%, which is less than the average striking efficiency for foraging Tricolored Herons (33.0%). Little Blue Herons never initiated foraging associations.

Prey Handling

Only 1.6% of the captured prey was handled for more than two seconds. Little Blue Herons took longer than two seconds to handle 10 of 23 fish which were equal in length or longer than the bill, ranging from 25 seconds for an Atlantic Needlefish (Strongylura marina) to three minutes for a Red Drum (Sciaenops ocellata). Six of 8 fish equal in length or longer than the bill were handled longer than two seconds by Snowy Egrets (range 7 sec - 3.5 sec). Tricolored Herons handled 17 of 31 of the fish equal in length or longer than the bill for two seconds or longer (range 3 sec - 10 sec). On all occasions the Tricolored Herons delayed immediate swallowing to dip the prey in the water.

Little Blue Herons handled Blue Crabs (Callinectes sapidus) equal to the bill in length for an average of 5.25 min (n = 2, range 2.5 - 8 min). The crabs were held in the bill of the Little Blue Heron by their dorsal and ventral surfaces and positioned in the bill such that their long axes were perpendicular to the length of the

bill. The Little Blue Herons flattened the crabs, rotated the crabs such that their long axes were parallel to the length of the bill, and swallowed. Legs which had droped off during the flattening process were subsequently eaten. Snowy Egrets swallowed Blue Crabs without manipulation.

Defecation

Heron defecation was observed on 28 occasions during foraging periods. Little Blue Herons (n = 8) and Tricolored Herons (n = 9) always walked quickly out of the water to shore before defecating. Snowy Egrets followed the same procedure on 9 occasions but twice they defecated in the water. One Snowy Egret defecated while foot-stirring in a pool with a second Snowy Egret within one meter. The other Snowy Egret defecated while following a White Ibis.

HABITAT USE

Microhabitat

The habitat was divided into five microhabitats: 1) shore - terrestrial, 2) shoreline - in the water near the shore, 3) pool - a body of water separated or nearly separated from the main body of water, 4) open water - an area away from the shoreline (a bird foraging in open water does so without reference to the shoreline), and, 5) canal an extended, narrow body of water open at one end. Two canals occurred within the study area.

Snowy Egrets (χ^2 = 641.18, $p < 0.001$), Tricolored Herons (χ^2 = 909.85, $p < 0.001$), and Little Blue Herons (χ^2 = 525.93, $p < 0.001$) all used microhabitats with a frequency which was not random. Snowy Egrets preferred the shoreline (47.2% of total observation time) and pools (34.5%) to open water (9.9%), the shore (4.3%), and canals (4.3%, Figure 6). Tricolored Herons preferred the shoreline (46.7%) to other microhabitats (Figure 7). Tricolored Herons never foraged on the shore. Little Blue Herons showed a preference for the shoreline (32.2%) and pools (42.1%) and spent little time foraging in open water (8.5%) or in the canals (2.0%, Figure 8).

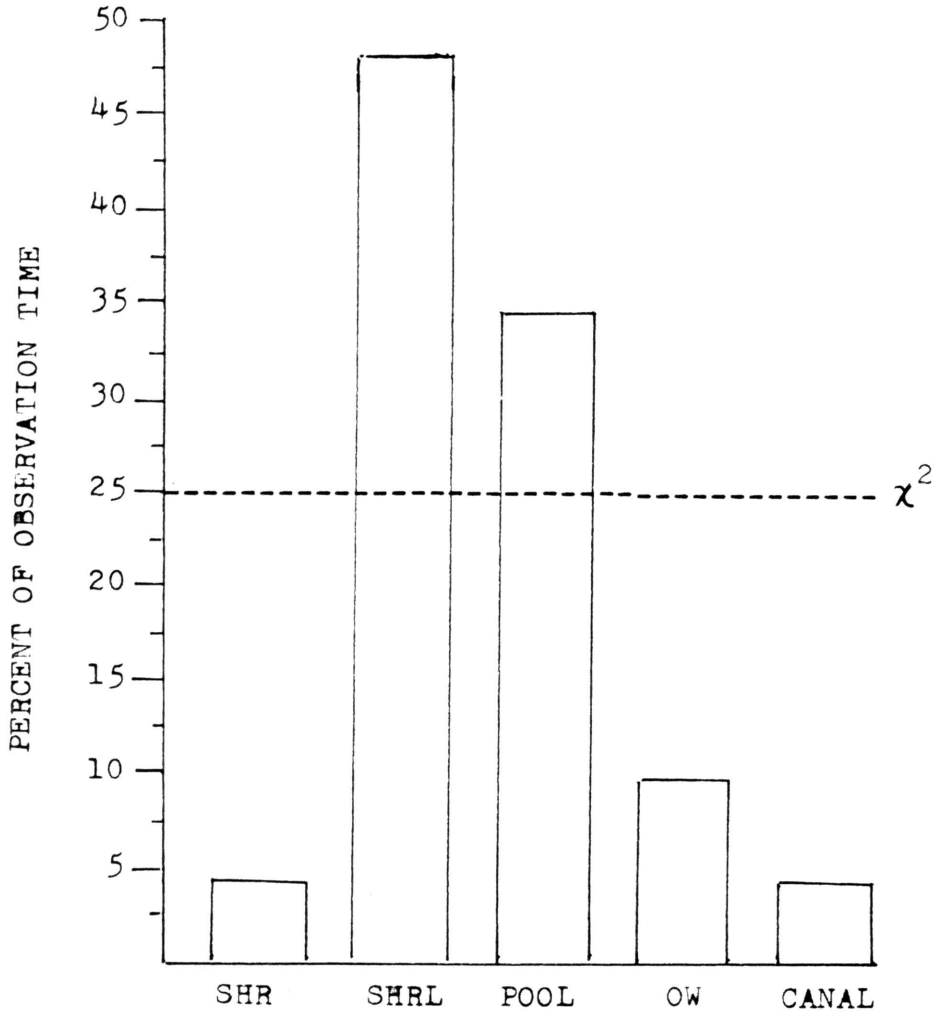

Figure 6. Snowy Egret foraging habitat use (total observation time) in Old Tampa Bay and Safety Harbor, Florida. SHR = shore, SHRL = shoreline, OW = open water.

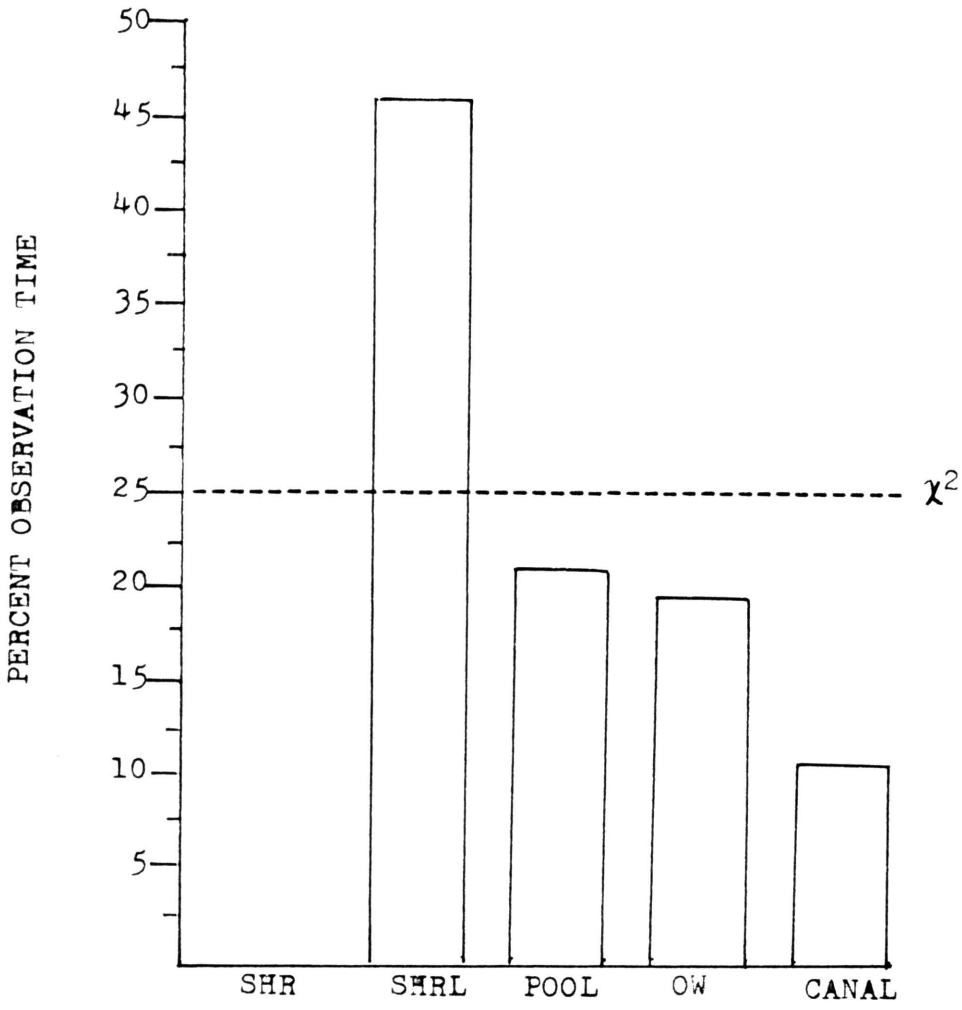

Figure 7. Tricolored Heron foraging habitat use (total observation time) in Old Tampa Bay and Safety Harbor, Florida. SHR = shore, SHRL = shoreline, OW = open water.

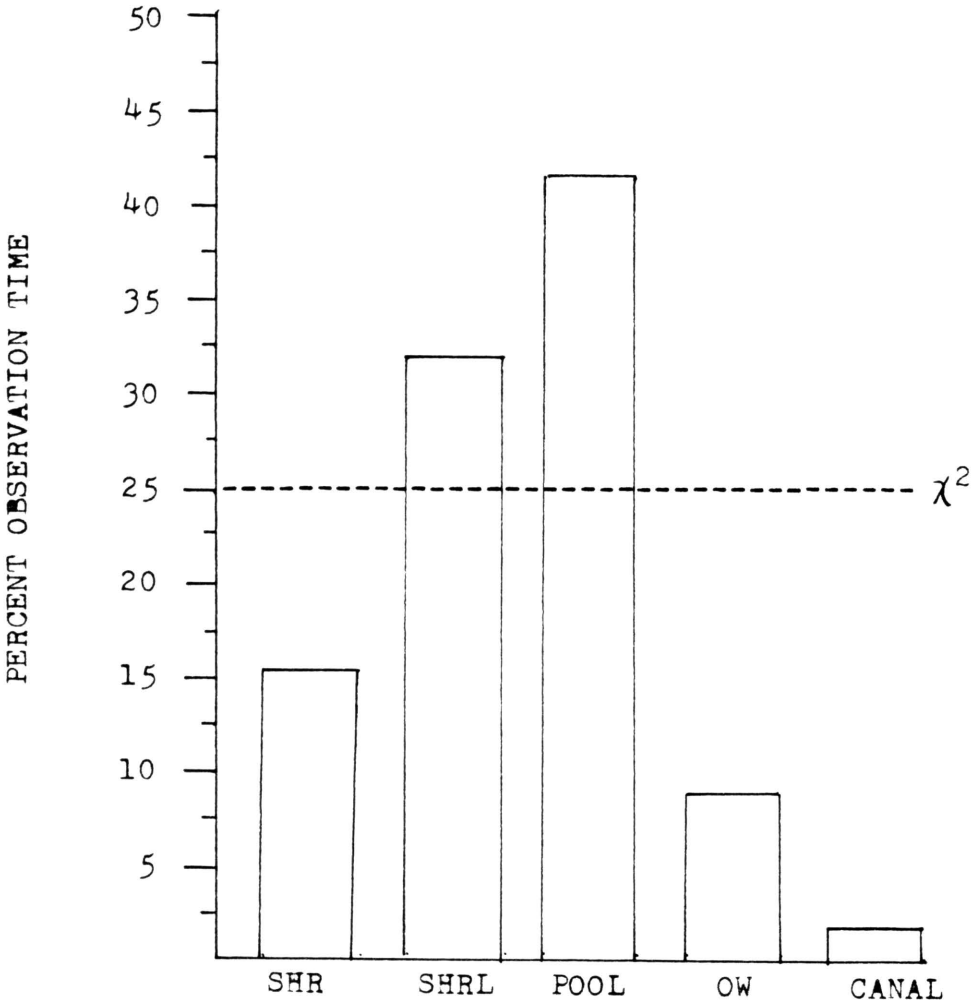

Figure 8. Little Blue Heron foraging habitat use (total observation time) in Old Tampa Bay and Safety Harbor, Florida. SHR = shore, SHRL = shoreline, OW = open water.

The degree of association of a particular species with a particular microhabitat is small (χ^2 = 529.18, $p<0.001$, $\hat{C}_\lambda$ = .37). All three species preferred the shoreline and pools. Extremely high microhabitat overlaps were found between Little Blue Herons and Snowy Egrets ($\hat{C}_\lambda$ = 0.94) and between Snowy Egrets and Tricolored Herons ($\hat{C}_\lambda$ = 0.95). A high overlap was also found between Little Blue Herons and Tricolored Herons ($\hat{C}_\lambda$ = 0.83, Tables 5 and 7).

Foraging Depth

Snowy Egrets (χ^2 = 138.15, $p<0.001$), Tricolored Herons (χ^2 = 412.35, $p<0.001$), and Little Blue Herons (χ^2 = 195.59, $p<0.001$) foraged at different depths with a frequency which was not random. Snowy Egrets spent more time foraging at depths of 23 mm (21.9% of total observation time), 45 mm (21.8%), 90 mm (24.1%), and 68 mm (16.0%), than at 142 mm (5.0%) or from shore (11.2%, Figure 9). Tricolored Herons foraged more frequently at depths of 23 mm (23.8%) and 90 mm (31.1%) than at other depths (Figure 10). Little Blue Herons foraged most frequently at 90 mm (29.4%), and least frequently at a depth of 142 mm (5.3%, Figure 11).

The degree of association between a particular heron species and a particular foraging depth is extremely weak (χ^2 = 121.10, $p<0.001$, C = .19). Overlap of foraging depth

Table 7. Frequency of foraging habitat use, as percent of total observation time, for Little Blue Herons (LBH), Snowy Egrets (SE), and Tricolored Herons (TH) in Old Tampa Bay and Safety Harbor, Florida. SHR = shore, SHRL = shoreline, OW = open water.

	Microhabitat				
Species	SHR	SHRL	POOL	OW	CANAL
LBH	15.25	32.20	42.06	8.47	2.01
SE	4.30	47.02	34.49	9.90	4.30
TH	0	46.74	21.69	19.77	11.79

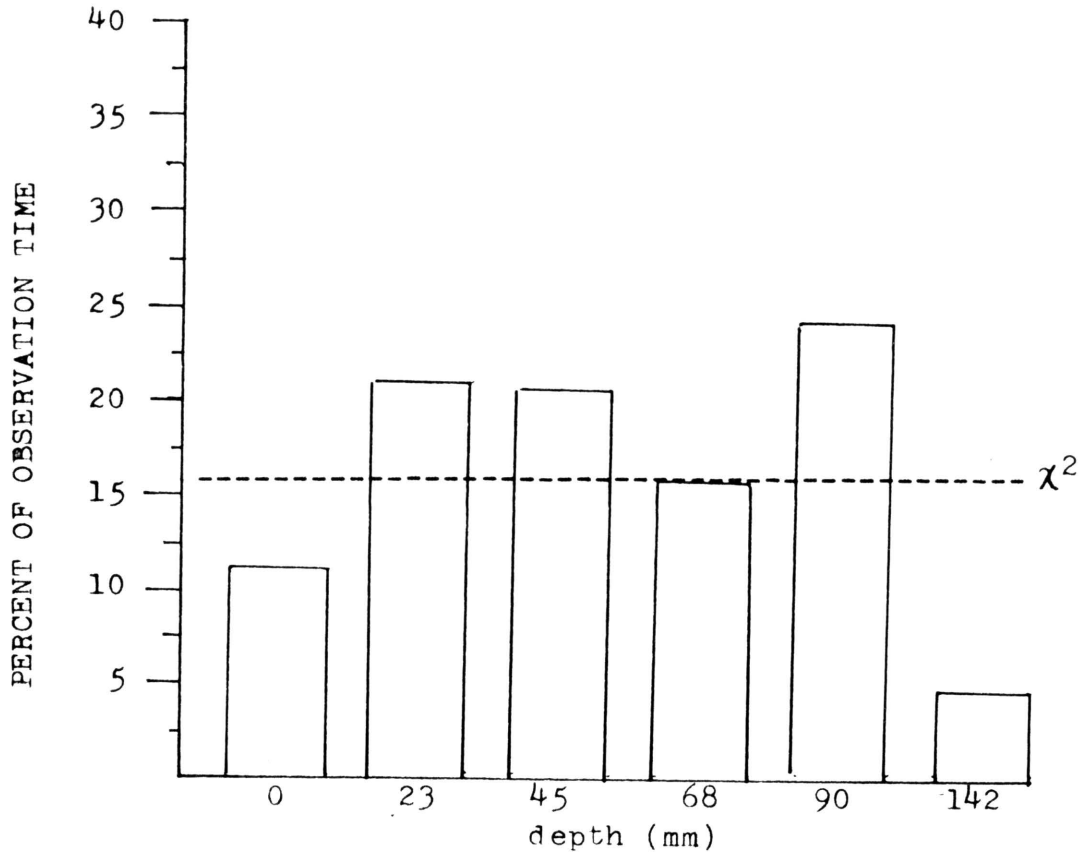

Figure 9. Snowy Egret foraging depth (total observation time) in Old Tampa Bay and Safety Harbor, Florida.

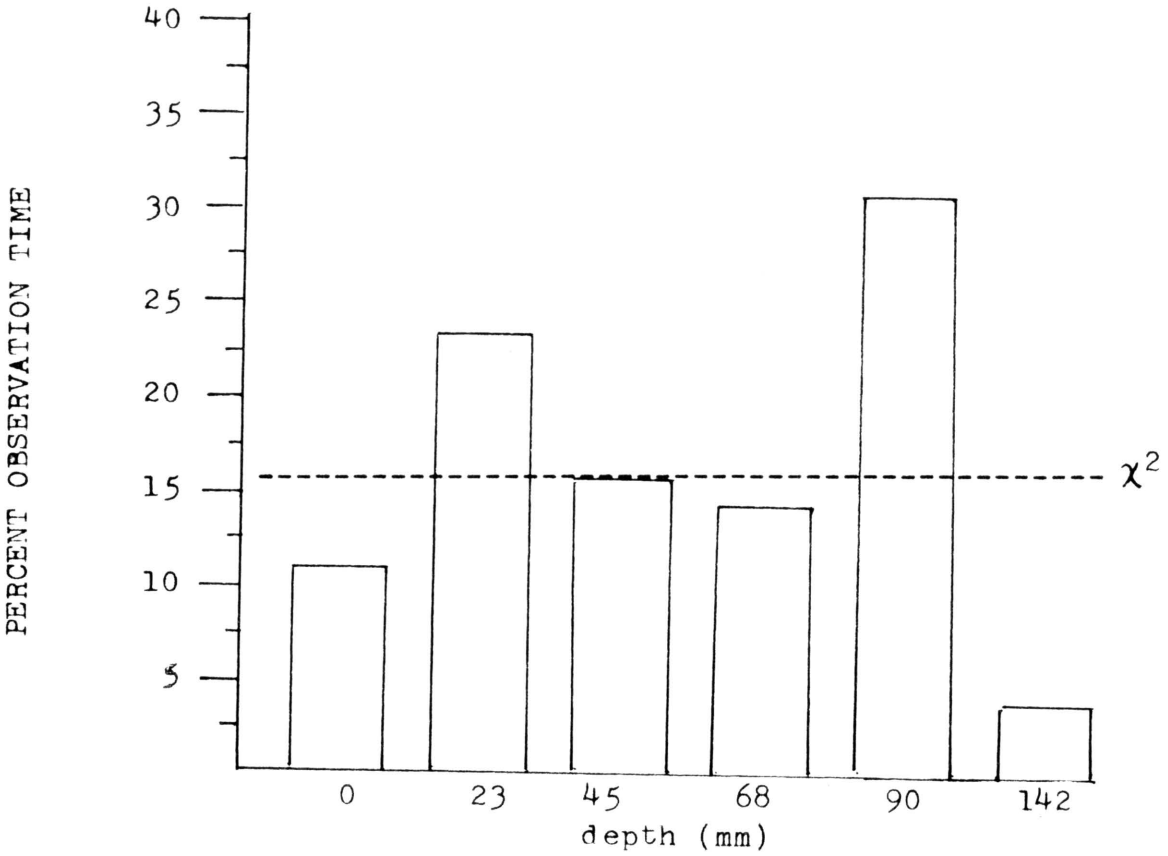

Figure 10. Tricolored Heron foraging depth (total observation time) in Old Tampa Bay and Safety Harbor, Florida.

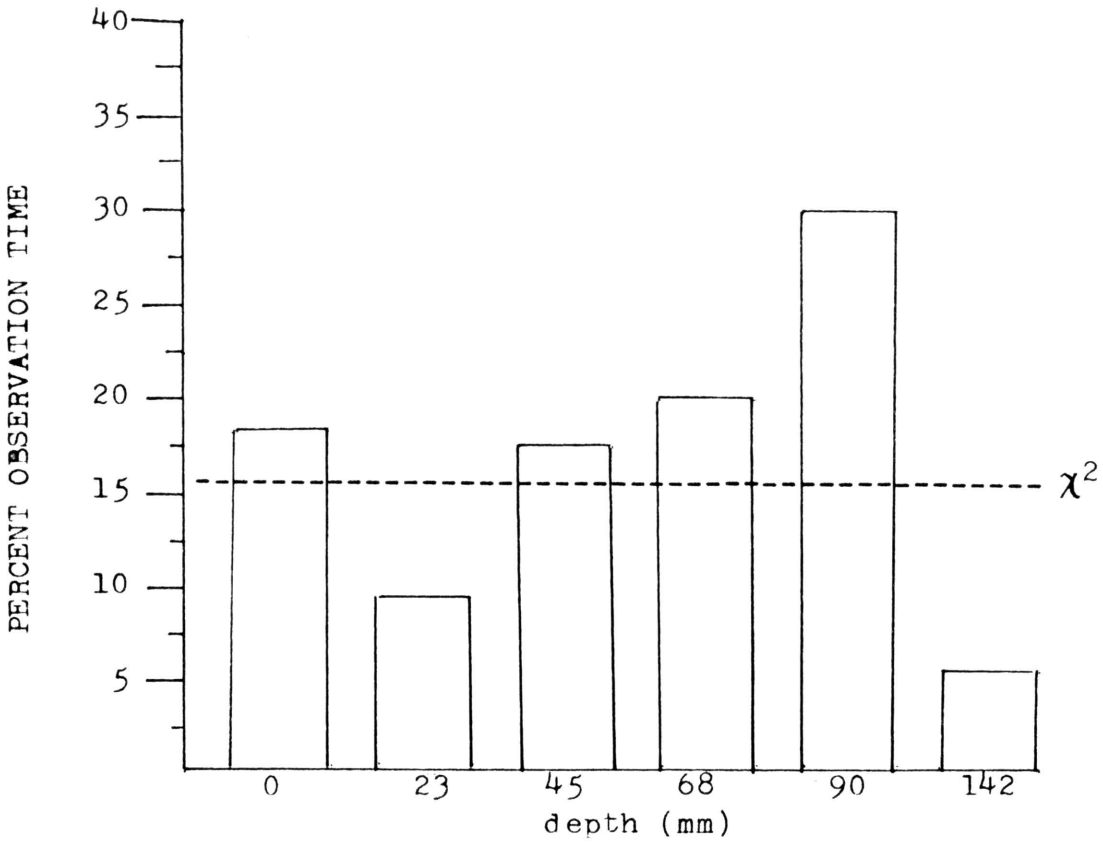

Figure 11. Little Blue Heron foraging depth (total observation time) in Old Tampa Bay and Safety Harbor, Florida.

distribution was extremely high between Little Blue Herons and Snowy Egrets ($\hat{C}_\lambda$ = 0.93), Little Blue Herons and Tricolored Herons ($\hat{C}_\lambda$ = 0.94), and Snowy Egrets and Tricolored Herons ($\hat{C}_\lambda$ = 0.98, Tables 5 and 8). There was no difference between these three species for habitat use.

Behavior and Microhabitat

Little Blue Herons used walk-slow in all microhabitats. Snowy Egrets used walk-slow exclusively when foraging on shore (8 of 63 observations). Along the shoreline, Snowy Egrets used walk-slow (19 of 53 observations), disturb-and-chase (15 of 53 observations), and foot-stirring (11 of 53 observations) most often, while Tricolored Herons used walk-slow (37 of 79 observations) and disturb-and-chase (28 of 79 observations). In pools, Snowy Egrets used mostly foot-stirring (20 of 20 observations) and Tricolored Herons used walk-slow (10 of 25 observations), disturb-and-chase (7 of 25 observations), and stand (6 of 25 observations) most often. Snowy Egrets used disturb-and-chase (7 of 19 observations) and walk-slow (6 of 19 observations) more than other behaviors in open water. Disturb-and-chase (21 of 41 observations) was the predominant behavior of Tricolored Herons in open water. Walk-slow, disturb-and-chase, and foot-stirring were used equally as often (each 2 of 6 observations) by Snowy Egrets in canals.

Table 8. Frequency of foraging depth, as percent of total observation time, for Little Blue Herons (LBH), Snowy Egrets (SE), and Tricolored Herons (TH) in Old Tampa Bay and Safety Harbor, Florida.

	Foraging Depth					
Species	0 mm	23 mm	45 mm	68 mm	90 mm	142 mm
LBH	18.4	9.8	17.5	19.5	29.4	5.3
SE	11.2	21.9	21.8	16.0	24.1	5.0
TH	12.0	23.8	15.4	14.4	31.1	3.3

Tricolored Herons used walk-slow (14 of 27 observations) and disturb-and-chase (12 of 27 observations) more than other behaviors when foraging in canals (Figures 12 and 13).

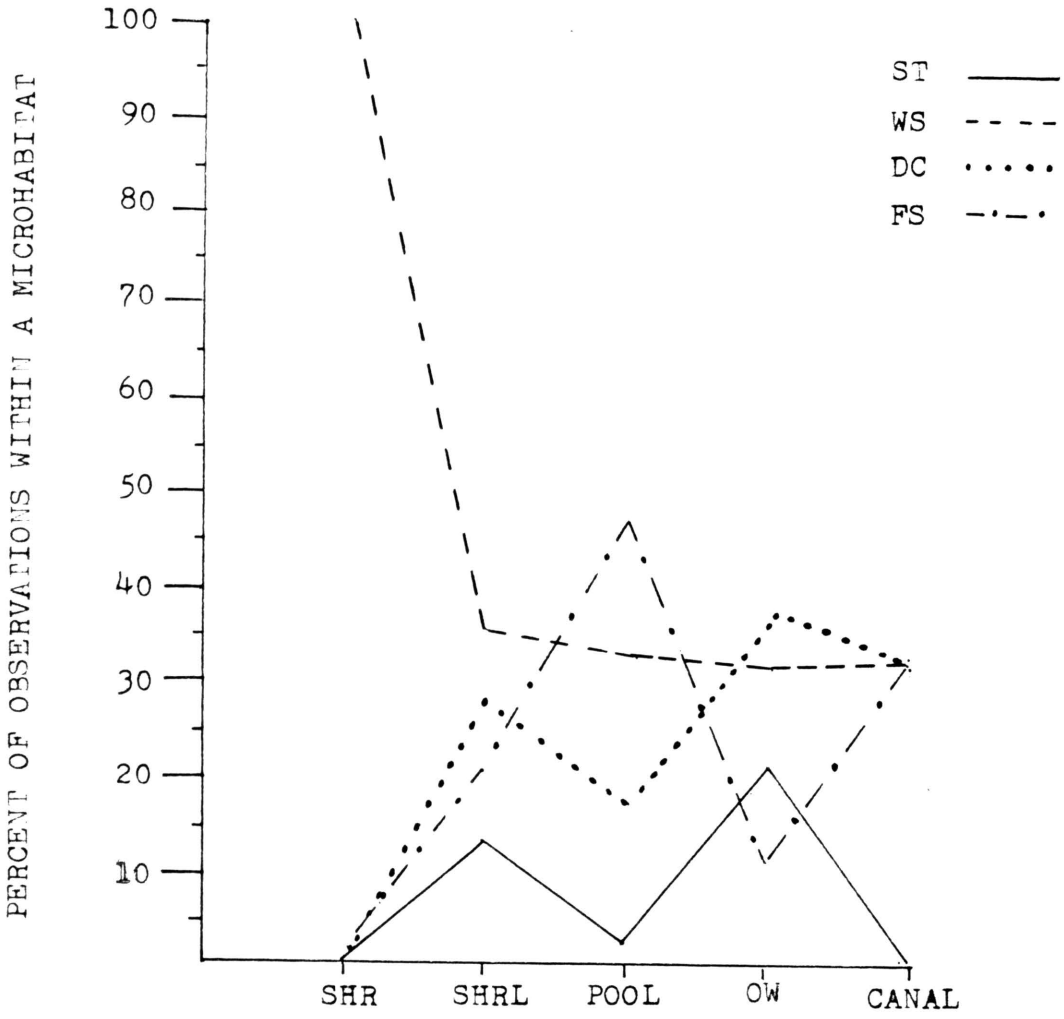

Figure 12. Snowy Egret foraging behavior within microhabitat in Old Tampa Bay and Safety Harbor, Florida. SHR = shore, SHRL = shoreline, OW = open water, ST = stand, WS = walk-slow, DC = disturb-and-chase, FS = foot-stirring.

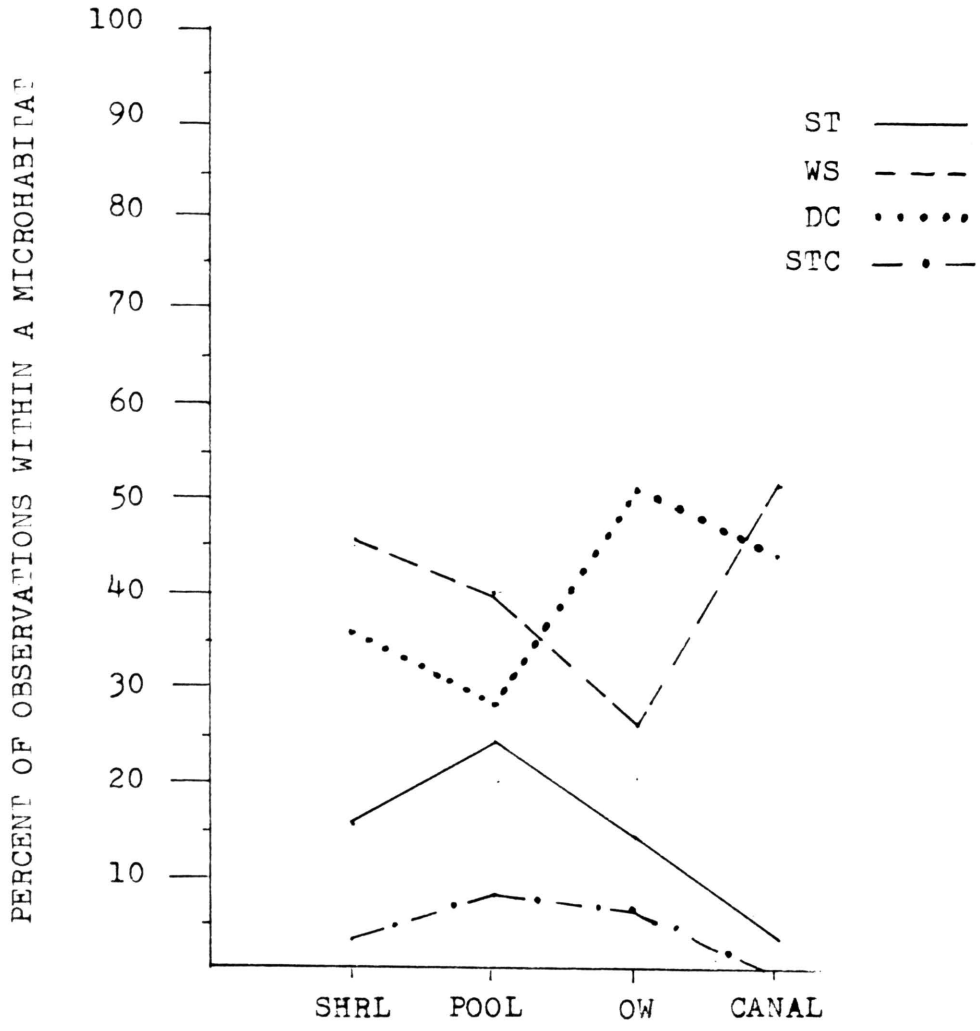

Figure 13. Tricolored Heron foraging behavior within microhabitat in Old Tampa Bay and Safety Harbor, Florida. SHRL = shoreline, OW = open water, ST = stand, WS = walk-slow, DC = disturb-and-chase, STC = stand-and-chase.

FOOD

Prey Type

Table 9 summarizes the prey types of Little Blue Herons, Snowy Egrets, and Tricolored Herons in Old Tampa Bay and Safety Harbor, Florida. Fish which were caught with a cast-net in the foraging area but were too small or not readily distinguishable before being consumed by the herons are listed in Table 10.

Little Blue Herons ate a wide variety of prey with polychaetes (30.3%) and fish (33.6%) occurring most frequently. Fish (50.5%) and crabs (40.7%) accounted for most of the biomass of the diet of Little Blue Herons. Snowy Egrets ate prawns (37.6%) and fish (42.2%) most frequently, with fish (45.8%) accounting for much of the biomass. Tricolored Herons had a less diverse diet than Little Blue Herons and Snowy Egrets. Fish (83.0%) occurred with the greatest frequency in the diet of Tricolored Herons and accounted for most of the biomass (97.1%). Tricolored Herons never ate crabs, isopods, or flatfish, and a polychaete was eaten once.

A moderately high overlap ($\hat{C}_\lambda = 0.82$) exists between the types of prey in the diets of Little Blue Herons and

Table 9. Food of Little Blue Herons (LBH), Snowy Egrets (SE), and Tricolored Herons (TH) foraging in Old Tampa Bay and Safety Harbor, Florida.

Food Item	LBH n	LBH % of diet	LBH % total wt.	SE n	SE % of diet	SE % total wt.	TH n	TH % of diet	TH % total wt.
Insects	4	0.99	0.33						
Polychaetes (*Nereis* spp.)	122	30.27	3.03	57	12.90	3.29	1	0.25	0.03
Isopod (*Ligia exotica*)	51	12.66	4.22	24	5.44	3.29			
Prawn (*Palaemonetes pugio*)	75	18.61	1.22	166	37.64	19.73	68	16.96	2.80
Fiddler Crab (*Uca* sp.)	4	0.99	2.05						
Blue Crab (*Callinectes sapidus*)	11	2.73	37.70	3	0.68	22.50			
Crab spp.	1	0.25	0.91	5	1.13	5.68			
Total crab spp.	15	3.97	40.66	8	1.81	28.18			
Flounder spp.	12	2.98	16.80	6	1.36	13.72			
Pipefish (*Syngnathus* spp.)	11	2.73	0.68	5	1.13	0.38	21	5.24	0.44
Atlantic Needlefish (*Strongylura marina*)	1	0.25	0.58	1	0.23	0.99	18	4.49	7.40
Red Drum (*Sciaenops ocellata*)	7	1.74	2.51						
Fish spp.	104	25.81	29.90	174	39.46	30.70	293	73.07	89.30
Total fish spp.	135	33.58	50.47	186	42.18	45.79	332	82.79	97.14
Total	402	100.0	99.93	441	99.97	100.3	401	99.99	99.97

Table 10. Fish found in the foraging areas of Little Blue Herons, Snowy Egrets, and Tricolored Herons in Old Tampa Bay and Safety Harbor, Florida.

Species	Relative Abundance
Cyprinodontidae	
Fundulus grandis	Abundant
Fundulus similis	Abundant
Adinia xenica	Common
Cyprinodon variegatus	Common
Lucania parva	Rare
Poecilidae	
Poecilia latipinna	Common
Atherinidae	
Menidia beryllina	Common
Mugilidae	
Mugil cephalus	Rare

Snowy Egrets and between Tricolored Herons and Snowy Egrets ($\hat{C}_\lambda$ = 0.80). There was less dietary overlap between Little Blue Herons and Tricolored Herons ($\hat{C}_\lambda$ = 0.59).

Prey Size

The size of prawns and fish in the diet of Little Blue Herons, Snowy Egrets, and Tricolored Herons was compared for overlap. There was high overlap for size of prawns in the diet of Little Blue Herons and Snowy Egrets ($\hat{C}_\lambda$ = 0.99), Little Blue Herons and Tricolored Herons ($\hat{C}_\lambda$ = 0.97), and Snowy Egrets and Tricolored Herons ($\hat{C}_\lambda$ = 0.98, Tables 5 and 11). Most prawns taken were approximately 20 mm in length. This comparison may be meaningless because of the limited size of prawns available in the habitat and the fact that all sizes of prawn are easily manipulated by each heron species.

The overlap for size of fish in the diet of Little Blue Herons and Snowy Egrets was low ($\hat{C}_\lambda$ = 0.31). A moderate overlap ($\hat{C}_\lambda$ = 0.79) in fish size was found between Little Blue Herons and Tricolored Herons. This overlap was for fish 20 - 41 mm in length. There was moderate overlap ($\hat{C}_\lambda$ = 0.79) for the size of fish in the diets of Snowy Egrets and Tricolored Herons, primarily for fish 20 mm in length (Tables 5 and 12).

Table 11. Frequency of prawn-size eaten by Little Blue Herons, Snowy Egrets, and Tricolored Herons foraging in Old Tampa Bay and Safety Harbor, Florida.

	Prawn-Size	
Species	20 mm	41 mm
LBH	84	16
SE	83	17
TH	71	29

Table 12. Frequency of fish-size eaten by Little Blue Herons, Snowy Egrets, and Tricolored Herons foraging in Old Tampa Bay and Safety Harbor, Florida.

	Fish-Size				
Species	20 mm	41 mm	62 mm	82 mm	111 mm
LBH	10.37	49.63	23.00	15.56	1.48
SE	79.00	9.68	7.00	3.76	0.54
TH	42.60	33.70	14.50	8.46	0.90

Behavior and Food

Little Blue Herons ate four insects on one occasion when a bird foraging in a canal walked onto an adjoining grassy field. Isopods were eaten by Little Blue Herons which foraged along a rock wall when the tide was not yet low enough to allow foraging in the water. Snowy Egrets foraged for isopods along the same walls but did so even when the tide was low.

Food was considered as a function of behavior to determine if a particular behavior results in a particular prey type. As Little Blue Herons used only the walk-slow behavior and ate a diversity of prey types, no association can be demonstrated for this species. There is an association of behavior with prey (polychaetes, prawns, and fish) with Snowy Egrets ($\chi^2 = 303.13$, $p < 0.001$, $C = .64$). Snowy Egrets used the walk-slow behavior to eat polychaetes, and primarily stand to catch fish. Walk-slow, disturb-and-chase, and foot-stirring were used to catch prawns (Table 13).

Tricolored Herons had a weakly significant relationship between prey type and behavior ($\chi^2 = 69.68$, $p < 0.001$, $C = .39$). Prawns were eaten with walk-slow; and fish with stand, walk-slow, and disturb-and chase (Table 14). Combining the results for all three species indicates a relationship between foraging behavior and the type of prey captured ($\chi^2 = 482.83$, $p < 0.001$, $C = .55$). Walk-slow be-

Table 13. Prey caught by Snowy Egrets as a function of behavior in Old Tampa Bay and Safety Harbor, Florida. ST = stand, WS = walk-slow, DC = disturb-and-chase, FS = foot-stirring.

	ST	WS	DC	FS
polychaete	1	56		
prawn	5	46	39	76
fish	128	30	10	21

Table 14. Prey caught by Tricolored Herons as a function of behavior in Old Tampa Bay and Safety Harbor, Florida. ST = stand, WS = walk-slow, DC = disturb-and-chase, STC = stand-and-chase.

	ST	WS	DC	STC
prawn	2	52	5	3
fish	155	97	64	8

havior was used to capture prawns and polychaetes, and stand and walk-slow behaviors were used to capture fish (Table 15). A prey item cannot be predicted with certainty by observing a behavior.

Table 15. Prey caught by Little Blue Herons, Snowy Egrets, and Tricolored Herons as a function of behavior in Old Tampa Bay and Safety Harbor, Florida. ST = stand, WS = walk-slow, DC = disturb-and-chase, FS = foot-stirring, STC = stand-and-chase.

	ST	WS	DC	FS	STC
polychaete	1	178	1		
prawn	7	173	44	76	3
fish	283	261	66	10	27

FORAGING EFFICIENCY

Efficiency and Behavior

Little Blue Herons had a greater percentage of successful strikes ($\bar{x}$ = 59.0%) than Snowy Egrets ($\bar{x}$ = 42.8%; $Z = 3.62$, $p > 0.001$) or Tricolored Herons ($\bar{x}$ = 33.0%; $Z = 4.64$, $p > 0.001$). Snowy Egrets and Tricolored Herons were equally proficient at striking while foraging ($Z = 0.05$, $p = 0.480$; Figure 14).

Little Blue Herons used walk-slow for all foraging. Snowy Egrets had a greater percentage of successful strikes using the stand behavior (74.28%) than walk-slow (39.14%), disturb-and-chase (31.94%), or foot-stirring (44.17%) behaviors (Table 16, Figure 15). Walk-slow resulted in a greater percentage of successful strikes for Snowy Egrets than did disturb-and-chase. Snowy Egrets were more successful striking when they used foot-stirring than when using disturb-and-chase behavior. Tricolored Herons were equally proficient at striking with all foraging behaviors (Table 17, Figure 16).

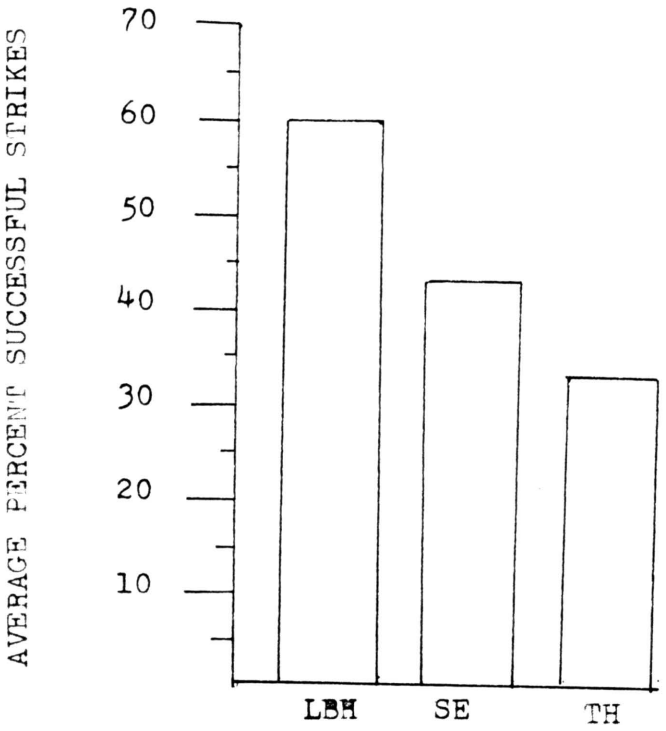

Figure 14. Striking efficiency of Little Blue Herons (LBH), Snowy Egrets (SE), and Tricolored Herons (TH) foraging in Old Tampa Bay and Safety Harobor, Florida. Calculated as the average of the efficiency for each observation (n: LBH = 63, SE = 71, TH = 96).

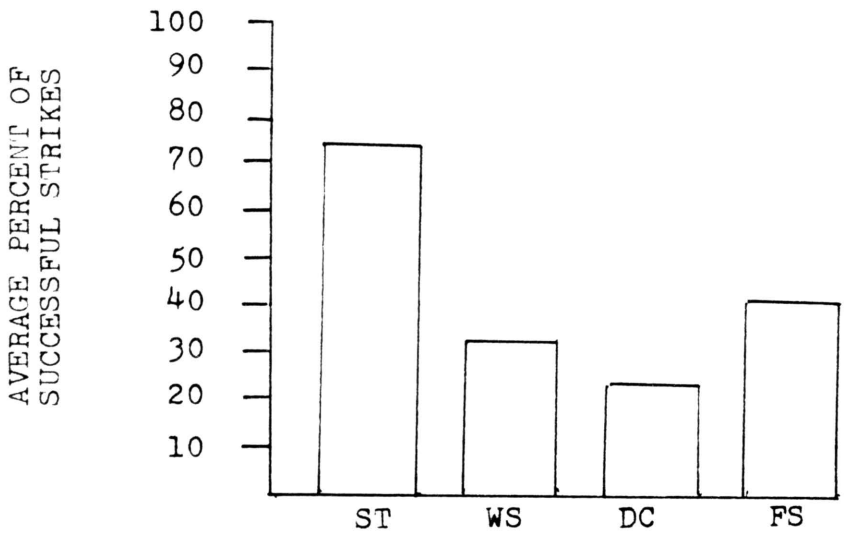

Figure 15. **Snowy Egret** efficiency by foraging behavior in Old Tampa Bay and Safety Harbor, Florida. Calculated as the average of the efficiency for each observation (n: ST = 10, WS = 39. DC = 24, FS = 30). ST = stand, WS = walk-slow, DC = disturb-and-chase, FS = foot-stirring.

Table 16. Comparative efficiency of Snowy Egret foraging behavior in Old Tampa Bay and Safety Harbor, Florida. ST = stand, WS = walk-slow, DC = disturb-and-chase, FS = foot-stirring.

ST X WS Z = 3.87, p > 0.001**

ST X DC Z = 2.83, p = 0.0023**

ST X FS Z = 2.75, p = 0.0030**

WS X DC Z = 1.79, p = 0.0367*

WS X FS Z = 0.74, p = 0.2296

DC X FS Z = 2.79, p = 0.0026**

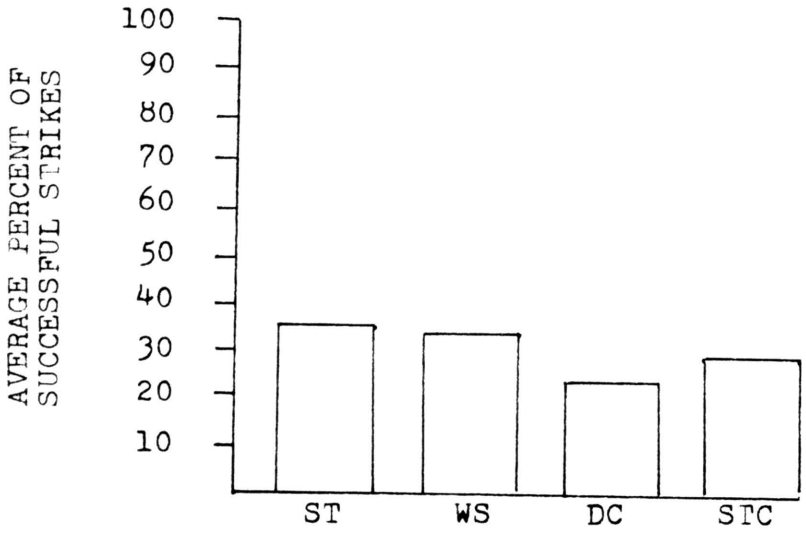

Figure 16. Tricolored Heron efficiency by foraging behavior in Old Tampa Bay and Safety Harbor, Florida. Calculated as the average of the efficiency for each observation (n: ST = 19, WS = 59, DC = 55, STC = 6). ST = stand, WS = Walk-slow, DC = disturb-and-chase, STC = stand-and-chase.

Table 17. Comparative efficiency of Tricolored Heron foraging behavior in Old Tampa Bay and Safety Harbor, Florida. ST = stand, WS = walk-slow, DC = disturb-and-chase, STC = stand-and-chase.

ST X WS $Z = 0.42$, $p = 0.3372$

ST X DC $Z = 0.52$, $p = 0.3015$

ST X STC $U = 73$, $p > 0.05$

WS X DC $Z = 1.49$, $p = 0.0681$

WS X STC $Z = 0.65$, $p = 0.2578$

DC X STC $Z = 0.22$, $p = 0.4129$

Grams of Food Per Minute

Little Blue Herons obtained 0.86 grams wet weight of prey/minute. Snowy Egrets obtained food at a rate of 0.61 grams wet weight of prey/minute. Tricolored Herons obtained 0.68 grams wet weight of prey/minute (Table 18). At these rates of food intake, Little Blue Herons would need to forage for approximately 76.0 minutes/day, Snowy Egrets would need to forage approximately 98.4 minutes/day, and Tricolored Herons would need to forage approximately 80.9 minutes/day to meet daily food requirements.

Efficiency and Microhabitat

Little Blue Herons had a greater percentage of successful strikes when foraging on shore (73.4%) than in pools (48.6%), and in open water (77.5%) than in pools or canals (33.3%, Table 19 and Figure 17). Little Blue Herons were equally proficient in all other microhabitats. Snowy Egrets were equally proficient at striking in all foraging microhabitats (Table 20 and Figure 18). Tricolored Herons were more successful striking along the shoreline (37.3%) than in open water (17.7%), and in canals (32.3%) than in open water (Table 21 and Figure 19). There was no difference in Tricolored Heron striking efficiency between the shoreline, pools (27.7%), and canals, or between pools and open water.

Table 18. Comparative foraging efficiency of Little Blue Herons (LBH), Snowy Egrets (SE), and Tricolored Herons (TH) in Old Tampa Bay and Safety Harbor, Florida.

Species	foraging time in min	g wet wt. identif. prey	est g total wet wt.	g wet wt. prey per min
LBH	944	604.62	816.24	0.86
SE	838	364.46	513.89	0.61
TH	1525	965.88	1036.88	0.68

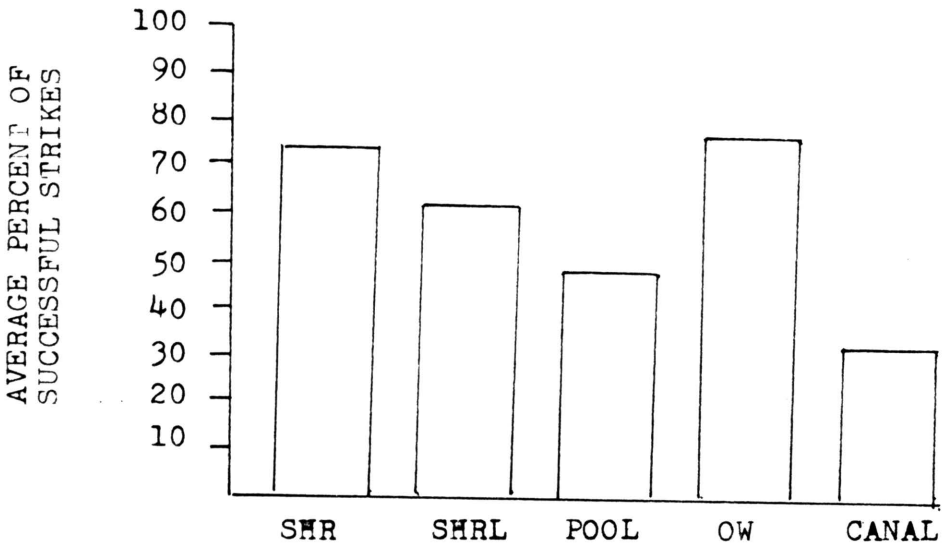

Figure 17. Little Blue Heron foraging efficiency by microhabitat in Old Tampa Bay and Safety Harbor, Florida. Calculated as the average of the efficiency for each observation (n: SHR = 7, SHRL = 25, POOL = 28, CANAL = 3, OW = 8). SHR = shore, SHRL = shoreline, OW = open water.

Table 19. Comparative efficiency of microhabitat use by Little Blue Herons in Old Tampa Bay and Safety Harbor, Florida. SHR = shore, SHRL = shoreline, OW = open water.

SHR X SHRL $Z = 0.87$, $p = .1922$

SHR X POOL $Z = 0.30$, $p = 0.0013$**

SHR X OW $U = 50$, $p > .05$

SHR X CANAL $U = 12.5$, $p > .05$

SHRL X POOL $Z = 0.53$, $p = 0.2981$

SHRL X OW $Z = 1.22$, $p = 0.1112$

SHRL X CANAL $U = 32$, $p > .05$

POOL X OW $Z = 1.98$, $p = 0.0239$*

POOL X CANAL $Z = 0.80$, $p = 0.2119$

OW X CANAL $U = 12$, $p < .05$ *

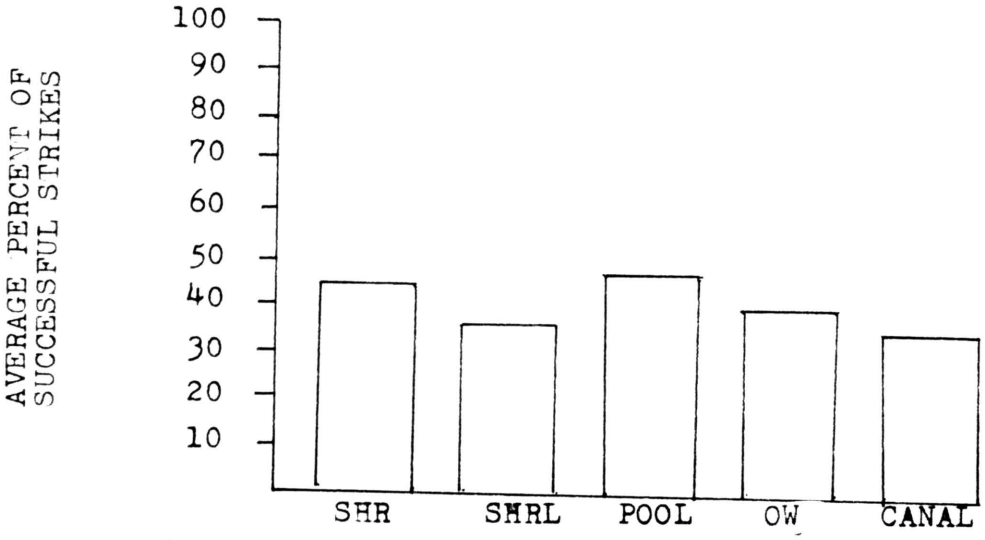

Figure 18. Snowy Egret foraging efficiency by microhabitat in Old Tampa Bay and Safety Harbor, Florida. Calculated as the average of the efficiency for each observation (n: SHR = 2, SHRL = 30, POOL = 33, OW = 11, CANAL = 3). SHR = shore, SHRL = shoreline, OW = open water.

Table 20. Comparative efficiency of microhabitat use by Snowy Egrets in Old Tampa Bay and Safety Harbor, Florida. SHR = shore, SHRL = shoreline, OW = open water.

SHR X SHRL $U = 46$, $p > .05$

SHR X POOL $Z = 0.17$, $p = 0.4325$

SHR X OW $U = 13.5$, $p > .05$

SHR X CANAL too few observations to test

SHRL X POOL $Z = 1.05$, $p = 0.1469$

SHRL X OW $Z = 0.85$, $p = 0.1977$

SHRL X CANAL $U = 58.5$, $p > .05$

POOL X OW $Z = 0.23$, $p = 0.4090$

POOL X CANAL $Z = 0.54$, $p = 0.2946$

OW X CANAL $U = 20$, $p > .05$

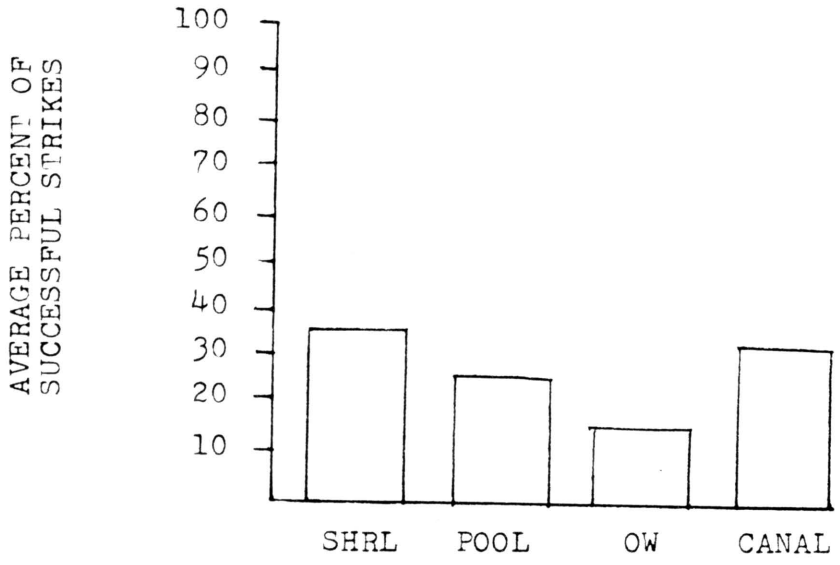

Figure 19. Tricolored Heron foraging efficiency by microhabitat in Old Tampa Bay and Safety Harbor, Florida. Calculated as the average of the efficiency for each observation (n: SHRL = 49, POOL = 14, OW = 26, CANAL = 16). SHRL = shoreline, OW = open water.

Table 21. Comparative efficiency of microhabitat use by Tricolored Herons in Old Tampa Bay and Safety Harbor, Florida. SHRL = shoreline, OW = open water.

SHRL X POOL	Z = 0.92, p = 0.1778
SHRL X OW	Z = 3.31, p = 0.0005**
SHRL X CANAL	Z = 0.69, p = 0.2451
POOL X OW	Z = 0.11, p = 0.4562
POOL X CANAL	U = 204.5, p 0.05
OW X CANAL	Z = 2.44, p = 0.0073**

DISCUSSION

One of the goals of this study was to determine the mechanism of resource partioning among similar herons within the confines of a single habitat. Little Blue Herons, Snowy Egrets, and Tricolored Herons did not overlap significantly in their use of foraging behaviors. A difference in foraging behavior was found in comparative studies of other species of herons (Meyerriecks, 1962; Jenni, 1969; Williard, 1977). These authors suggested that a difference in behavior was sufficient to partition the available resources. The present study showed that Little Blue Herons and Snowy Egrets used different foraging behaviors but ate the same type of prey. Snowy Egrets and Tricolored Herons used the same behaviors under some circumstances, but the prey types included in the diet were similar. Thus, behaviors should not be considered to be sufficient by themselves to partition resources.

Habitat differences have also been suggested as a mechanism for partitioning resources (Williard, 1977; Whitfield and Blaber, 1979). The present study found that high overlap in microhabitat use existed among the three species. This high overlap was also found for foraging depth so that it appears that Little Blue Herons,

Snowy Egrets, and Tricolored Herons used the same microhabitats at the same depth. No partitioning of the resources was achieved for these three heron species in this study area by mechanisms of habitat segregation. All three species showed preferences for the same portion of the habitat, 23 - 90 mm depth in pools and along the shoreline.

Jenni (1969) conducted a study of partitioning among four mid-sized herons in a freshwater habitat. He found that partitioning was achieved primarily through a difference in major food items, and to a lesser degree by behavior and microhabitat. The present study found an insignificant overlap for prey type between Little Blue Herons and Tricolored Herons. A significant overlap was found for prey type between Little Blue Herons and Snowy Egrets and between Snowy Egrets and Tricolored Herons. Fish, which comprised much of the diet of Snowy Egrets and Little Blue Herons, overlapped little when partitioned by size. This contrasts with Williard's (1977) study in which Snowy Egrets and Little Blue Herons took fish of identical size. Williard suggested that Snowy Egrets used slightly different habitats than Little Blue Herons but his data (Table 2) indicate significant habitat overlap in four of the six months during which the two species occurred together.

Williard found moderate overlap between Tricolored Herons and Little Blue Herons for size of fish eaten but little overlap in habitat use. Significant overlap was

found in the present study for the size of fish eaten by Tricolored Herons and Little Blue Herons. This overlap may be meaningless in light of the low dietary overlap of these two species. However, this study shows a significant dietary overlap and fish-size overlap for Tricolored Herons and Snowy Egrets. Pianka (1974) demonstrated that sympatric competing species of lizards which exhibit high overlap on one dimension generally overlap little on another dimension. This appears to be the case for Little Blue Herons and Snowy Egrets foraging sympatrically in a shallow estuary but does not explain the observed relationship between Tricolored Herons and Snowy Egrets. It may be that Tricolored Herons and Snowy Egrets are eating different species of fish and therefore the overlap is not real. The detection of such a subtle difference in diet between these two species is beyond the scope of the present study. Alternatively, food may not be a limiting resource and a difference in diet would not be necessary.

Head and neck tilts and the use of the wings by foraging herons were most recently reviewed by Kushlan (1978). Tricolored Herons used neck tilts when standing or walking slowly, especially on sunny days. The tilt apparently is a device designed to reduce glare on the surface of the water, much in the way that the head tilt does for Little Blue Herons (Krebs and Partridge, 1973).

Twice Tricolored Herons foraged with an open-winged

behavior. The use of the open-winged behavior reduced glare on the water and may have attracted fish to the false refuge of the shadow created by the open wings. Meyerriecks (1960) has seen fish swim toward the shadow created by a Reddish Egret (Egretta rufescens) canopy feeding. Wing-flicking has been proposed as a device for startling motionless prey into activity so that they may be seen and captured (Meyerriecks, 1962). The frequent wing-flicking by Snowy Egrets and Tricolored Herons walking quickly in this study were perceived to be intention movements. The herons were already moving quickly enough to disturb prey. Wing-flicking, along with the opening of the wings while running or preparing to strike, probably aids in balancing the heron.

Species which possess a repertoire of foraging behaviors might be expected to change their behavior to suit a particular microhabitat. This was not true for Little Blue Herons in this study which only used the walk-slow behavior. Snowy Egrets used foot-stirring in pools and occasionally in other microhabitats that offered shallow-water and cryptic prey. Disturb-and-chase behavior was used by Snowy Egrets and Tricolored Herons foraging in open water. Tricolored Herons used walk-slow or walk-quickly (disturb-and-chase) behaviors along the shoreline.

A species with a repertoire of foraging behaviors might also be expected to use different behaviors to

capture different prey. Snowy Egrets ate polychaetes only when they used the walk-slow behvior , but this behavior was also used to catch prawns and fish. Walk-slow was generally the behavior used by Tricolored Herons to catch prawns. Snowy Egrets used the stand behavior as the predominant means for catching fish, generally when the fish were trapped in small pools. Tricolored Herons caught fish by standing, but usually along the shoreline and from a crouch position. This crouch of the Tricolored Heron resembled a posture used by the Reef Heron (Egretta sacra) when approaching a small pool or detecting a fish at a distance (Recher and Recher, 1972). Recher and Recher suggested that the crouch reduces the chance of being seen. I suggest that the Tricolored Herons crouched to prepare for striking, and flattened the body by partially extending the wings to better balance themselves. Flattening the body may increase the amount of body visible to the fish and not reduce it.

Cody (1971) suggested that birds in areas of renewable resources increase foraging efficiency by flocking. An individual would reduce the chances of foraging in an area which had recently been depleted. Caldwell (1981) suggested mixed heron flocks in Panama gain an advantage of this nature. This did not occur in the present study as herons arrived at, and departed foraging sites independently of other individuals. Individuals often foraged in areas recently vacated by others.

Caldwell suggested that Little Blue Herons and Tricolored Herons benefit by increasing foraging success when foraging near Snowy Egrets. Snowy Egrets benefit by supplanting other species from food supplies. Snowy Egrets did not supplant the other species from food on a regular basis in the present study. Snowy Egrets were the object of aggression as often as they were the aggressor. Russell (1978) suggested that Snowy Egrets are subordinate in mixed aggregations and that their efficiency is reduced in such situations. The mechanisms operating in Caldwell's aggregations which allowed Snowy Egrets to benefit by supplanting Little Blue Herons and Tricolored Herons did not operate in this study.

Snowy Egrets engaged in foraging associations with White Ibises on a few occasions but their striking efficiency was well below the average striking efficiency of Snowy Egrets foraging alone. Courser and Dinsmore (1975) report over 70% of the Snowy Egrets in an area foraging with White Ibises. Meyerriecks (pers. comm.) has seen Snowy Egrets defend their White Ibises against conspecifics. This was not observed in this study. The low number of successful strikes observed for Snowy Egrets and Tricolored Herons engaged in foraging associations may be misleading. An occasional food item of high quality may justify the associations.

Unlike Little Blue Herons and Tricolored Herons, Snowy Egrets were seen to defecate in the water. Recher and

Recher (1972) said that defecation out of the water is probably designed to reduce prey avoidance. The situations in which Snowy Egrets defecated in the water suggest that they did not want to lose a favored position which they at that time held.

Search path, an important element of foraging, is generally not considered in studies of heron ecology. Herons which used the walk-slow behvior tended to walk a straight line until a food item was encountered and then the rate of turning increased, presumably so that the heron stayed in a productive area. This pattern has been observed in bees (Pyke, 1978), fish (Beukema, 1968), and birds (Cody, 1971). Disturb-and-chase behavior began in a similar manner but quickly degenerated as chases ensued. No path was discerned from observations of foot-stirring because the foci of attention in most cases were randomly located patches of submerged vegetation. Once prey was encountered, the bird reduced the search area to the immediate vicinity.

There have been studies of foraging efficiency for single species (Recher and Recher, 1969, 1972; Quinney and Smith, 1980) but not between species or for behaviors within a species. The present study found that the striking efficiency of Little Blue Herons is consistent with the earlier observations of Recher and Recher (1969). A more realistic measure of foraging efficiency is grams of food eaten/minute foraging time. It appears that foraging

need only occupy a relatively small portion of a heron's day. Little Blue Herons foraged at a greater rate of grams of food/minute than Tricolored Herons or Snowy Egrets. Outside of the breeding season there are few constraints on herons other than foraging, and so feeding at a faster rate should convey little advantage as long as food supplies are adequate.

During the breeding season it may by advantageous for a bird to minimize time for foraging (Schoener, 1971), allowing more time to be spent establishing a nesting territory, incubating eggs, and feeding young. In this case, Little Blue Herons, and Tricolored Herons, which also need to spend less time foraging than Snowy Egrets, may possess an advantage for gaining the best nest sites and/or increasing reproductive output through increased parental investment. Long term studies of colony formation and reproductive output for mixed colonies of Little Blue Herons, Snowy Egrets, and Tricolored Herons correlated with foraging studies, are needed to determine the consequences of differential foraging rates.

To forage optimally, a heron should use a behavior which maximizes the energy return for the least energy expenditure (Schoener, 1971). Conditions permitting, foraging herons might be expected to stand and eat fish of the largest size which did not require lengthy handling. In a temporally variable environment like the coastal

marine habitat, foraging herons might be expected to develop tactics to meet changing conditions. Little Blue Herons did not vary their foraging behavior to meet different conditions. Little Blue Herons used walk-slow behavior in all microhabitats and were most efficient on shore, along the shoreline, and in open water. Most of their time was spent foraging in pools and along the shoreline. The fact that Little Blue Herons spent so much time in a microhabitat in which they were less than maximally efficient may be related to the distribution of prey.

Snowy Egrets were most proficient using stand, a behavior which can be used on a limited number of occasions. They were equally successful in all microhabitats and spent most of their time along the shoreline and in pools, reinforcing the idea of prey distribution. Behavior was modified greatly by Snowy Egrets only in pools where foot-stirring increased and disturb-and-chase behavior decreased.

Tricolored Herons were most successful along the shoreline, in pools, and in canals. This was correlated with the time Tricolored Herons spent in microhabitats. Disturb-and-chase was the most frequently used behavior by Tricolored Herons in open water, which was the least successful microhabitat. The fact that disturb-and-chase behavior was the predominant behavior in the least successful microhabitat, but was not any less successful overall suggests that different behaviors have different

success rates in different microhabitats. It may be that because of prey characteristics and features of the microhabitat, disturb-and-chase behavior provides the maximum energy return allowable in open water. Less productive microhabitats are probably used when other areas are unavailable or foraging has been unsuccessful. Regardless of the circumstances, an optimally foraging heron should select the behavior which is most efficient for the particular microhabitat it is in.

The present study showed that a combination of prey type and prey size partitioned the resources available to Little Blue Herons and Snowy Egrets, and Little Blue Herons and Tricolored Herons. No obvious partitioning was detected for Snowy Egrets and Tricolored Herons. All three species differed in their use of foraging behaviors. The majority of aggressive interactions involved conspecifics. Foraging associations were few and immediately unproductive. All species foraged most often in pools and along the shoreline. Little Blue Herons had a greater percentage of successful strikes than did Snowy Egrets of Tricolored Herons. Little Blue Herons obtained food at a greater rate of grams wet weight/minute. All three species could obtain their daily food requirement in a relatively small portion of the day. Snowy Egrets need to spend more time foraging/day than Little Blue Herons or Tricolored Herons.

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