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Aspects of colonial nesting in four species of herons in Virginia

Paula Christine Frohring
College of William & Mary - Arts & Sciences

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ASPECTS OF COLONIAL NESTING IN FOUR SPECIES OF HERONS IN VIRGINIA

A THESIS

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In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

by

Paula C. Frohring

1981

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirement for the degree of

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Paula C. Frohring
Author

Approved, June, 1981

Mitchell A. Byrd
Mitchell A. Byrd, Ph.D.

Norman J. Fashing
Norman J. Fashing, Ph.D.

Stewart A. Ware
Stewart Ware, Ph.D.

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ABSTRACT

This study investigated aspects of interspecific nesting in four herons (Ardeidae) including the Snowy Egret (Egretta thula), the Louisiana Heron (Hydranassa tricolor), the Little Blue Heron (Florida caerula) and the Cattle Egret (Bulbulcus ibis) on Fishermans Island, Virginia.

The four heron species initiated nesting in a similar sequence during 1976 and 1977. Each species moved into subzones in which other species were already nesting. Interspecific social stimulation was proposed to be an important factor in nest site selection. Tests showed that all species were not synchronously nesting. The slight asynchrony of nesting stage within a subzone could be advantageous in reducing predation, as only a small number of eggs or small chicks were available at a specific time.

Interspecific colonial nesting would be advantageous if individuals increased their probability of finding food by nesting with other species. Observations of feeding flight movements indicated that the colony itself was not important as a center for feeding information exchange. The continuous presence of flight movement and of nearby feeding aggregations was possibly more important in increasing the probability of an individual finding food.

Premises of the information exchange hypothesis were that species were capturing the same prey types, and that these prey were patchy in occurrence. Three species had as high a degree of overlap in number and type of prey as one species did in two different years. Trapping samples from feeding areas showed that size classes and types of prey that were temporally and locally most abundant were those most frequently encountered in food samples of heron chicks.

It was expected that parents nesting interspecifically would distinguish their own young to avoid contributing to another genotype, or to another species. Despite a similar degree of nest permanency and the same development schedule, the four species differed in recognitive abilities.

Intraspecific growth rates were related to individual parental care, hatching sequence, and nesting success among years. It was hypothesized that mixed-species nesting was selectively adaptive in enabling fledglings to find food. Although growth strategies differed among species, a common minimum and maximum growth rate was detected in both years suggesting the possibility that all four herons could fledge young within a similar time interval.

ASPECTS OF COLONIAL NESTING IN FOUR SPECIES OF HERONS IN VIRGINIA

INTRODUCTION

This thesis presents observations and data relating to interspecific nesting among four heron species at Fishermans Island, Virginia. The Snowy Egret (Egretta thula), Louisiana Heron (Hydranassa tricolor), Little Blue Heron (Florida caerula), and Cattle Egret (Bulbulcus ibis) were selected for comparative study. Nesting habitat was not completely utilized in this large colony. It appeared that several species selectively nested among other species rather than in interspecific groups. It was hypothesized that mixed-species nesting was more advantageous to these colonial nesting ardeids.

Darling (1938) proposed that colonial nesting birds would benefit from social stimulation by neighboring birds. If hatching were synchronized, predator numbers would increase only during the short period when young were available as prey. The possibility of a higher degree of interspecific synchrony was examined at Fishermans Island in 1976. Potential advantage of interspecific nesting in relation to predation pressure was explored.

More recently, emphasis has been placed on coloniality being an adaptation for exploiting food when prey is spatially unpredictable (Krebs, 1974; Ward and Zahvi, 1973).

The colony may act as an information center in which less successful feeders locate new feeding sites by following nesting neighbors (Krebs, 1974).

If such an adaptation occurs at an interspecific level, one would expect to observe nonspecific neighbors following one another in and out of the colony to feeding habitats. The possibility of information exchange is presented for species nesting at Fishermans Island during the 1976 nesting season. Information exchange could only be advantageous if each species were obtaining the same types of food in the same habitats. Therefore, food analysis is presented for samples emitted from chicks of each of the four species. Information exchange theory is applicable when food is spatially unpredictable. Trapping and seining collections, made during the nest building and incubation period in 1977, indicate availability of prey, which was correlated with prey selectivity as indicated by food sample analysis.

If interspecific colonial nesting was advantageous to these herons, one would expect that selection for specific recognition would have occurred. If a young bird is fledged among extraspecific neighbors and joins mixed-species feeding aggregations, then at some point it must learn to identify its own species to maintain species integrity. Investigations have shown that among colonial, intraspecific ground nesting birds, individual recognition exists between parents and young. This behavior allows adults selectively to care for their own offspring rather than reduce their own fitness through contributing to other genotypes (Shugart, 1978). If recognition was important enough to be selected from among some ground nesters before chicks leave the nest, it is reasonable to assume that this characteristic will be expressed in a situation involving more than one species, i.e., gene pool. Crossfostering experiments are presented to compare recognitive ability among the four parent and young heron species.

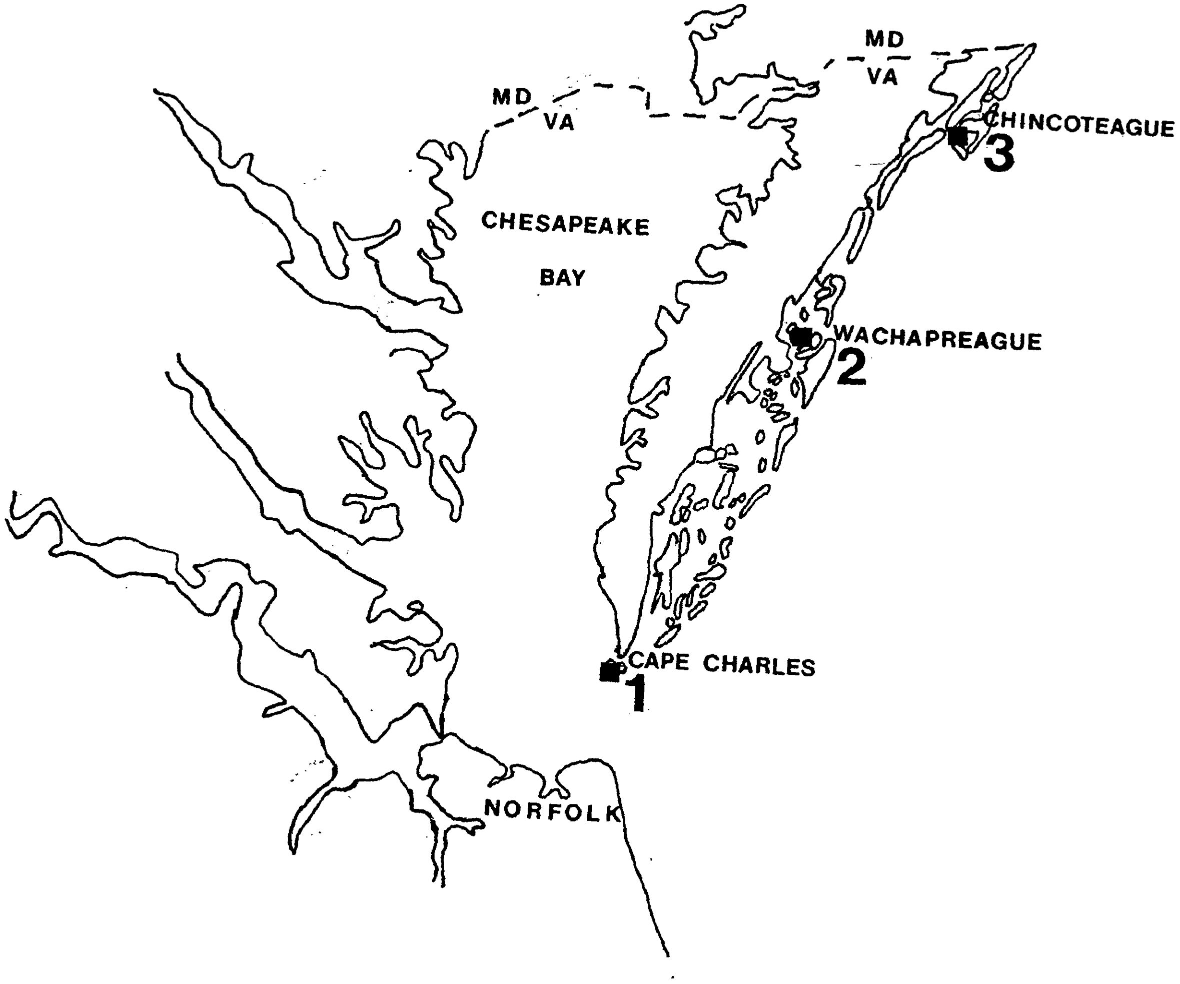
In order to interpret crossfoster growth results and to determine average age of broods, intraspecific growth rates are analyzed. The intrapsecific growth study was not planned as a correlate to coloniality. However, results of all analyses and observations are presented as intraspecific growth offers further insight into comparative growth strategies and success among the four ardeids.

DESCRIPTION OF THE STUDY AREAS

Most of this investigation was conducted on Fishermans Island ($37^{o}29'$ Lat., $75^{o}58'$ Long.) located in the mouth of Chesapeake Bay. The island has an area of about 1.2 square km. and is located 2 km. south of Cape Charles at the southern tip of the Delmarva Peninsula (Figure 1). The island is partially controlled and maintained by the U. S. Fish and Wildlife Service.

The heronry is located in woodland and thicket, which have grown for the past forty years to a size of approximately 4 ha. Expansion of the Wax-myrtle thicket was noticeable from the 1976 to 1977 nesting season, accompanied by increased utilization of peripheral areas by nesting herons. The heron colony appeared to be growing as indicated by a comparison of survey figures of adult birds from 1975 and 1976: Black-crowned Night Herons (Nycticorax nycticorax), 905 to 1965; Snowy Egrets, 305 to 760; Louisiana Herons, 42 to 400; Great Egrets (Casmerodius albus), 115 to ?; Little Blue Herons, 88 to 188; Cattle Egrets, 400 to 500; and Glossy Ibis (Plegadis falcinellus), 50 to 70. In 1977, one pair of White Ibis (Eudocimus albus) fledged two young in the colony, the first known breeding record for White Ibis in Virginia (Frohring and Beck, 1978).

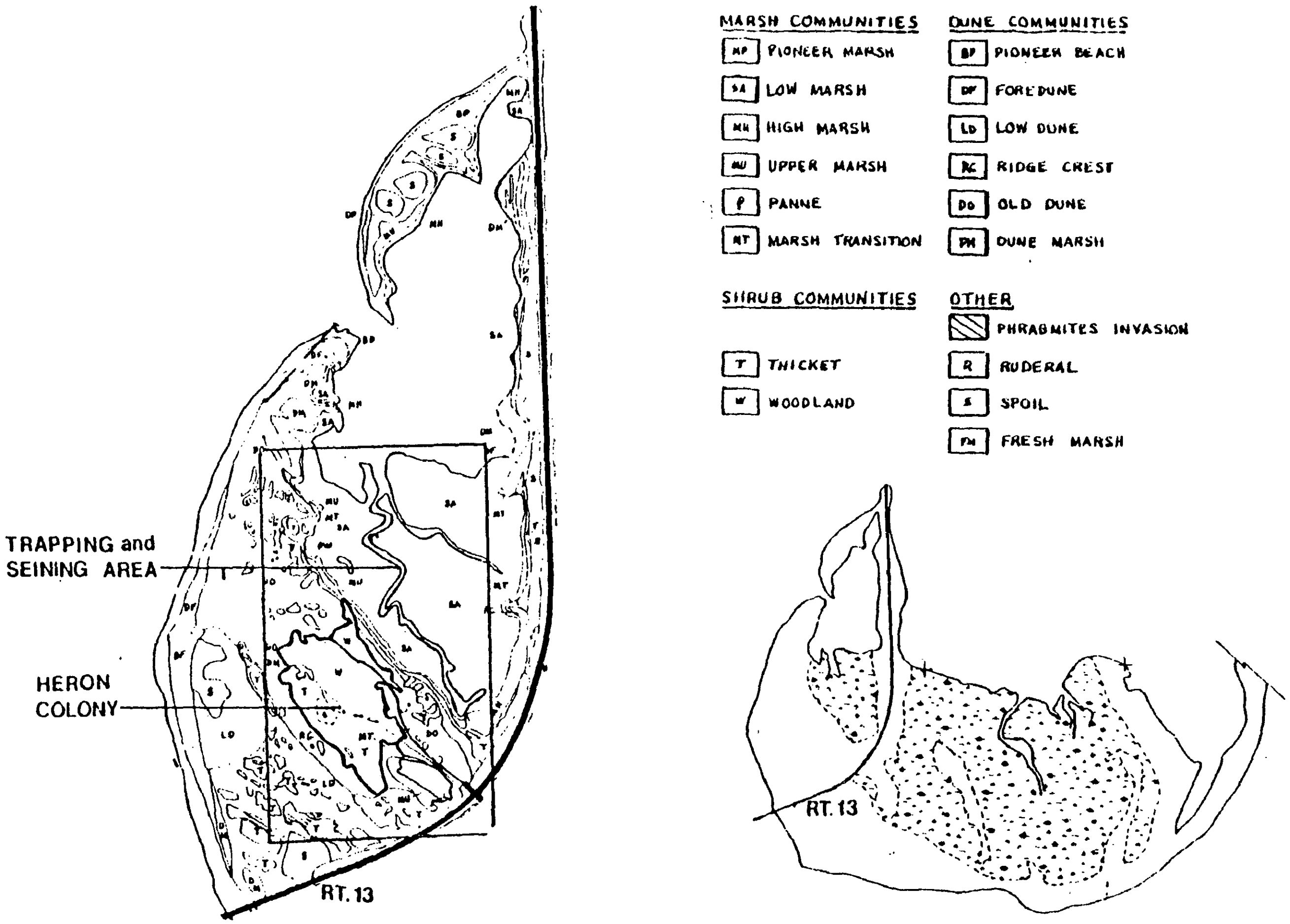
Figure 1. Location of Fishermans Island (1), Clubhouse Point (2), and Walkers Marsh (3) Heron Colonies on the Delmarva Peninsula, Virginia


MD
VA
MD
VA
CHESAPEAKE
BAY
CHINCOTEAGUE
3
WACHAPREAGUE
2
CAPE CHARLES
1
NORFOLK

Yellow-crowned Night Herons (Nyctanassa violacea) also nested in small numbers in the northern portion of the woodland and in a thicket on the eastern side of the highway (Route 13). The eastern beach area of the island supported one to three mixed Black Skimmer (Rynchops nigra) - Common Tern (Sterna hirundo) Colonies as well as nesting populations of Royal Terns (Thalasseus maximus), Laughing Gulls (Larus atricilla), Herring Gulls (Larus argentatus), Willets (Catoptrophorus semipalmatus), rail species, (Rallus sp.), and Oystercatchers (Haematopus palliadus). One pair of Canada Geese (Branta canadensis) also nested on the island along with other nesting marsh birds in 1976 and 1977.

Figure 2 shows the vegetational composition of the heron colony area and other portions of the island. The woodland understory was from 3 - 5 m. high and the top of the canopy from 10 - 15 m. high. Sassafras (Sassafrass albidium) accounted for 60-70% of the canopy with black cherry (Prunus serotina) as the other major component of the overstory. Scattered specimens of red cedar (Juniperus virginiana), as well as two specimens of Loblolly pine (Pinus taeda) have also been noted (Boulé, 1977). It was in this vegetation that approximately 66 per cent of the Black-crowned Night Herons, all the Great Egrets and scattered Yellow-crowned Night Herons nested at an average height of 10 m. Below the canopy, Black crowned Night Herons occasionally nested in American holly (Ilex opaca). Wax-myrtle (Myrica cerifera) and bayberry (M. pennsylvanica) was mostly

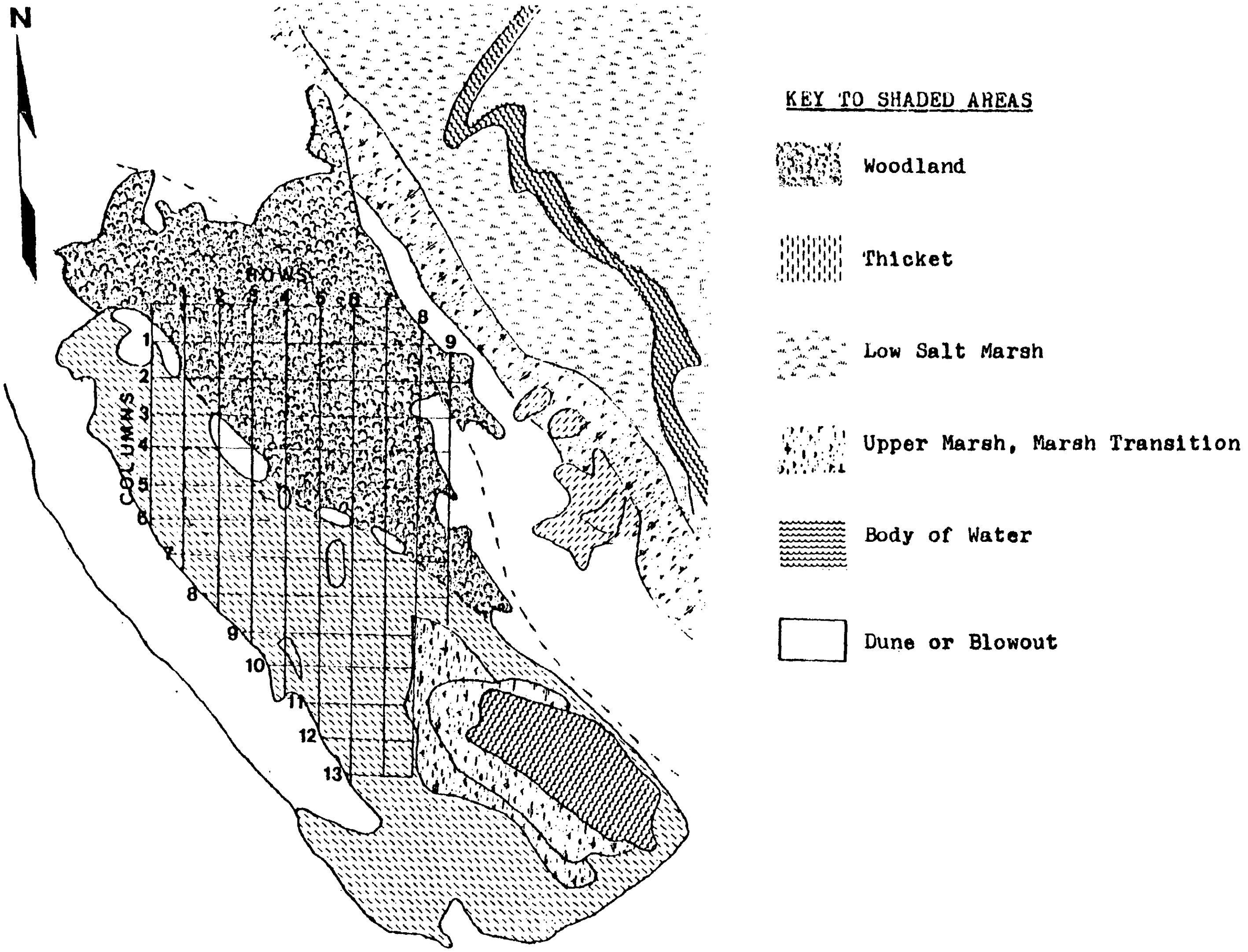
Figure 2. Vegetational Communities on Fishermans Island, Virginia from Boulé (1977), Showing Location of the Study Area. See Figure 3 for Details.


TRAPPING and SEINING AREA
HERON COLONY
RT. 13
RT. 13
MARSH COMMUNITIES
MP PIONEER MARSH
SA LOW MARSH
MH HIGH MARSH
MU UPPER MARSH
P PANNE
MT MARSH TRANSITION
DUNE COMMUNITIES
BP PIONEER BEACH
DF FOREDUNE
LD LOW DUNE
RC RIDGE CREST
DO OLD DUNE
DM DUNE MARSH
SHRUB COMMUNITIES
T THICKET
W WOODLAND
OTHER
PHRAGMITES INVASION
R RUDERAL
S SPOIL
FM FRESH MARSH

old and dying in this zone. The understory was composed of Japanese honeysuckle (*Lonicera japonica*), Virginia-creeper (*Parthenocissus quinquefolia*), poison-ivy (*Rhus radicans*), greenbriar (*Smilax spp*.) and other lianas. Snowy Egrets and more frequently Louisiana Herons, used this understory vegetation for nesting as did late nesting Black-crowned Night Herons, especially in the transitional zone between the woodland and a thin line of tall, old wax-myrtle.

The thicket area (Figure 3) has characteristic subzones, that aided in locality orientation. From within, it appeared to be a dense area, with medium sized herons and scattered Glossy Ibis nesting at an average height of 4.5 m. The most densely vegetated area had a damp ground surface remnant of the old lagoon that remains as a depression. During several very high tides, water inundated a portion of the heronry floor. There were several small blow-out grassy areas unoccupied by nesting birds. These regions are portions of the old dune ridges that remain dry with the thicket around them. The older portion of the thicket contained groundsel tree (*Baccharis halimifolia*), sumac (*Rhus coppalina*), and black cherry (*Prunus serotina*). Individual clumps of Hercules' club (*Zanthoxylum clava-herculis*) were common on the southern edge of the colony, a portion apparently never used for nesting. In partially sunny areas, lianas included, in order of abundance Japanese honeysuckle climbing hempweed (*Mikania scandens*), poison ivy, virginia creeper, and trumpet vine (*Campsis radicans*). The first of these plant species

Figure 3. Map of the Study Site Showing the Major Vegetation Types in and Near the Heron Colony at Fishermans Island. The Grid System is Explained in Text. See Figure 2 for Location.


N
ROWS
1
2
3
4
5
6
7
8
9
COLUMNS
1
2
3
4
5
6
7
8
9
10
11
12
13
KEY TO SHADED AREAS
Woodland
Thicket
Low Salt Marsh
Upper Marsh, Marsh Transition
Body of Water
Dune or Blowout

was frequently used by Louisiana Herons, sometimes as the entire nest support; any of these vines often formed a portion of any heron species' nest in areas in which they occurred.

Supplemental studies were conducted at Walker's Marsh, Accomack County, Virginia ($37^{o}54'$ Lat., $75^{o}27'$ Long.) near Chincoteague, Virginia in 1976. In 1977, this colony was inactive, and additional crossfostering data were collected at Clubhouse Point ($37^{o}35'$ Lat., $75^{o}38'$ Long.) near Wachapreague, Accomack County, Virginia (Figure 1). Colony sites at both Walker's Marsh and Clubhouse Point were smaller, 1.8 and 0.8 hectares, respectively. Heron species nested at an average height of 1 m. At Walker's Marsh, the nesting vegetation was primarily marsh elder (<u>Iva fructescens</u>). Vegetation at Clubhouse Point was slightly more heterogeneous with shrubs from 0.6 to 1.8 m. in height comprised of marsh elder and groundsel tree. Some Little Blue Herons nested at the edge of the colony in red cedar (<u>Juniperus virginiana</u>) and poison ivy vegetation taller than that in the rest of the colony. The periphery of both colonies was characterized by plant species common to marsh transition zones. Both colony sites were spoil disposal sites dating back to at least 1945 (M. Byrd, personal communication).

INFORMATION CENTER THEORY

Methods

The possibility of information exchange was investigated in this study. Movement in and out of the colony was recorded from an observation platform outside the colony in 1976. Specific time intervals were not reported because movement was continuous during some periods, but sporadic, with longer intervals of time between incoming or outgoing flights at other times. Observations were initially made for one minute's duration. However, even within one minute, several separate trips might be made by individuals. An individual was considered to be leaving or arriving with a group if that group remained intact for the duration of the observation. Period of observation was defined as the amount of time a group could be followed with the spotting scope (a distance of approximately 3 to 4 km). Observations were pooled from six days in April, before clutches had been completed.

Several days each in March, April, June, July and August of 1976 and 1977 were spent covering most of the Fishermans Island marsh system and inlets to find and to observe feeding aggregations.

Tables and Figures in this section and in succeeding sections contain abbreviations for common names of each heron species. Abbreviated species codes are consistent throughout the text. The list of common and scientific heron species' names and their abbreviations are given in Table 1.

Results

Snowy Egrets, Little Blue Herons, and to a lesser extent Louisiana Herons were noted moving into and out of the colony in mixed-species groups. Some individuals accompanied Great Egrets, so movements and feeding habitat observations collected on this larger species were included with the other four herons studied.

At low tide, Great Egrets and Snowy Egrets concentrated in the mouth of a tidal creek opening into a large inlet on the northwest side of the island (Figure 2). Edges of the entire inlet were most heavily used by Snowy Egrets. Great Egrets more frequently flew out toward the southwest and to the north or northeast. Their feeding destination was unknown. When Snowy Egrets returned with Great Egrets, it was usually from the north, so it is expected that some of the smaller species were feeding in the same unknown habitats of the north.

Platform observations summarized in Figures 4 and 5 suggested that some form of feeding information exchange may have been operative for Snowy Egrets and Great Egrets. However, several qualifications must be noted. Neither species necessarily followed nearest neighbors from the colony but often came up from opposite sides of the colony to join an

TABLE 1

COMMON NAMES, SCIENTIFIC NAMES AND ABBREVIATIONS OF HERON SPECIES REFERRED TO IN THE TEXT

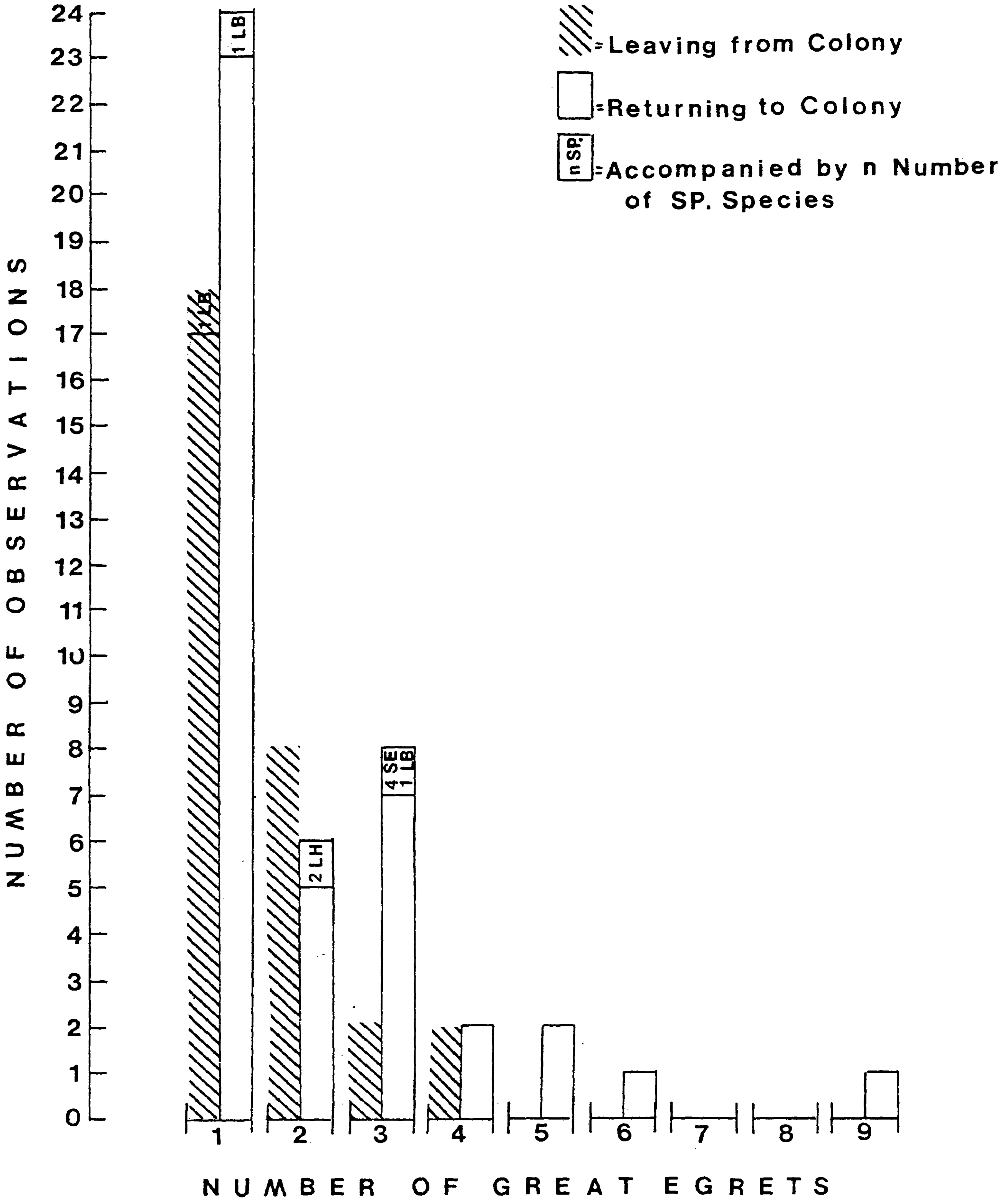
Common Name	Scientific Name	Abbreviation
Great Egret	*Casmerodius albus*	GE
Snowy Egret	*Egretta thula*	SE
Louisiana Heron	*Hydranassa tricolor*	LH
Cattle Egret	*Bulbulcus ibis*	CE

outgoing group. A group often dispersed after leaving the colony, and birds feeding in the marsh often joined groups in flight. Separate returning groups were often seen coming together before landing in the colony and then landing in separate locations within the colony. Generally, Snowy Egrets joined groups of Great Egrets, but the reverse was never observed. Snowy Egrets moved in larger intraspecific groups than Great Egrets, Louisiana Herons, or Little Blue Herons.

Little Blue Herons were observed feeding in small aggregations with Snowy Egrets and/or Louisiana Herons, or alone along marsh creek mud flats. Because Little Blue Herons had the most frequent number of interspecific flights returning to the colony (Figure 7) this species may have joined feeding flocks north of Fishermans Island, then returned with these groups. This species was never observed following nearest neighbors of any species out from the colony.

Data in Figure 6 suggests that Louisiana Herons most frequently departed and returned to the colony either alone or with 1 or 2 other Louisiana Herons. This species was observed feeding singly along marsh creek edges on the east side of Fishermans Island. Individuals frequently were observed flying low and erratically over the east side marsh system. On three occasions, I observed an individual of this species land close to another Louisiana Heron or to a Snowy Egret that was feeding or standing along a marsh creek.

Figure 4. Number of Observations of Great Egrets Leaving or Returning to the Colony Alone or in a Group.



NUMBER OF OBSERVATIONS
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
1 LB
1 LB
2 LH
4 SE
1 LB
1
2
3
4
5
6
7
8
9
NUMBER OF GREAT EGRETS
=Leaving from Colony
=Returning to Colony
n SP.
=Accompanied by n Number of SP. Species

Figure 5. Number of Snowy Egrets Observed Leaving or Returning to the Colony Alone or in a Group.

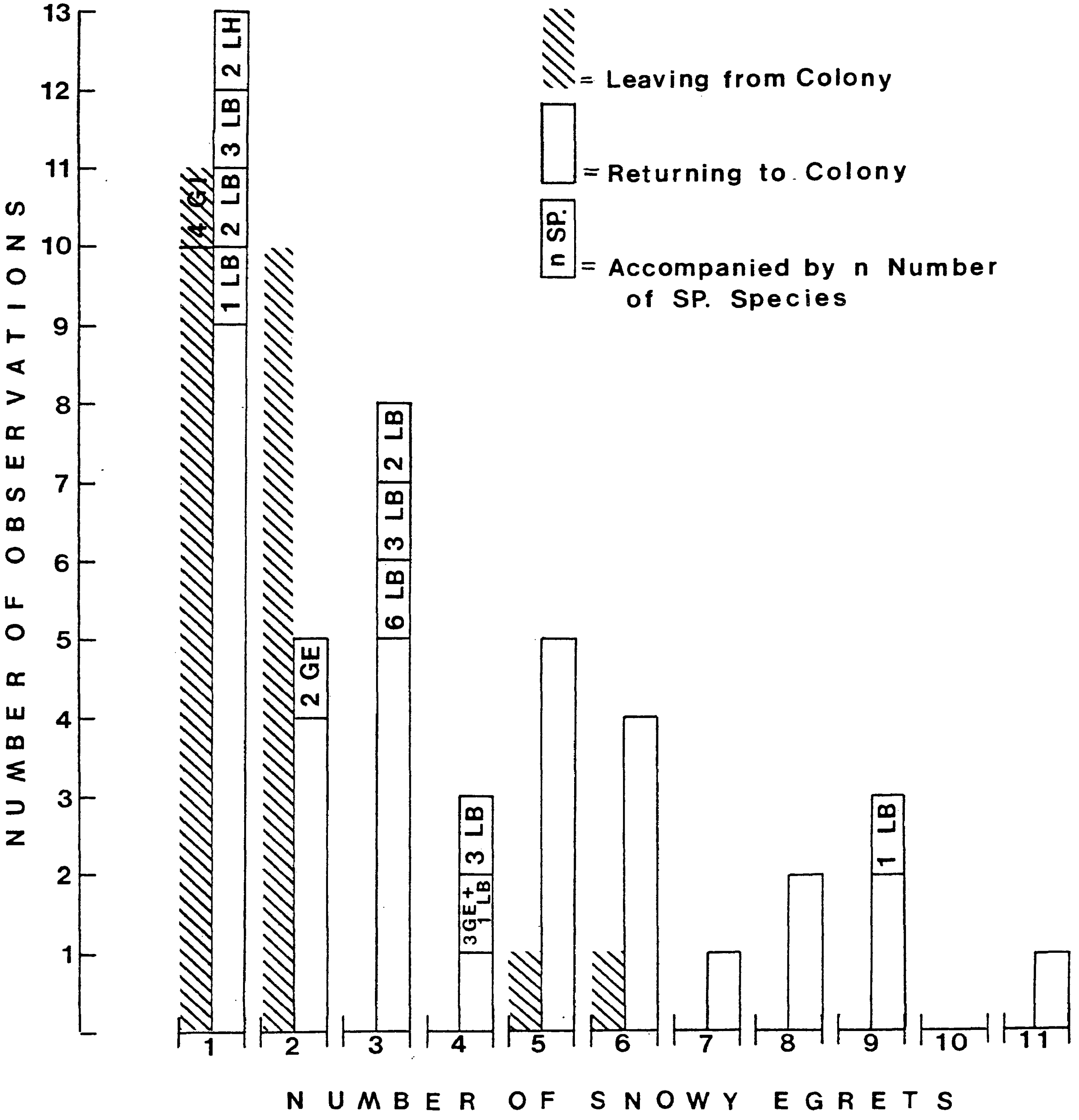

NUMBER OF OBSERVATIONS
13
12
11
10
9
8
7
6
5
4
3
2
1
NUMBER OF SNOWY EGRETS
1
2
3
4
5
6
7
8
9
10
11
= Leaving from Colony
= Returning to Colony
n SP.
= Accompanied by n Number of SP. Species
4 GE
1 LB
2 LB
3 LB
2 LH
2 GE
6 LB
3 LB
2 LB
3GE+1LB
3 LB
1 LB

Figure 6. Number of Louisiana Herons Observed Leaving or Returning to the Colony Alone or in a Group.

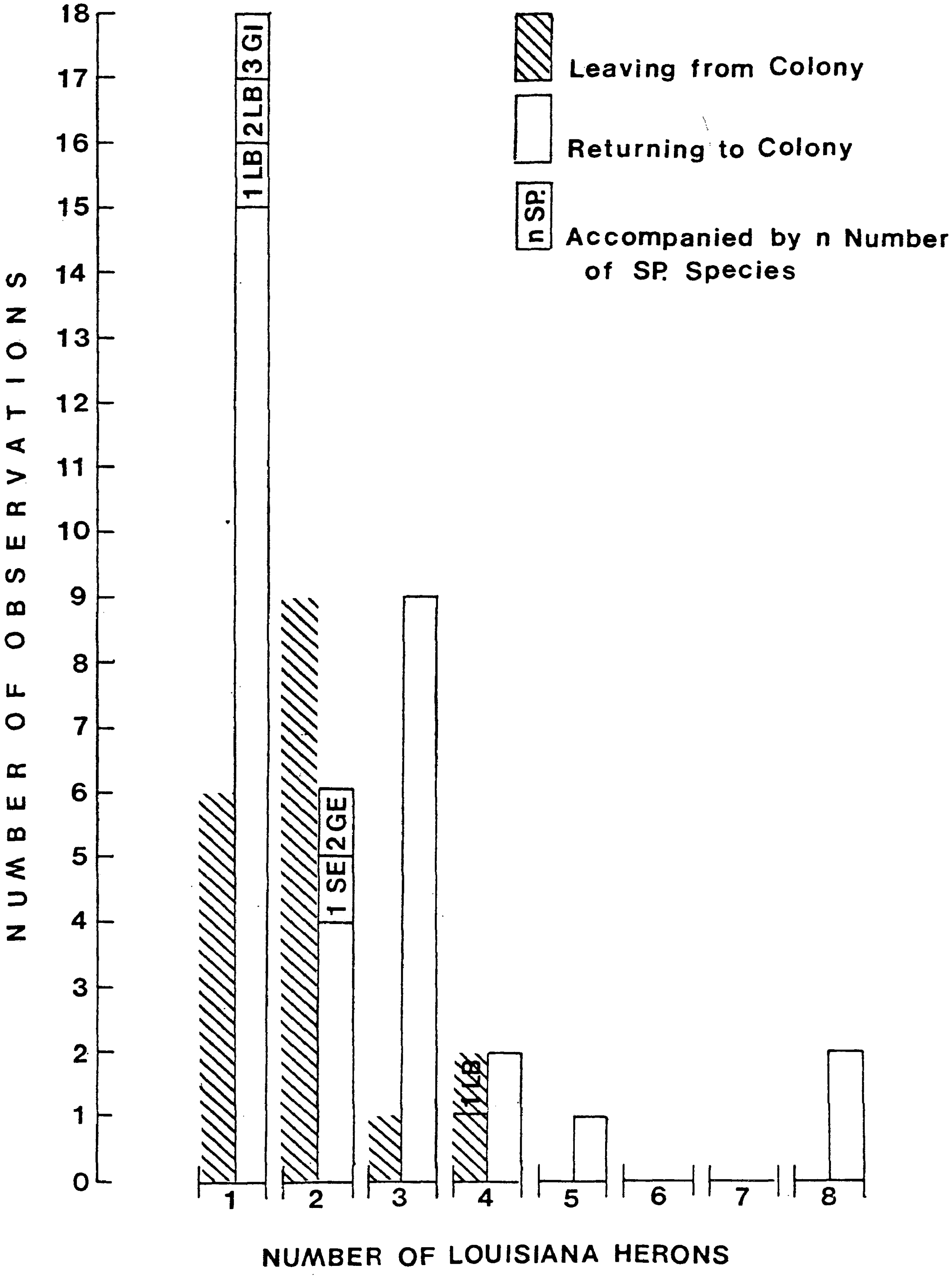
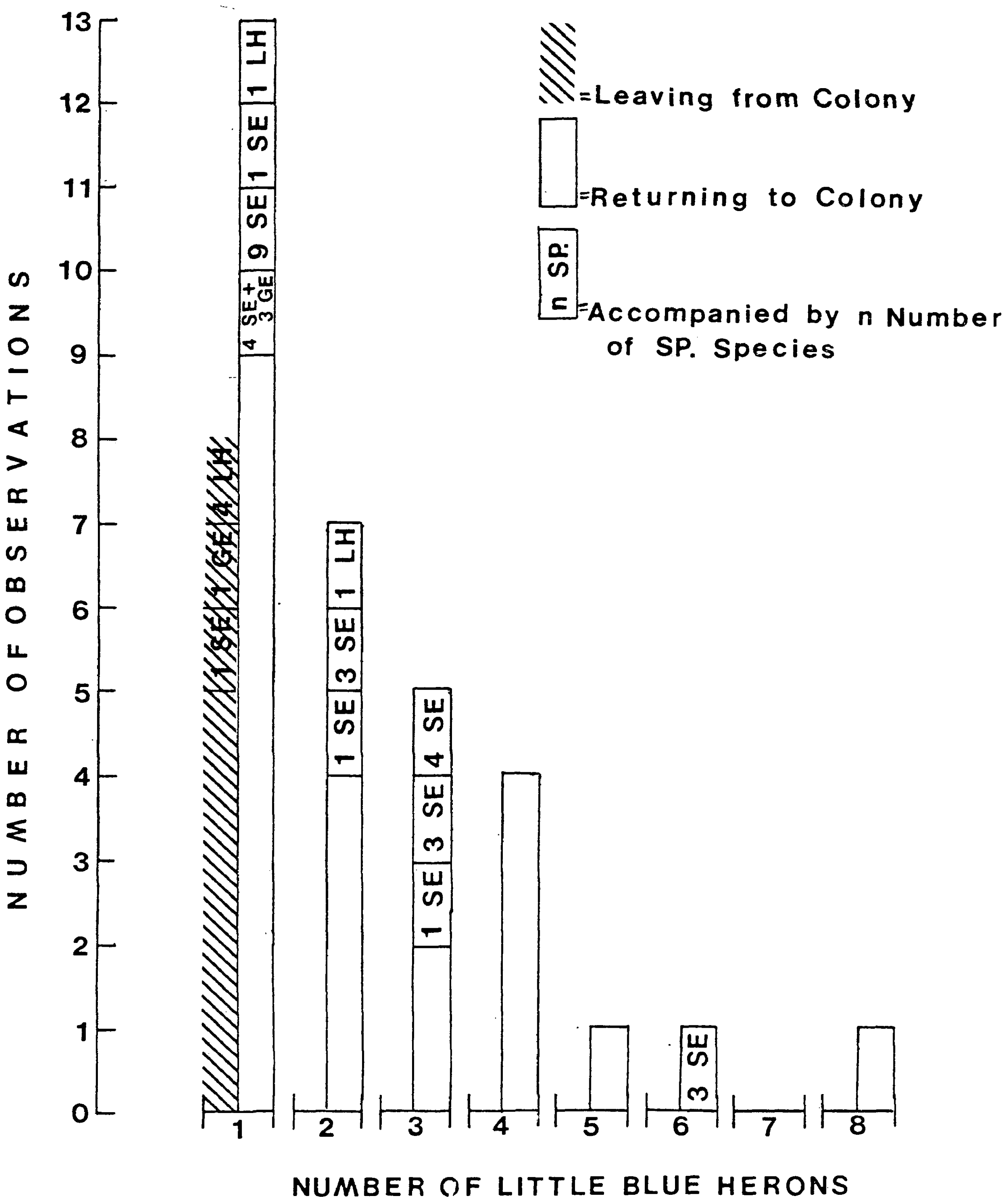

18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
NUMBER OF OBSERVATIONS
1 LB
2 LB
3 GI
1 SE
2 GE
1 LB
1
2
3
4
5
6
7
8
NUMBER OF LOUISIANA HERONS
Leaving from Colony
Returning to Colony
n SP.
Accompanied by n Number of SP. Species

Figure 7. Number of Little Blue Herons Observed Leaving or Returning to the Colony Alone or in a Group.



NUMBER OF OBSERVATIONS
0
1
2
3
4
5
6
7
8
9
10
11
12
13
NUMBER OF LITTLE BLUE HERONS
1
2
3
4
5
6
7
8
=Leaving from Colony
=Returning to Colony
n SP.
=Accompanied by n Number of SP. Species
1 SE
1 GE
4 LH
4 SE+3 GE
9 SE
1 SE
1 LH
1 SE
3 SE
1 LH
1 SE
3 SE
4 SE
3 SE

Discussion

Investigations on a variety of unrelated bird species show that coloniality can be an adaptation for exploiting food when food sources are distributed in spatially unpredictable local patches (Horn, 1968; Ward and Zahavi, 1973; Krebs, 1974). The hypothesis that the colony itself may act as an information center was tested on several colonial nesting species by these authors. Krebs (1974) and Davies (1973) enhanced this theory by showing that Great Blue Herons (Ardea herodius) and Herring Gulls (Larus argentatus), respectively, followed neighbors out from the colony to feed in the same location. Less direct evidence for neighbor following was found by Ashcroft (1976) in his study of Common Puffins (Fratercula artica). Young in neighboring nests in the colony gained weight in synchrony while young from different parts of the colony were out of phase.

Kushlan (1977) and Krebs (1977) noted that interspecific feeding information exchange may occur among several species of wading birds because of overlap in food habits or feeding sites. If such a relationship occurs, mixed species nesting would be advantageous. Ogden (1977) tested the possibility of such exchange in Snowy Egrets and Louisiana Herons nesting in the same colony. He found that the two species did not disperse in the same direction or distance as would be predicted if an unsuccessful feeder was randomly choosing the species to follow out from the colony. He did find that the two species had similar diets both in percentage and size of prey species.

White-colored waders feed together in open areas and may attract dark colored birds (Kushlan, 1977). Interspecific colonial nesting would be advantageous for dark colored birds if locally abundant food supplies were patchy. A less social species of unsuccessful feeding bird nesting in the colony would benefit by increasing its (random) chances of sighting a visible (white) feeding aggregation which happens to be finding the same choice of prey as is taken by the food-searching species.

Feeding advantage would be expected to be accrued by fledglings, which are able to increase their foraging efficiency when feeding among juveniles and adult heron species (Kushlan, 1978). Time and energy in finding food would be minimized by "parasitizing" information from other colony members (Emlen and Demong, 1975). Fledglings from Fishermans Island were most often observed following single adults, frequently attempting in-flight food begging gestures. Interspecific food beggging or following was not observed (with the exception of a crossfostered fledgling to be discussed later). However, Louisiana Heron fledglings spent a considerable amount of time finding food items in vacant nests. Post-fledgling feeding aggregations found throughout the island were interspecific and included adults of any combination of species nesting within the colony. Most frequently young and adults of Snowy Egrets, Louisiana Herons and Little Blue Herons were found feeding distinctly together, but in varying numbers and proportions.

More data collected on movements and feeding habitat of each species just before, during, and after nesting might clarify the relative importance of the colony itself as an information center, and the proportion of each nesting species that joins interspecific feeding aggregations.

Results of flight movements and feeding aggregations in this study do not show that the colony itself acts as an information center. However, observations do indicate that an individual bird's chances of finding food may be enhanced by increased probability of finding a nearby feeding aggregation and by the option of joining one of the continuous flights to and from feeding areas.

SEQUENCE OF ARRIVAL AND NESTING

Methods

To investigate the degree of intra or interspecific nesting synchrony, the colony was partitioned into a grid system before any nesting birds arrived in 1976. Individual rows and columns were spaced approximately 50 feet (15.2 m.) apart. Distances were measured with marked string, so slight deviations occurred, especially in densely vegetated areas. A compass was used in forming the north to south rows and east to west columns. Each row-column intersection was identified by a labelled piece of surveyor's tape around the nearest tree. Because visitation in the colony during egg laying and incubation caused excessive fish crow predation, nests were visited only after peak hatching.

Between May 19 and June 6, 1976, data was collected on a sample of accessible nests throughout the colony around the row-column intersections. Chick weights or egg numbers were recorded from each marked nest. After growth curves had been constructed (Intraspecific Growth) each clutch was assigned an average age based upon the weights of the first and second chick. In all but a few cases, each clutch matched one age according to the growth curve better than any other age. All data were then adjusted to one date, May 24. For example, if, on May 22 in one brood the first hatched chick's weight matched age 9 on the growth curve and the second matched 7, then the average brood age was 8, and on May 24, it would have been 10 days old. The date May 24 was selected because the largest useable sample was collected on this date and so did not require adjustment of date. Data were collected on 140 Snowy Egret nests, 82 Louisiana Heron nests, 40 Little Blue Heron nests, and 92 Black-crowned Night Heron nests.

Density of nests varied, as did species composition, density and maturity of dominant types of vegetation, throughout the sampled area. Six areas within the colony were selected as separate subzones defined by such parameters as homogeneous vegetation, heron species composition, or as naturally partitioned from other subzones by blowouts, or presence of certain vegetation patterns (Figure 8). The age data collected from sampled nests within the six subzones was used to compare mean brood age of different species in each subzone. A Kruskal-Wallis test (Sokal and Rohlf, 1969) was performed to evaluate the degree of intra and extraspecific synchrony within and among subzones.

Results

Synchronized nesting has been suggested as being advantageous to intraspecific colonial nesting species. If interspecific heronries and single species colonies are similar in function, then synchronization of nesting time should be manifested by the former group as well.

Figure 8. Map of the Heron Colony at Fishermans Island Showing Subzones by the Row, Column Grid System, with Accompanying Description of Each Subzone. See Figure 3 for Location.

R3C6: vegetated with large, dying *Myrica* interdispersed with large *Prunus*, bordered on west side by a dead stand of uprooted *Myrica*.

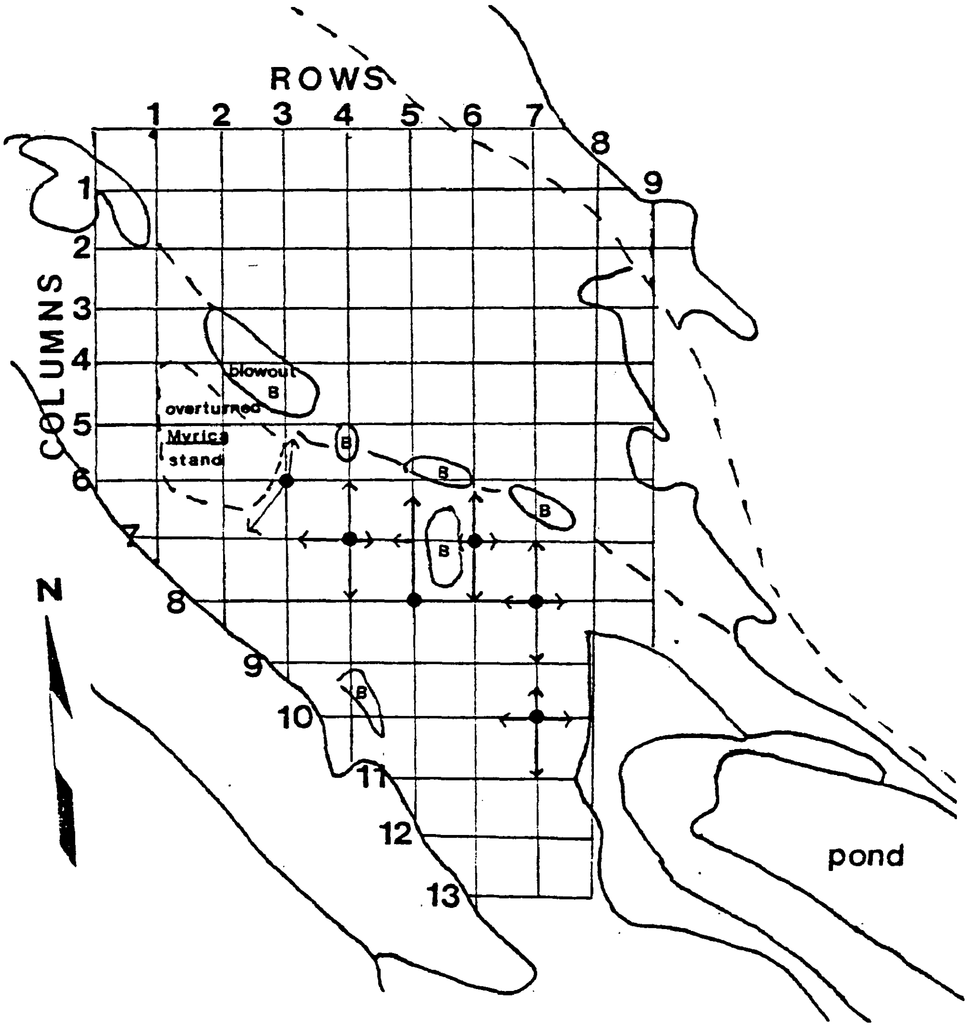
R4C6-7: discontinuous with R5C8 because of several larger sized *Myrica* with understory of vines including *Lonicera* and *Mikania*.

R5C8: stand of *Myrica* bordered on east by a blowout area.

R6C7: continuous stand of *Myrica* stopping abruptly at west side at blowout area vegetated with grasses.

R7C8: continuous stand of *Myrica* with no understory.

R7C9-11: adjacent to R7C8 with eastern portions more dense, containing smaller *Myrica* branching out low to the ground.



The degree of synchrony among species within the Fishermans Island colony was investigated in 1976. Review of data collected throughout the colony indicated that if synchrony could be demonstrated, it would be most evident in six contiguous zones which are described in Figure 8. Data presented in Figure 9 depicts distribution of mean brood ages of each species within each selected subzone listed in Table 2.

The first null hypothesis tested was that nestlings between subzones did not differ in mean brood age independent of species type. Hereafter, distribution of nestlings within a subzone is referred to as "age-location." A Kruskal-Wallis test demonstrated a significant difference between subzones (H/D - 111.73, $P < 0.005$). The possibility that differences could be explained by species type alone was tested. Average brood ages of each individual species were pooled from all subzones, and the three groups, Snowy Egrets, Louisiana Herons and Little Blue Herons, were compared again using the Kruskal-Wallis test. Results confirmed that each species differed from each other in age-location (H/D - 136.27, $P < 0.005$). Using the same test, it could be shown that intraspecifically, Snowy Egrets did not differ in age-location among five subzones ((R5C8 was omitted because of small sample size) H/D - 4.32, $P > 0.10$)). Louisiana Herons showed a significant difference at the 0.05 level (H/D - 9.64). Little Blue Herons were tested among the two subzones with adequate sample size using the Wilcoxon test (Table 3). Age-

TABLE 2

MEAN BROOD AGE, STANDARD DEVIATION AND SAMPLE SIZE OF EACH HERON SPECIES AND OF THE GROUP OF SPECIES IN EACH SUBZONE OF FISHERMANS ISLAND, 1976

Subzone[1]	Heron Species	N	Mean Brood Age	SD
R7C8	SE	16	8.41	4.236
	LH	13	7.23	3.225
	Group	29	8.43	3.970
R7C9-11	SE	15	9.27	4.423
	LH	11	4.41	2.567
	Group	26	7.23	4.434
R6C7	SE	7	12.50	4.330
	LH	11	8.04	3.446
	Group	18	9.78	4.312
R5C8	LB	8	7.5	5.581
	SE	2	9.25	3.182
	Group	10	7.85	5.088
R4C6-7	SE	16	7.94	5.822
	LH	7	5.28	3.684
	LB	11	8.09	4.206
	Group	34	7.43	4.927
R3C6	SE	8	8.00	4.590
	LH	5	9.30	3.768
	LB	2	6.00	1.414
	Group	15	8.17	3.985

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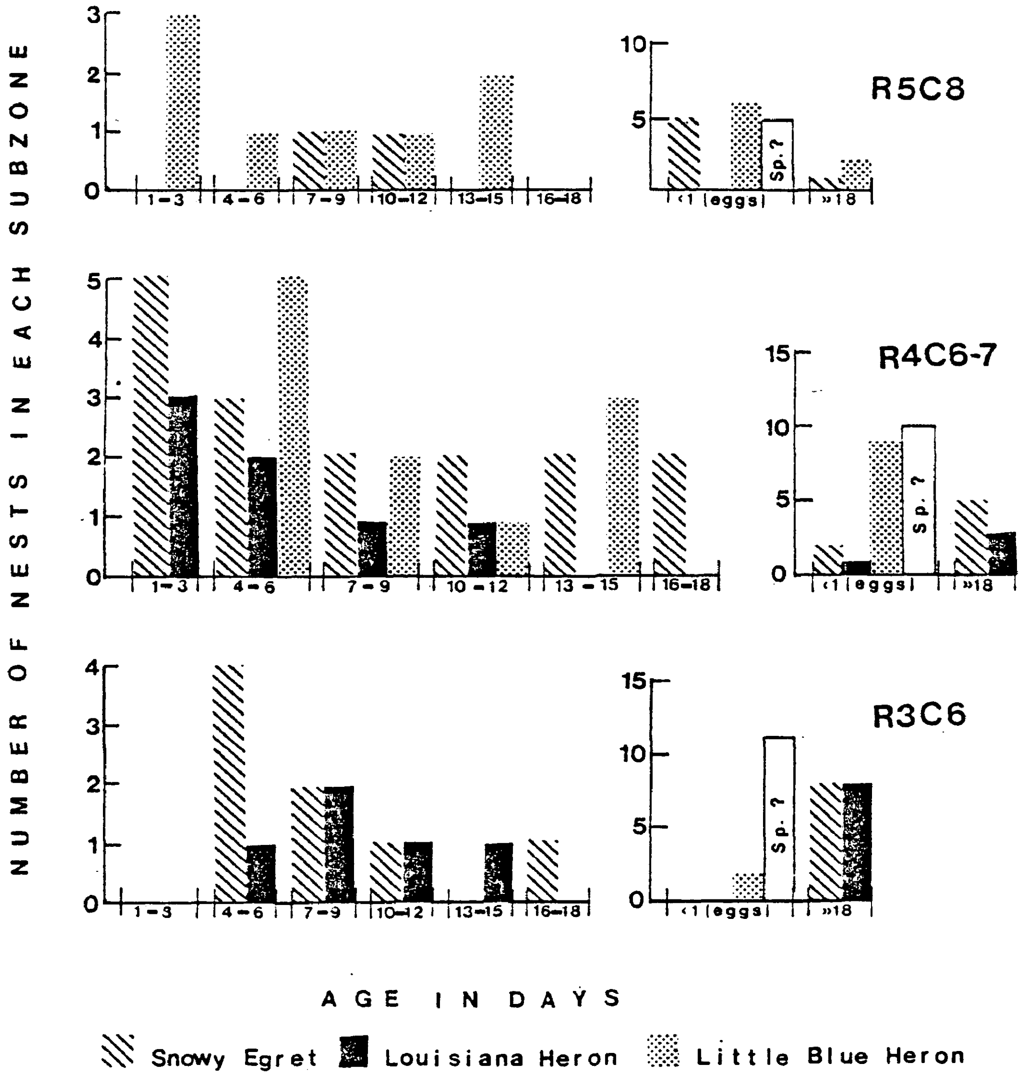
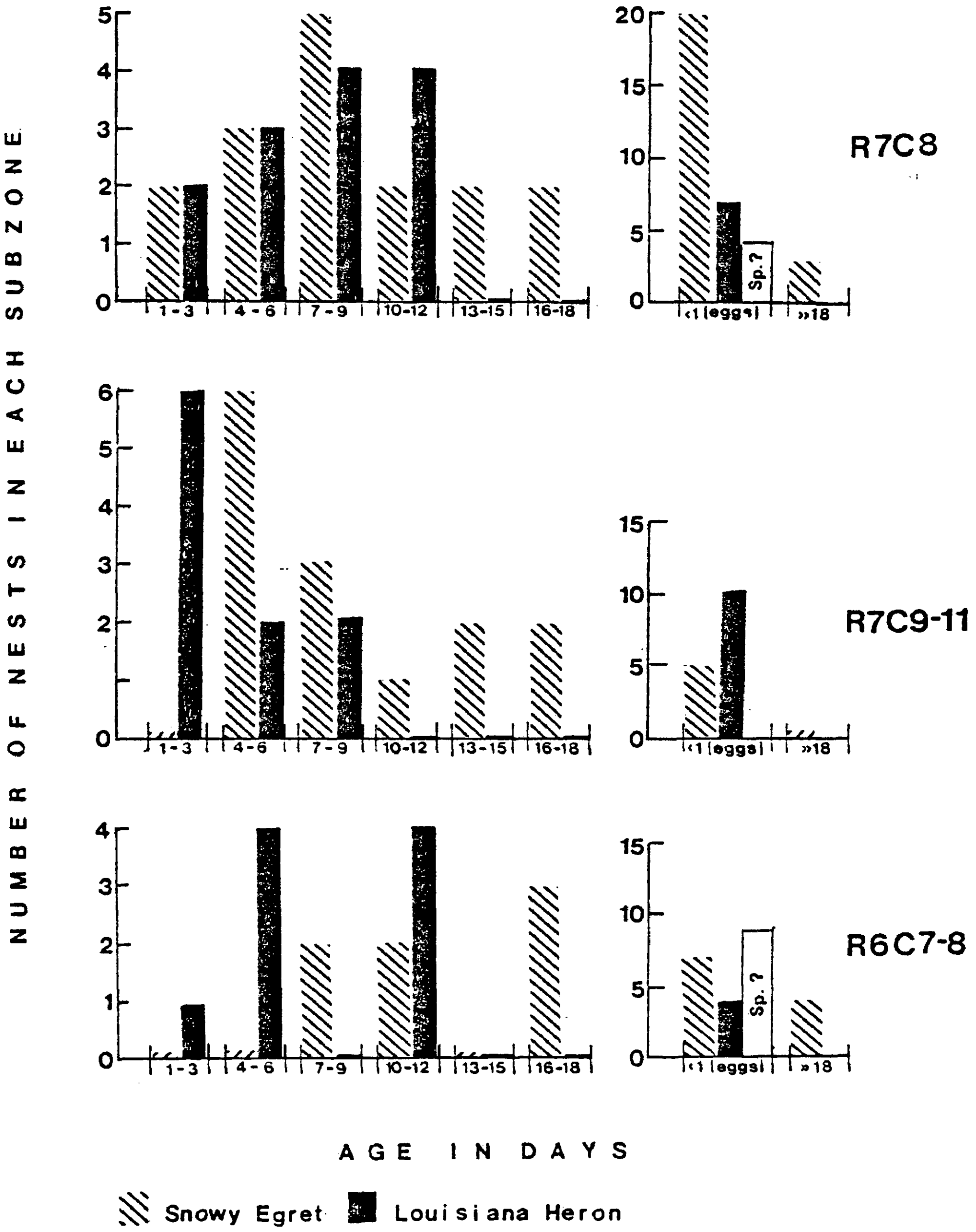
[1] See Figure 8 for location and description of subzones.

Figure 9. Distribution of Mean Brood Ages of Each Species in three Subzones at Fishermans Island, 1976.


NUMBER OF NESTS IN EACH SUBZONE
R5C8
3
2
1
0
1–3
4–6
7–9
10–12
13–15
16–18
10
5
Sp. ?
<1 (eggs)
>18
R4C6-7
5
4
3
2
1
0
1–3
4–6
7–9
10–12
13–15
16–18
15
10
5
0
Sp. ?
<1 (eggs)
>18
R3C6
4
3
2
1
0
1–3
4–6
7–9
10–12
13–15
16–18
15
10
5
0
Sp. ?
<1 (eggs)
>18
AGE IN DAYS
Snowy Egret
Louisiana Heron
Little Blue Heron


NUMBER OF NESTS IN EACH SUBZONE
R7C8
0
1
2
3
4
5
1-3
4-6
7-9
10-12
13-15
16-18
0
5
10
15
20
<1 (eggs)
>18
Sp. ?
R7C9-11
0
2
3
4
5
6
1-3
4-6
7-9
10-12
13-15
16-18
0
5
10
15
<1 (eggs)
>18
R6C7-8
0
1
2
3
4
1-3
4-6
7-9
10-12
13-15
16-18
0
5
10
15
<1 (eggs)
>18
Sp. ?
AGE IN DAYS
Snowy Egret
Louisiana Heron

location for this species did not differ among the two subzones (C = 50.5, $P > 0.10$). To test the degree of interspecific synchronization, separate tests were done comparing age-location between Snowy Egrets and Louisiana Heron broods in each of the four largest subzones. Table 3 lists results of these comparisons. There was not a significant difference in age location between species in R7CB, yet in the two subzones on either side, R7C9-11, and R6C7-8 there was a significant difference. Comparison of means in Table 2 for the two species in these subzones reflects the greater age discrepancy in the two bordering subzones. The R7C8 subzone was the first location in which the peak number of clutches of both species was first observed. In subsequent days, hatching radiated out from this area into adjacent zones. There was more of a temporal gap between the time of arrival of earlier Snowy Egrets and later Louisiana Herons at the colony than in eventual initiation of egg laying for both species. Possibly the social displays of the white-plumed Snowy Egrets stimulated Louisiana Herons into physiological readiness for nesting. As subzone R7C8 became saturated with territories, both species began occupying new areas. The increased difference in species-specific age may have been caused by the longer persistence of Louisiana Herons in competing for a nest site in the central area before selecting a nest site peripheral to this zone.

Because extreme peripheral nests within subzones were not included in the analysis, the first Little Blue Heron

TABLE 3

COMPARISON OF MEAN BROOD AGE BETWEEN SPECIES PAIRS IN EACH SUBZONE USING WILCOXON TESTS

Species compared (n broods)		Subzone	Wilcoxon Statistic C	P
SE(15)	LH(11)	R7C9-11	142.1	$p < 0.001$
SE(16)	LH(13)	R7C8	131	$p > 0.10$
LH(11)	SE(7)	R6C7-8	59	$p < 0.05$
SE(16)	LH(7)	R4C6	70.5	$p > 0.10$
SE(16)	LB(11)	R4C6-7	84.5	$p > 0.10$

clutches to hatch at the western border of R6C7 do not appear in the data. Initiation of nesting among Little Blue Herons was in the two subzones R5C8 and R4C6-7.

Movement into the eventual major nesting subzones, R4C6-7 can be seen through the increased numbers of egg nests from R5C8 to R4C6-7. Many of the egg nests listed as unknown in Figure 9, R4C6-7, eventually proved to be those of Little Blue Herons. Because this species nested slightly later, and more intraspecifically in location, social stimulation by other species during initiation of nesting seems to have been operative.

Subzone R3C6 was the location in which the first Snowy Egret and Louisiana Heron clutches hatched. Most of these nests were adjacent to Black-crowned Night Heron nests. During the time in which nests were being marked in this area, Black-crowned Night Heron clutches were generally in the second major wave of hatching throughout the colony. Nesting within this species may have stimulated nest initiation among the two smaller species, despite the fact that Black-crowned Night Herons are known predators of heron chicks (see Predation Pressure). Had the presence of night herons not been important, it is expected that initiation of the nesting in Snowy Egrets and Louisiana Herons would have occurred in R6C7-8 and R7C8 where larger concentrations eventually formed.

Discussion

Several conclusions were drawn from analysis of age distribution of young throughout the colony. The overall age distribution among species differed in age location according to subzone. Interspecific synchrony was not manifested at the colony level. A significant difference in age-location of separate species, independent of subzone, indicated that synchronous nesting might be more a species-specific phenomenon than one of subzone location. Further testing showed that Snowy Egrets and Little Blue Herons each did not differ in age-location among subzones. For these two species, intraspecific nesting was synchronous on a colony level. Louisiana Herons did differ significantly suggesting that initiation of nesting was influenced by some other factor, possibly visual stimulation from displaying Snowy Egrets. As expected from previous testing, Snowy Egret and Louisiana Heron broods were significantly different in age-location within two of the four subzones tested. The age discrepancy probably accounted for most of the former test group differences. Interspecific social stimulation was suggested in the choice of location for nest initiation by Snowy Egrets, Louisiana Herons, and Little Blue Herons.

Later-nesting Cattle Egrets also initiated nesting among still active Little Blue Heron nesting zones. Later Cattle Egret nesting concentrations were adjacent but distinctly apart from other species. The pattern of sequential nesting among the former three species was duplicated in subsequent waves of hatching in the same season. The entire nesting pattern among all species was repeated in 1977 within the same subzones. Cattle Egrets did shift in nesting location, perhaps because of noticeable vegetational damage in their nesting areas each year. (The site labelled "overturned *Myrica* stand" in Figure 8 was the area used by nesting Cattle Egrets in 1975).

The age data presented in Figure 9 and in Table 2 are based on the largest number of nests that could be treated within a reasonably short period of time among the three species that nested synchronously. By May 14, 1976, the major peak of hatching had occurred among Louisiana Herons and Snowy Egrets. Many more waves of hatching continued through June, including the major peak in hatching in Little Blue Heron clutches. Data from later dates showed increased asynchrony among the smaller numbers of clutches available to compare. Thus the analyses done on data most likely to show synchrony included less than half of the sampled population of three heron species.

The relative degree of synchrony exhibited by each species in part may have resulted from other factors. The most obvious differential factor noted in this and other colonies was time of arrival among different species. Other workers have indicated that the sequence of arrival and nesting among medium sized herons is probably more influenced by local conditions than by latitude along the coastal United States (Teal, 1955; Jenni, 1969; Simersky, 1971; Burger, 1977; Gaston and Johnson, 1977; Maxwell and Kale, 1977). Among ardeids there is a tendency to nest as high as possible and still have enough cover above the nest. Vertical stratification in a vegetationally homogeneous colony depends upon the following list in order of importance: 1. time of nesting; 2. size of nesting species; 3. the competitive ability of the species (Dusi, 1968; Jenni, 1969; Weber, 1975; Maxwell and Kale, 1977; Burger, 1977). Later birds nest higher (Jenni, 1969; Maxwell and Kale, 1977; Burger, 1977) after density declines.

At Fishermans Island, Black-crowned Night Herons and Great Egrets arrived and began nesting over two weeks before smaller sized herons. Both of these larger species did nest higher than the later arriving, smaller herons. The latest nesting Louisiana Herons did select very high nest sites near abandoned Black-crowned Night Heron nests in the cherry stand.

Further space partitioning by different species has been attributed to specific nest site variables within a colony (Custer and Osborn, 1977; McCrimmon, 1975; Burger, 1978). Warren (1977) studied two vegetationally similar colonies with different numbers and types of species. Significant differences between nest site components for Snowy Egrets and Louisiana Herons were not the same in both colonies. I have noted different species occupying the same marked nest later in the same season, or in different seasons. Thus, if the first two dependent factors vary, and if preferred nest site components change from one colony to the next, competitive ability might influence species-specific nest site distribution.

Burger (1977) made an extensive study of extra and intrapspecific behavioral interactions before and during nesting. The sequence of arrival and species composition in this New Jersey heronry was similar to that at Fishermans Island, and greater synchrony was noted within subareas than throughout the colony. Burger's study examined comparative aggressiveness of several species that initiated egg laying within three days of each other in one area. Conspecific encounters comprised 50% of the encounters of Little Blue Herons, 40% of Louisiana Herons, and 38% of Snowy Egret aggressive encounters. These percentages alone do not reflect any species-specific behavioral differences. More conspecific encounters among Little Blue Herons would be expected as individuals of their species. Herons more frequently nest nearer to each other than to other species. Had proportions of extra to intrapsecific nearest neighbors been correlated with percentage of conspecific encounters, relative species specific aggressiveness could have better been evaluated. Burger's analysis showed an inverse relationship between aggressiveness while nesting and the percentage of wins during encounters. Snowy Egrets were most aggressive and least successful at winning extra specific encounters, followed by Louisiana Herons, with Little Blue Herons being least aggressive and most successful at winning encounters.

Comparison with a colony in which Louisiana Herons initiate nesting slightly before Snowy Egrets might elucidate the relationship between time of nestling and competitive ability to defend nest site. A most instructive observation in Burger's work was that there was an overall decline in aggression during incubation. Aggression increased after hatching, except for Snowy Egrets which were less aggressive than previously.

At Fishermans Island, increased packing of nests within any subzone occurred during the incubation period of the first group of nesting birds. A portion of those nests in Figure 9 and 10 listed as egg nests hatched before those nests that held one to three day old chick broods reached twenty-one days. Although Snowy Egrets and Little Blue Herons tended to concentrate in the center of a subzone, there was dispersed distribution of ages throughout the one-to-eighteen-day range for all three species. Mean ages and standard deviations listed in Table 8 reinforced the observed distribution. It would be expected that if Snowy Egrets were more aggressive while Louisiana Herons were more successful at winning encounters, the only way Snowy Egrets could continue to secure nesting sites in the presence of Louisiana Herons on territories would be the availability of sites outside the chasing distance of either species. As space became limited, newcomers would spread into newer areas. Later nesting within the originally packed subzones would perhaps be possible as soon as clutches had been laid, and nesters became less aggressive.

A decrease in agonistic behavior may be a significant factor influencing nesting at Fishermans Island. If aggression does influence nest site selection, the presence of such behavior, and its decline after initiation of incubation may explain the original dispersal of nests in contrast to eventual increased packing of nest sites within subzones later in the nesting season. Among the smaller heron species in this study, nest site selection appears more associated with existent nesting than with any species specific nest site characteristic.

These behaviors may have conferred advantages on nesting herons in several ways. If a bird was trying to find a safe place to nest, the presence of other surviving nests was an indication of immunity from predation (Krebs, 1977). Social stimulation has been documented among intraspecific breeding birds. (Lehrman (1961) showed the interaction between social stimulation and endocrine function in the Ringed Dove (*Streptopelia risoria*), and Southern (1974) demonstrated that wing flagging behavior among wild colonial nesting Ring-billed Gulls (*Larus delawarensis*) was a synchronizing mechanism.) If visual and/or vocal behavior of one species is general enough to be recognized by another species, increased nesting synchrony would be expected among species nesting close to one another. For example, dark colored waders are attracted to white colored wading bird feeding aggregations (Kushlan, 1977; personal observation). It is reasonable to speculate that dark colored wading birds are attracted, and possibly stimulated into nesting readiness by courtship behavior especially among white plumed, Snowy and Great Egrets.

Less experienced and later arriving birds may be stimulated into a physiological state of readiness to nest by those members of a colony that are displaying nesting behavior. It is speculated that selecting a nest site among already nesting, brooding, birds may be less energy demanding than competing for space among other members of the same species in the same behavioral, aggressive, stage associated with establishment of territory.

After eggs are laid, it may be disadvantageous to spend time chasing neighbors, leaving eggs susceptible to fish crow predation. In a subzone with asynchronous hatching, smaller young might gain increased safety in that older nestlings are aggressive toward intruders. As age increased, nestling response toward the author changed from food begging to freezing. At still later stages, nestlings showed varied responses such as neck lunging, pecking, and fleeing. Two older Louisiana Heron chicks were observed effectively chasing adult Cattle Egrets from perches near the respective nests. This behavior appeared to be selective since Cattle Egret adults nest in both unoccupied nests of other species. (Burger, 1977) and occupied nests of Little Blue Herons (Dusi and Dusi, 1970; McKitrick, 1975; Werkschkul, 1977). McKitrick cited several instances in which juvenile Little Blue Herons retaliated against occupancy of their nest by Cattle Egrets. Extraspecific or intraspecific aggression between nestlings could be of selective advantage. Smaller neighbors might be discouraged from wanderings. The resulting tenacity to nest site could increase the probability of obtaining food from the appropriate parent, especially if parents recognize nest site rather than specific offspring.

Gochfeld (1977) studied the concept of synchrony in relation to very large nesting colonies. He noted several studies in which synchrony of egg laying was not apparent. His study of nesting skimmers showed that a higher degree of synchrony occurred on the level of subcolonies. At Fishermans Island, Snowy Egrets, Louisiana Herons, early nesting Little Blue Herons, and a continuum of later arrivals (or less successful birds) nested over a continuous period. Thus, over a period of weeks these species could be considered to be nesting synchronously. However, equal emphasis could be placed on the degree of asynchrony when measured in terms of one to three days. From the perspective of an individual nester, one to three days difference in reproductive stage could mean the difference between availability or unavailability of nesting space within a subzone. The relative decline in movement and vocalizing once nesting had begun at Fishermans Island indicated that competitition and aggression waned rapidly. Growth of chicks was also rapid, particularly from date of hatching to the date at which young began moving into branches to receive food (less than two weeks). Within three weeks, the nest territory declined in importance and newcomers could establish themselves between earlier nesting birds. Short term asynchronous nesting of the colony as a whole, and within subzones possible, allowed a larger population of nesting individuals to benefit from longer term synchronous colonial nesting. Social facilitation in nesting was proposed as the active mechanism producing overall synchronization although time of arrival, aggressive behavior, nest site selection, and size of species caused asynchrony within a shorter time frame.

PREDATION PRESSURE

Results

Mixed species colonial nesting has been considered to be an adaptation to reduce predation pressure. Observed predation pressure, and its possible effect upon nest clustering, was examined at the Fishermans Island heronry. Predation pressure was indicated by a denser packing of nests than would be necessitated by availability of nesting sites in the colony.

The population of the predominant predator, Fish Crows (Corvus ossifragus), increased from 1976 to 1977. Crows roosted in groups of up to 100 birds at the highest count (May 31, 1977) near the colony. Food remains below crow roosts consisted exclusively of eggs. Although the author has no evidence that fish crows do not eat chicks, most observed cases of nest robbing by crows were during the incubation period. There was a decrease in the numbers of roosing crows and no noted crow raids occurred later in the season. Further indirect indication that crows predated primarily on eggs was that edible-sized chicks lost from marked nests were most frequently left to decompose or were partially consumed by Catbirds (Dumatella carolinensis). Thus, the fates of most dead or missing chicks of this size class were known. Most unexplained disappearances occurred among chicks of wandering size rather than among small, sedentary nestlings.

If eggs were the primary prey source for Fish Crows, availability would be limited to the incubation period. Any one subzone of the Fisherman Island colony contained variously aged chicks and eggs at any given time. Any egg nest might be more obscured if a great deal of movement occurred around it. This would be a modified "confusion effect" (Neill and Cullen, 1974) in which the aerial predator Fish Crow would be distracted enough by varied movements depending on the ages of chicks and not be able to focus upon egg nests.

The problem of predator or intruder defense may also be alleviated by nestling aggression, which increases with age. Older chicks were observed defending their nest when other young or adults came near. Chicks neck-lunged and pecked at me, and I noted one young Louisiana Heron peck and chase an adult Cattle Egret from a nearby branch.

The only other known predator at Fishermans Island was the Black-crowned Night Heron (Teal, 1963; Peck, personal communication). Earliest nesting Snowy Egrets and Louisiana Herons selected nest sites among night heron nesting areas rather than in the larger, unoccupied habitat later used for nesting. Apparently, the presence of other nesting birds more strongly influenced nest site selection than did the possibility of heightened predation.

All nesting heron species responded to some disturbances. At the onset of my work within the colony in 1976, my entrance evoked massive departures from active nesting and extensive circling flights by all species. Within two weeks, daily visitations elicited less of a response. Adult birds only in my vicinity left their nests and perched in higher branches. Parents began exchanging calls with chicks being handled. Up to eight adult Little Blue Herons gathered above and circled me, vocalizing with increased intensity on several occasions. Snowy Egret parents most often vocalized individually, occasionally head lunging toward me; on one occasion an adult Snowy Egret attempted to peck my face. Louisiana Heron adults also remained perched within sight of the nest eliciting low "ut-ut" calls, which I interpreted to be agonistic warning vocalizations. When walking around the periphery of the colony, I often startled nearby deer. Their fleeing into the colony area never caused a single alarm cell or flight response by any nesting heron species. One would think that rapid motion by an audible, large animal would cause at least as much alarm response as a "stealthy" person. The crackling and swishing sounds by displaced vegetation caused no response. Talking and other human vocalizations were also accepted at later dates. However, my breaking branches in this and other colonies always caused high intensity alarm evidenced by flights and vocalizations. Ironically, the characteristically aggressive Cattle Egret was the only species which did not become accustomed to my presence. Presumed parents of nestlings being handled were never within view. In 1977, the majority of these birds nested in the only portion of the colony in which <u>Myrica</u> trees were too tall and too devoid of lower branches to get access to nests.

Discussion

Cullen (1960) proposed that clustering in space reduces the chances of a predator finding food. Synchronized nesting is clustering in time. If the total number of predators is limited by the amount of food present throughout the year, then a peak in food during a short time period should not increase the predator population (Kruuk, 1964). At Fishermans Island, the increased population of Fish Crows of 1977 had discovered a potential food source. However, this predator population declined later in the nesting season. Therefore, it would appear that after a food source is discovered, the degree of predation accomplished by Fish Crows may be minimized by the small period in which eggs are available and by the accessibility of that limited supply. Once the stimulus of moving food begging chicks is present, parent birds may be less prone to leave the site unless threatened themselves, as by larger ground predators. Observed chick aggression may also reduce overall predation by Fish Crows and by other intruders.

No colonial nesting species yet studied maximizes by achieving the degree of synchrony or density that is potentially possible. Intraspecific aggression and predation have been found to be operative among colonial nesting gulls. Hunt and Hunt (1976) noted intrapsecific predation among Glaucous Gulls (<u>Larus glaucescens</u>). Patterson (1965) demonstrated that the upper limit in clustering of the Black-headed Gull (<u>Larus</u>

ridibundus) was determined by predation by neighbors despite the fact birds nested closer than the average aggression distance they defended. This was caused by "househunters" who persisted in trying to land in a densely populated nesting area. This behavior is analagous to earliest nesting Snowy Egrets and Louisiana Herons nesting among Black-crowned Night Herons. The upper limit in clustering must have been reached, because the majority of smaller herons nesting slightly later established nest sites in areas unoccupied by Black-crowned Night Herons. It is possible that only those individuals that have experienced active aggression or predation avoid this larger species.

Communal mobbing is a response to predation. This behavior has been demonstrated to be advantageous to center oriented, colonial nesting species (see Krebs, 1977, for review). This may be a more specialized behavior among intraspecific nesters which have an entire behavioral repertoire in common. Mobbing response has not been documented in herons and was not evident at Fishermans Island except in the small number of Little Blue Herons that mobbed me. Mobbing response could be more confusing than advantageous to an interspecific nesting group. Lower levels of aggression among some ardeids may permit selection of nest sites among a wider range of nesting associates including Brown Pelicans (Pelicanus occidentalis), Cormorants (Phalacrocorax sp.), and potential predators such as Herring Gulls and Black-crowned Night Herons.

It must be that chances are better of a bird surviving among the group despite the presence of certain types of predators.

Although predation pressure was evidenced in clustering of nests in space and time, the four heron species studied at the Fishermans Island colony did not demonstrate any defensive behavior or avoidance of actual predators. (Perhaps only adults that actually lose a clutch to a predator then avoid that intruder.) These herons did flee from disturbance, but habituation altered the type and intensity of response elicited. The fact that two species became relatively more aggressive toward me implied that this behavior exists but is perhaps only elicited to a known passive intruder. Reduction of predation could best be explained in this colony to be a result of nesting colonially.

FOOD HABITS

Methods

Food items emitted by chicks were collected whenever possible. Collection was limited because the largest percentage of samples were issued from young birds old enough to climb into branches. Thus, it was often difficult to identify from which species the sample had come.

In 1976, each fish sample from boluses was measured and identified. Aquatic invertebrates, amphibians, reptiles, and mammals were identified and included in the percentage of total number of food items. Many of the Cattle Egret samples were too mutilated to identify individual prey items. Only those samples in which all items were identified were used in the food sample analysis. In 1977, food samples were recorded in the field. Overlap in food selection was compared using Horn's (1966) overlap equation, $C = \Sigma X_i Y_i / X_i^2 = Y_i^2$ where X_i and Y_i are proportions of prey species i consumed by species x and y in the same year, or for one species in x and y years.

Results

Analysis of food samples from four heron species show that the most common food items taken by Louisiana Herons, Little Blue Herons and Snowy Egrets were essentially the same in both years. Tables 4 and 6 show that Fundulus heteroclitis was the most frequently occurring food item comprising the greatest percent of total diet followed by grass shrimp (Palaemonetes vulgaris), for all three heron species. Striped killfish (Fundulus majalis), a larger sized food item, occurred in many more Louisiana Heron samples than in the other species (Table 4). Spot (Leistomus xanthurus) were taken by all species but occurred most frequently in Snowy Egret samples. Naked gobies (Gobiosoma bosci) were found in only one Snowy Egret sample and occurred more frequently in Little Blue Heron samples. American eel (Anguilla rostrata) also occurred infrequently among the same heron species. Atlantic silversides (Menidia menidia) occurred only among Louisiana and Little Blue Heron samples, again representing a small percentage of the total fish items. Sheepshead minnow (Cyprinodon variegatus) and flounder (Eutropis sp.) were only found in Little Blue Heron samples. This latter heron species showed a more varied diet than the other two herons in 1976 (Table 4).

Table 5 lists by sample the number and type of food items consumed by ten Cattle Egret chicks in 1976. More samples were collected, but analysis could not be made as the items were too mutilated. These samples and many observed in the colony indicated that caterpillars, adult blowflies, and maggots were major sources of food for the young. In these samples, larger prey items did not occur. In 1976, there was a slight overlap in type of prey taken by Cattle Egrets and Little Blue Herons. Both species obtained Bufo woodhousei, spiders, crickets, and Rana catsbieana in more than one sample.

TABLE 4

FOOD OF CHICKS OF THREE HERON SPECIES AT FISHERMANS ISLAND, 1976

Food Item	Snowy Egret (16) N Items (%)	 % Occurrence	Louisiana Heron (10) N Items (%)	 % Occurence	Little Blue Heron (31) N Items (%)	 % Occurrence
Fundulus heteroclitus (Mummichog)	79 (31.0)	75.0	51 (51.5)	90.0	388 (43.2)	80.6
Palamonetes vulgaris (Grass shrimp)	70 (27.4)	56.0	25 (25.2)	20.0	365 (40.6)	51.6
Emerita talpoida (Mole crab)	46 (18.0)	31.2	0 ----	----	0 ----	----
Leistomus xanthurus (Spot)	38 (14.9)	31.0	1 (1.0)	10.0	1 (0.1)	0.03
Menidia menidia (Atlantic silverside)	11 (4.3)	18.8	0 ----	----	16 (1.8)	6.4
Fundulus majalis (Striped killifish	9 (3.5)	18.8	16 (16.2)	50.0	17 (1.9)	9.7
Callinectes sapidus (Blue crab)	2 (0.8)	12.5	0 ----	----	3 (0.3)	9.7
Gobiosoma bosci (Naked goby)	0 ----	----	3 (3.0)	10.0	18 (2.0)	22.6
Alpheus heterochaelis (Pistol shrimp)	0 ----	----	2 (2.0)	10.0	2 (0.2)	6.4
Cyprinodon variegatus (Sheepshead minnow)	0 ----	----	0 ----	----	26 (2.9)	12.9
Anguilla rostrata (American eel)	0 ----	----	1 (1.0)	10.0	17 (1.9)	6.4
Uca pugnax (Marsh fiddler crab)	0 ----	----	0 ----	----	15 (1.7)	25.8
Belostomatidae (Giant water bug)	0 ----	----	0 ----	----	13 (1.4)	6.4
Bufo woodhousei (Woodhouse's toad)	0 ----	----	0 ----	----	5 (0.6)	3.2
Gryllidae (Crickets)	0 ----	----	0 ----	----	5 (0.6)	3.2
Polycharis sp. (Hermit crab)	0 ----	----	0 ----	----	4 (0.4)	12.9
Arachnida (Spiders)	0 ----	----	0 ----	----	4 (0.4)	6.4
Rana catesbeiana (Bullfrog)	0 ----	----	0 ----	----	4 (0.4)	6.4
Eutropis sp. (Flounder)	0 ----	----	0 ----	----	2 (0.2)	3.2
Lepidoptera (Moth)	0 ----	----	0 ----	----	1 (0.1)	0.03
Acris crepitans	0 ----	----	0 ----	----	1 (0.1)	0.03

TABLE 5

FOOD OF CATTLE EGRET CHICKS AT FISHERMANS ISLAND, 1976

Food Item	Chick Sample 1	2	3	4	5	6	7	8	9	10	N Items ()	% Occurrence
Acrididae (Grasshoppers)	30	--	24	--	13	5	10	--	--	--	82 (16.4)	50
Gryllidae (Crickets)	8	--	4	--	8	9	9	--	--	--	38 (7.6)	50
Lepidoptera (Caterpillar)	58	--	--	6	97	--	3	--	--	--	164 (32.9)	40
Rana catesbeiana (Bullfrog)	--	--	1	--	2	3	--	--	--	--	6 (1.2)	30
Bufo woodhousei (Woodhouse's toad)	1	1	--	1	--	--	1	1	--	--	5 (1.0)	50
Callaphoridae (Blowflies)	--	9	--	--	--	--	--	--	--	77	86 (17.2)	20
Muscoid dipterans (Maggots)	--	86	--	--	--	--	1	--	--	--	87 (17.4)	20
Popillia japonica (Japanese beetle)	--	--	--	--	2	--	--	--	--	--	2 (0.4)	10
Carribidae (Ground beetles)	--	--	--	1	2	--	--	--	--	2	5 (1.0)	30
Zygoptera (Damsel fly)	--	--	--	--	1	--	--	--	--	--	1 (0.2)	10
Lepidoptera (Moth)	--	--	--	--	1	--	--	--	--	--	1 (0.4)	10
Curculionidae (Weevil)	--	--	--	--	--	--	--	1	--	--	1 (0.4)	10
Microtis sp. (Vole)	--	--	--	--	--	--	--	--	--	1	1 (0.4)	10
Arachnida (Spider)	--	--	--	--	--	--	--	--	4	--	4 (0.8)	10
Palamonetes vulgaris (Grass shrimp)	--	--	--	--	--	--	--	--	2	--	2 (0.4)	10
Fundulus heteroclitus (Mummichog)	--	--	--	--	--	--	--	--	14	--	14 (2.8)	10

TABLE 6

FOOD OF CHICKS OF THREE HERON SPECIES AT FISHERMANS ISLAND, 1977

Food Item	Snowy Egret (17)[1]		Louisiana Heron (12)		Little Blue Heron (19)	
	N Items (%)	% Occurrence	N Items (%)	% Occurrence	N Items (%)	% Occurrence
Fundulus heteroclitus (Mummichog)	32 (17.5)	16.4	7 (3.8)	50.0	16 (12.1)	57.9
F. heteroclitus <1 cm[2] (Mummichog)	45 (24.6)	17.6	75 (41.0)	41.7	45 (30.2)	15.8
Leistomus xanthurus (Spot)	72 (39.3)	52.9	45 (24.6)	58.3	1 (0.7)	5.3
Palamonetes vulgaris (Grass shrimp)	18 (9.8)	35.2	48 (26.2)	50.0	65 (43.6)	47.4
Menidia menidia (Atlantic silverside)	0 ----	----	3 (1.6)	8.3	0 ----	----
Uca pugnax (Marsh fiddler crab)	6 (3.3)	5.9	0 ----	----	8 (5.4)	15.8
Callinectes sapidus (Blue crab)	4 (2.2)	17.6	1 (0.9)	8.3	7 (4.7)	15.8
Eutropis sp. (Flounder)	1 (0.5)	5.9	0 ----	----	2 (1.3)	10.5
Emerita talpoida (Mole crab)	5 (2.7)	5.9	0 ----	----	0 ----	----
Anchoa sp. (Anchovy)	0 ----	----	4 (3.5)	8.3	0 ----	----
Rana catesbeiana (Bullfrog)	0 ----	----	0 ----	----	2 (3.2)	10.5
Lizard tail	0 ----	----	0 ----	----	1 (0.7)	5.3

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[1] (N) Number of samples analyzed.

[2] Number given is based on an average of 15 tiny *F. heteroclitus* per sample.

These prey items, however, represented only a small proportion of the Little Blue Heron diet. Table 6 presents the total number of each prey species and the frequency of occurrence in the total number of samples analyzed among each chick species in 1977. Comparison of Tables 4 and 6 indicates that types and proportions of major prey items were quite similar in the two years. Samples were analyzed about two weeks earlier in the nesting season and over a shorter time period in 1977. This temporal difference and weather conditions could have caused the slight differences in diversity and proportions of prey items between the two years. Differences probably reflected local changes in prey abundance and availability. For example, 1977 samples included a distinctive class of small _F. heteroclitus_ not observed in 1976 samples. All three species emitted a food sample composed exclusively of these tiny fish at least once.

Both _L. xanthurus_ numbers and frequency of occurrence were greater in 1977 samples from Snowy Egret and Louisiana Heron chicks. Numbers of _M. menidia_ and _F. majalis_ were much lower in 1977 samples. Food samples of Little Blue Heron chicks contained a smaller diversity of prey items in 1977. However, _F. heteroclitus_ and _P. vulgaris_ accounted for the highest proportion of food items found in both years. Data were not collected from Cattle Egret chicks in the 1977 nesting season.

Measurement of overlap (Horn, 1966) in the proportion and type of prey items was compared for pairs of species.

Individual species were also compared for overlap in food diet among the two years. Results in Table 7 show there was a very high degree of overlap in the diets of Snowy Egrets, Louisiana Herons and Little Blue Herons in both years. Due to small sample size, overlap values, "C," between 0.80 and 0.92 were not considered indicative of notable dietary differences, other than those shown in Tables 4 and 6. The lower overlap value bewteen Little Blue Herons and Snowy Egrets in 1977 was due to a much higher proportion of P. vulgaris and a much lower proportion of L. xanthurus taken by Little Blue Herons than Snowy Egrets. Overlap in diet between Cattle Egrets and the aforementioned species was very low. Species-specific comparisons among years suggested that Little Blue Herons were more consistent in the types of prey species taken and that Snowy Egrets varied more in prey selection according to local availability of food items.

Discussion

Jenni (1969) found that Snowy Egrets, Louisiana Herons, Little Blue Herons and Cattle Egrets took different proportions of various classes of prey and differed in degree of diversification within each class of food. He noted that the four small herons were feeding in different feeding areas and proposed that habitat selection and differences in feeding behavior reduced competition for food. Willard (1977) noted that Louisiana Herons took fish of similar but somewhat larger size than the identically sized fish taken by Snowy Egrets and Little Blue Herons. He did not note much habitat segregation

TABLE 7

FOOD OVERLAP VALUES AMONG HERON CHICKS OF DIFFERENT SPECIES AT FISHERMANS ISLAND, 1976 AND 1977

Different species compared in same year	1976 overlap value[1]	1977 overlap value	Single species compared in two different years 1976 and 1977	1976, 1977 overlap value
SE, LH	.887	.826	SE	.771
SE, LB	.847	.514	LH	.871
LH, LB	.928	.814	LB	.990
CE, SE	.046	-		
CE, LH	.056			
CE, LB	.054			

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[1] Overlap value = $C = 2\ (\sum X_i Y_i)/\sum X_i^2 + \sum Y_i^2)$, where X_i and Y_i are the proportion of prey species i consumed by heron species x and y in the same year or in two years by the same species.

between Snowy Egrets and Louisiana Herons but found little overlap in habitat use between Louisiana Herons and Little Blue Herons. The three small species all hunted at similar depths suggesting that differences in feeding method resulted in finding and capturing different types of prey.

Ogden (1977) pooled food samples collected from three Everglades colonies and found that the two prey species representing the highest percentage of total diet were not significantly different in proportion of total diet, or in prey item length between Snowy Egrets and Louisiana Herons. This author's and my results differ from those of Jenni (1969) and Willard (1977). Possibly the degree of species specific food selection is dependent upon the potential diversity of feeding habitats available, and upon the type and diversity of available prey. Differences in feeding behavior would be of little import if prey type is limited.

Prey may be present but restricted in the predator diet because of specific habitat in which the prey most commonly occurs. Jenni (1969) and Ogden (1977) showed that the two most common fish species taken were not the largest species available. However, neither author demonstrated that larger prey were actually available to the herons studied. At Fishermans Island, the most common size class of _F. heteroclitus_ selected was smaller than _M. menidia_ and _F. majalis_ found in some samples. It does not necessarily follow that the latter species are equally available. The data from 1976 samples indicated that for Louisiana Herons and Snowy Egrets, grass shrimp, P. vulgaris, comprised a significant portion of the total diet. In 1977, Snowy Egrets took a higher percentage of the two most commonly captured prey, F. heteroclitus and L. xanthurus, and a decreased number of P. vulgaris. Diet may be flexible according to local, changing availability of several prey types. These changes may affect prey selection by different heron species. Little Blue Herons followed the same pattern as Snowy Egrets during the two years though change in proportions were minor, Louisiana Herons did not show the same shift in prey selection.

Availability of prey may dictate what types and proportions of food are consumed. Diversity of prey may also influence the degree of overlap in prey items selected by the three heron species despite any differences which can be shown in species specific feeding habitat (Custer and Osborn, 1977), or feeding techniques (see Kushlan, 1977, for review). Local and temporal abundance of potential prey relative to actual proportions of prey species taken should be correlated with species specific selectivity, feeding techniques, and habitat use. All of these factors are implicit in interpreting prey availability.

PREY AVAILABILITY

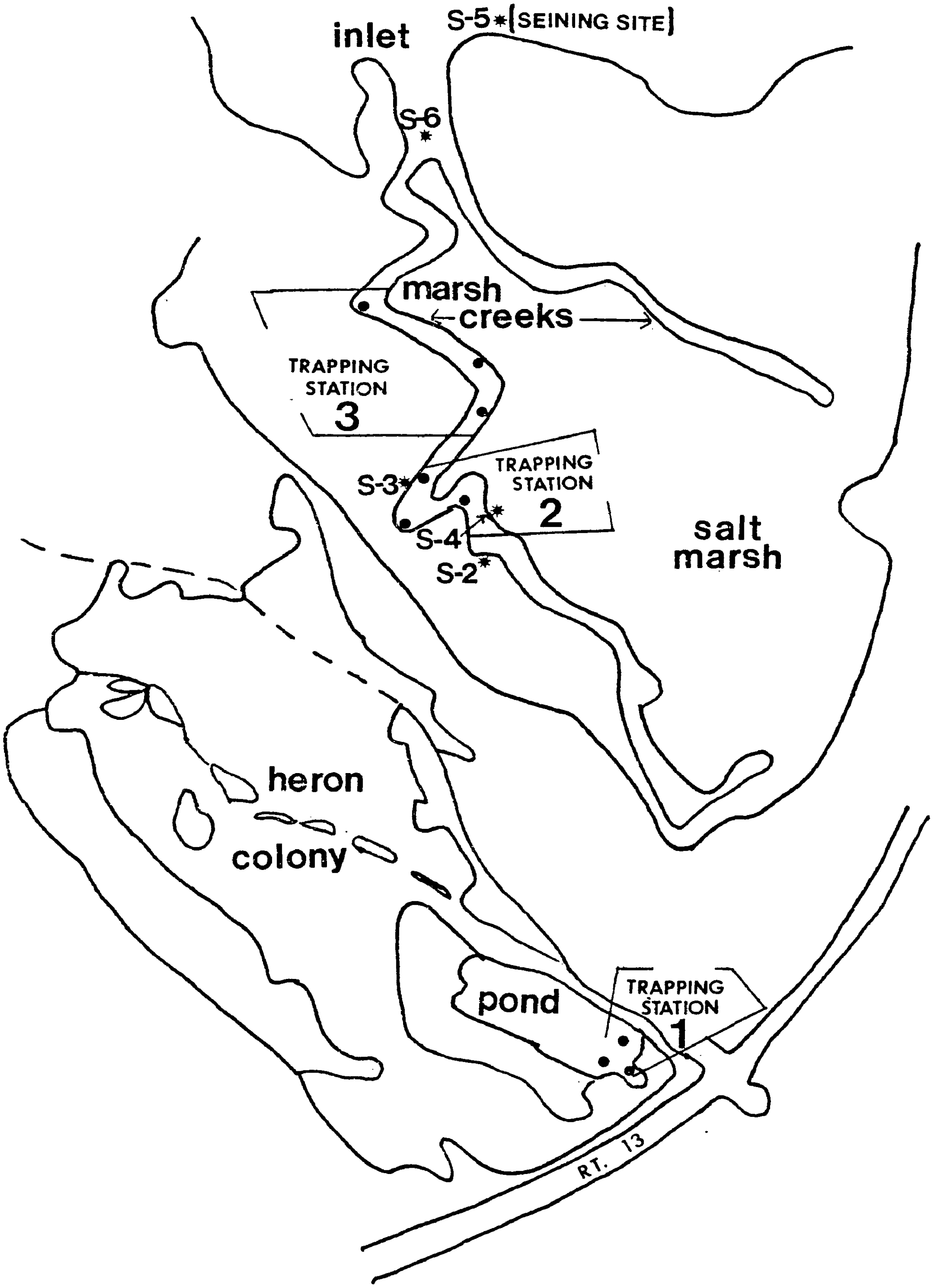
Methods

Three minnow traps baited with bread were set in each of two locations along the marsh creek system on the northwest side of Fishermans Island. Three more traps were placed in the pond adjacent to the heron colony. Traps 1 and 3 were in approximately the same water depth on either side of a mild current flowing in and out of the pond. Trap 2 was placed at the edge of a deeper pool receiving water from a tunnel under Route 13. The six trap sites are shown in Figure 10. Each trap was set for 2½ to 3 hours before low tide and reset for 2½ to 3 hours after low tide following collection of contents. On later dates trapping was done on a similar schedule around high tide. Fish trapping was conducted on April 16, 19, 22, 27, and on May 1, 5, 15 and 21, 1977.

Seining was done in three small guts projecting from the marsh creeks into the marsh (Figure 10). Sampling was done when tidal water was low enough that the marsh edge formed a barrier on three sides of the gut. At this time, most inhabitants of the gut could be collected by staking one end of a 10 foot (3m) seine at one end of the gut and encircling the entire gut manually with the other end.

Three more sites were sampled by seine where the large northwest inlet narrowed into the meandering tidal creek north

Figure 10. Trapping and Seining Sites for Food Availability at Fishermans Island, 1977.


inlet
S-5 * (SEINING SITE)
S-6
marsh
creeks
TRAPPING STATION 3
TRAPPING STATION 2
S-3
S-4
S-2
salt marsh
heron
colony
pond
TRAPPING STATION 1
RT. 13

of the colony. All species of herons under study had been observed feeding at the seining and trapping sites selected. Results from seining and trapping were analyzed, and literature pertaining to the most commonly captured prey species was reviewed.

Results

To determine if the three small heron species were taking the most locally abundant prey items, studies were conducted on the abundance and distribution of fish and invertebrates within the marsh system at Fishermans Island. The samples presented in Tables 8 and 9 are those collected when water levels were low enough for medium sized herons to feed. Despite the numerous environmental factors which could influence distribution and abundance of prey species, samples do reflect what was present in each location at the time and place waders were observed feeding.

Seining results indicated an overall patchiness in prey availability. The same site yielded different sample numbers at different times, and these differences did not appear to be correlated with date or with disturbance of the habitat from previous sampling. During the period of nest initiation, incubation and hatching, _Leistomus_ _xanthurus_ and _Palaemonetes_ _vulgaris_ were the most abundant potential prey items according to seining samples. _Fundulus_ _heteroclitus_ was more patchy, occurring in numbers greater than four in only two samples at different dates, and at different stations. _Fundulus_ _majalis_

TABLE 8

RESULTS FROM SEINING COLLECTIONS AT OBSERVED HERON FEEDING LOCATIONS, FISHERMANS ISLAND, 1977

		Prey Species				
Date	Seining[1] Station	Leistomus xanthurus	Palaemonetes vulgaris	Fundulus heteroclitus	Other species	Description of site
4/19/77	3	405	121	1		Small gut projecting into marsh from marsh creek 2 meters wide, 2.17 meters long
4/22/77	3	224	104	1		
4/27/77	3	120	104	0		
5/5/77	3	149	305	0		
5/7/79	3	588	>1000	26		
5/15/77	3	96	215	4		
4/19/77	5	68	>500	0	5 hermit crabs 1 *Callinectes sapidus*	Edge of large inlet, sandy substrate.

TABLE 8 (continued)

Date	Seining[1] Station	Prey Species Leistomus xanthurus	Palaemonetes vulgaris	Fundulus heteroclitus	Other species	Description of site
4/27/79	6	137	5			Mouth of creek leading into inlet
5/15/77	6	147	4		26 Fundules majalis	
4/22/77	4	164	55	78		Small gut projecting from creek into marsh 2.4 meters wide, 2.9 meters long with small lateral arms on either side.
4/27/77	4	58	210			
5/7/77	2	90	0	0		Small gut projecting from creek into marsh 2.1 meters wide, 3.6 meters long
5/15/77	2	55	0	3		

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[1] See Figure 11 for location of seining stations.

TABLE 9

RESULTS FROM TRAPPING SITE COLLECTIONS AT MARSH CREEK AND POND STATIONS, FISHERMANS ISLAND, 1977

Station	Date	Trap 1 Number in trap	Trap 1 Species trapped	Trap 2 Number in trap	Trap 2 Species trapped	Trap 3 Number in trap	Trap 3 Species trapped
Station 1: Pond adjacent to colony	4/22/77	32	*L.x.*[1]	312	*L.x.*	26	*L.x.*
		34	*F.h.*	13	*F.h.*	11	*F.h.*
						1	*C.v.*
		69	*F.h.*	26	*F.h.*	19	*F.h.*
				65	*L.x.*	3	(Anchovies)
	4/27/77	8	*P.v.*	85	*F.h.*	-	-
				6	*L.x.*	-	-
		15	*P.v.*	27	*F.h.*	-	-
		1	*L.x.*	6	*L.x.*	-	-
	5/1/77	40	*F.h.*			7	*F.h.*
				1	*L.x.*	3	*L.x.*
	5/5/78	8	*F.h.*			15	*F.h.*
		6	*P.v.*	1	*P.v.*		
				1	*L.x.*	3	*L.x.*
		7	*F.h.*	1	*L.x.*	1	*L.x.*
		12	*P.v.*			1	*P.v.*

TABLE 9 (Continued)

Station	Date	Trap 1 Number in trap	Trap 1 Species trapped	Trap 2 Number in trap	Trap 2 Species trapped	Trap 3 Number in trap	Trap 3 Species trapped
	5/7/77	5	*F.h.*	1	*F.h.*	1	*F.h.*
		3	*P.v.*	3	*P.v.*	26	*P.v.*
				2	*L.x.*		
	5/15/77	49	*F.h.*	2	*F.h.*	-	-
				4	*L.x.*	-	-
		1	*P.v.*	1	*P.v.*	-	-
	5/21/77	29	*F.h.*	12	*F.h.*	-	-
		5	*L.x.*	2	*L.x.*	-	-
Station 2: Edge of Marsh creek, distant from inlet	4/22/77	-	-	-	-	-	-
		-	-	-	-	-	-
		-	-	-	-	-	-
	4/27/77	-	-	-	-	-	-
		-	-	1	*L.x.*	-	-
		1	*F.h.*	-	-	-	-
		1	*P.v.*				
		1	(hermit crab)				
	5/1/77		-	-	-	-	-
				6	*P.v.*	12	*P.v.*

TABLE 9 (Continued)

Station	Date	Trap 1 Number in trap	Trap 1 Species trapped	Trap 2 Number in trap	Trap 2 Species trapped	Trap 3 Number in trap	Trap 3 Species trapped
	5/5/77	1	*L.x.*	1	*L.x.*	4	*L.x.*
				1	*F.h.*	2	*P.v.*
		8	*P.v.*	3	*P.v.*	33	*P.v.*
		1	*L.x.*	2	*L.x.*		
				1	*F.h.*		
	5/7/77	2	*P.v.*	2	*L.x.*	2	*L.x.*
				3	*F.h.*		
	5/15/77	0	-	-	-		
	5/21/77	3	*L.x.*	1	*L.x.*		
		1	*Uca pugnax*			63	*F.h.*
Station 3: Edge of Marsh Creek, closer	4/27/77	-	-	-	-	-	-
		-	-	-	-	-	-
	5/1/77	9	*P.v.*				
		1	*F.h.*				
	5/5/77	47	*F.h.*	3	*L.x.*	4	*L.x.*
				4	*P.v.*	3	*P.v.*
		-	-	-	-	9	*P.v.*
						1	*L.x.*

TABLE 9 (Continued)

Station	Date	Trap 1 Number in trap	Trap 1 Species trapped	Trap 2 Number in trap	Trap 2 Species trapped	Trap 3 Number in trap	Trap 3 Species trapped
	5/7/77	2	*F.H.*	1	*P.v.*	1	*L.x.*
	5/15/77	-	-	1 5 2	*P.v.* *L.x.* *F.h.*	30 2	*P.v.* *L.x.*
	5/21/77	19 2	*F.h.* *L.x.*	33 2	*F.H.* *L.x.*	4 3 3	*F.h.* *L.x.* *P.v.*

---

[1] *F.h.* = *Fundulus heteroclitus*, *L.x.* = *Leistomus xanthurus*, *P.v.* = *Palamonetes vulgaris*, *C.x.* = *Cyprinodon variegatus*

was only collected in one sample at seining site 3 where a large inlet narrowed into the tidal creek. Seining samples indicated a very low diversity of prey species within the creek area.

Trap results complemented seining results. However, F. heteroclitus did occur more frequently at station 3. Though stations 2 and 3 were only separated by about 450 meters, station 3 yielded larger samples. Specific trap catches reinforced the suggestion that prey items were patchy in occurrence. Comparison of trap with seine data indicated that traps did not represent the true abundance of P. vulgaris, although the species may collect in small guts in greater concentrations than along the edge of the creek. Fish captured in the trap at station 1 also showed irregular numbers per catch. Results from station 1 indicate that after the first catches either recruitment into that area was low, or that L. xanthurus had moved. Although abundance of the major food source, F. heteroclitus, was greater at station 1 than at any other station of seining site, herons were observed feeding there sporadically and not necessarily around low tide. Feeding aggregations were larger, and this location was more habitually used by juveniles. It is predicted that there was a more constant, predictable supply of prey in the pond than in marsh creeks. However, relative use of these feeding habitats by herons was not observed.

Discussion

One of the primary problems involved in sampling was unpredictability of tidal change relative to available tide tables. The lack of tide predictability was compounded by lag in ebb and flow which fluctuated according to height of tide within the creek system.

Although tidal fluctuation could not be correlated with prey abundance, both trapping and seining showed that in water levels within which herons feed, there was a varying abundance of prey according to site and date of collection. Both trapping and seining data also showed low diversity of prey types, suggesting that herons were eating what was most abundant. Catchability and feeding habitat available to herons may have further restricted prey selection. These factors would explain the high degree in overlap found among the diets of the Snowy Egrets, Louisiana Herons and Little Blue Herons.

Several studies have been conducted on movements and seasonal occurrence of the fish species most commonly trapped, seined, and collected in food samples from Fishermans Island. Richards and Castagna (1970) made a small trawl and beach seine survey from June, 1965 to July, 1966 of marine fish in seaside waters of Virginia's eastern shore. Fundulus heteroclitus was shown to be the second most abundant species as well as a permanent resident in the survey. Menidia menidia ranked as most abundant because of high species concentrations in inlet stations between barrier islands. This habitat would not generally be available to feeding wading birds except perhaps on the edges of the inlets and at low tide. *Menidia menidia* was 2.68 and 1.89 times as abundant as *F. heteroclitus* and *F. majalis*, respectively, in inshore beach stations from April to September. This was not a commonly used feeding habitat by any of the observed heron species. Furthermore, the peak of *Menidia* abundance was after nesting season (August and September), while both *Fundulus* species occurred in high numbers during the more critical nesting months of April and May.

If fish species follow the same pattern of movement in different geographical locations, local movements of *M. menidia* and *F. heteroclitus* in New York salt water channels and marshes further clarify potential differential availability of these prey items to herons. Buther and Brattstrom (1960) used mark and recapture procedures to show that *M. menidia* occurs offshore in small schools ascending streams as the tide rises presumably to avoid predation in the main channel, as well as to feed, breed and find warmer temperatures. When the tide goes out, *M. menidia* return to the main channel, moving up and down the channel enough so that they may or may not ascent the same stream on the subsequent tidal rise. *F. heteroclitus* do not remain in the channel. When the tide is high enough they feed in *Salicornia* and grass, following "the path of least resistence" as the water leaves higher ground as the tide ebbs. They remain near the mouth of the channel and usually closer to shore than *M. menidia*. The probability of returning up the same stream is greater for *F. heteroclitus* though the number of marked individuals will decrease from day to day.

Thus F. heteroclitus would be more available to feeding herons restricted by water depth.

F. heteroclitus has been shown to move seasonally in a Delaware tidal creek (Fritz, Meredith and Lotrich, 1975). From September to January, marking and recapture experiments showed that the majority of fish moved upstream into decreased salinities, or they remained at a single place. Photoperiod, and not temperature, appeared to be the primary cue for movement. It is presumed that a similar environmental cue initiates movements back downstream. During summer months, F. heteroclitus exhibited a home range of 36 m. (Lotrich, 1975) near the bank of a tidal creek. Although Lotrich's method did not adequately represent the size classes less than 6 cm (the size classes primarily eaten by herons), the dense population of this fish species within a tidal marsh system represents a potential food source that is essentially stationary but patchy in occurrence at one location over time. Unfortunately, neither study considered the factors that might be used to correlate food availability with time of nesting of herons. Information on time of movement downstream, and distribution of size class less than 6 cm. could substantially clarify the influence food abundance has on time and extraspecific synchrony of nesting, as well as the possible role of extraspecific food information exchange.

Seasonal population changes of Palaemonetes pugis in a Rhode Island saltmarsh embayment were reported by Welsh (1975). She found that shrimp numbers in March were 71 times those of July. Fundulus entered the embayment in peak numbers during April causing heavy predation of gravid shrimp females. By August, juveniles comprised 99 percent of the samples. Contribution of viable young was estimated at about 500 per adult. The quadrat net estimates showed shrimp were generally distributed as a mobile aggregation. If P. vulgaris has a similar ecology, then it and the main food item of three heron species are distributed differently but appear to peak in abundance during the two months when their availability might influence the onset of nesting. Increased availability and abundance in both items through the summer would ensure nesting success as energy demands would peak during nestling growth.

Data from the 1965-1966 survey of Richards and Castagna were different than the proportion of Leistomus xanthurus found in heron food samples. These investigators caught only a small number of juveniles by seine and then only in tidal creek stations. They were caught in varying numbers during May through June collections and in much lower numbers during July. In 1977, food samples were collected at Fishermans Island slightly earlier than in 1976. In 1977, L. xanthurus represented the second largest proportion of total diet of Snowy Egrets and Louisiana Herons whereas in 1976, this second ranking species consituted a smaller proportion of the Snowy Egrets' total diet. Only one L. xanthurus was found in all ten Louisiana heron samples. Differences in amount of this prey taken may reflect seasonal changes in abundance or may be due to the slight discrepancy in the time at which food samples were collected. It is speculated this size class of _L_. _xanthurus_ peaks in abundance for only a short time period early in the season.

It is known that abundances and/or availability can change seasonally and may in fact change during one nesting season. Owen (1960) suggested that the European Grey Heron (_Ardea_ _cinerea_) lays its eggs at a time such that young are in the nest during the period of maximum food availability. Jenni (1969) concluded that early peak nesting was adapted to food availability, noting that later clutches were significantly smaller in Louisiana Herons and Little Blue Herons and that food brought to late nesting broods differed. I noted that late nesting Little Blue Herons brought more insects and other invertebrates to young. These young appeared emaciated and slow growing. In South Florida colonies, smaller clutches are common in later nesting Snowy Egrets, Louisiana Herons and to a lesser degree, Little Blue Herons (personal observation). It may be food availability rather than lack of neighbors to follow that most strongly influences clutch size and nesting success.

Because diversity of prey items was relatively low and because preliminary trapping showed that the prey species eaten were also susceptable to sampling, feeding areas around the Fishermans colony would be ideal for further investigation on food availability. In particular, increases, dispersion, and decline of prey availability could be followed through one season to show whether initiation of nesting and degree of nesting and degree of nesting success are correlated with change in prey abundance.

SPECIES RECOGNITION

Methods

Several preliminary sets of cross fostering tests were made on newly hatched chicks at Fishermans Island in late May, 1976. Nests were revisited after one hour, then left for several days. No measurements were made initially as there was no knowledge of the possible stress cross fostering might have on resident nestlings, or on the cross fostered chicks. General size was noted and later translated into weight category. Statistical comparisons were run only on that sample in which cross fostered chicks had been measured at least three times so that the resulting "DWTINC" (See Intraspecific Growth) for each fostered group represented increases from each weight category. Preliminary trials and cross foster trials with unusual results were presented descriptively. Several cases involved more than one fostered species in a nest. Mixed-species broods of this type were not planned but were often necessary to balance brood sizes and to ensure placement of surplus chicks in broods. It was decided that extra chicks would be placed in already manipulated nests rather than in new nests with complete broods.

In all cross fostering experiments, I attempted to maintain original brood size, exchanging as often as possible the largest chicks in the nest, or using only second-hatched chicks in order to equate weight and/or age with that of young in nests receiving fostered young. Third hatched birds were never tested, and second or first-hatched birds that were obviously underweight for size and feather development were also avoided.

All aforementioned procedures were carried out on a small control group of 12 Louisiana Heron and 37 Snowy Egret nests at Walker's Marsh in 1976. At another colony, Clubhouse Point, several cross fostering trials were done on Louisiana Herons and Little Blue Herons during the 1977 nesting season. The resulting data from fostered chicks was treated in a descriptive table, but there were not enough cross fostered chick weights to compare with control groups.

Results

Because heron species nested in close proximity to one another, cross fostering tests were made to see if selective pressure has promoted at least species specific recognition of nestlings. Some results are interpreted descriptively in Table 10. The success of fostered chicks remaining in the nest long enough to be weighed three or more times was evaluated statistically. The variable "DWTINC" (mean daily weight increase) was used to evaluate success in cross fostering experiments. DWTINC was tested between cross fostered chick groups and their respective species control group. Growth in cross fostered chicks was also compared with that of species in which the foster chick had been placed. Results of comparative DWTINC values are presented in Tables 11 through 15.

TABLE 10

INFORMATION FROM CROSS FOSTERING TESTS AMONG FOUR HERON SPECIES

Colony Year	Nest species	Case No.	Resident original weight (grams)	Resident final weight (grams)	DWTINC (grams)	Fostered species	Foster original weight (grams)	Foster final weight (grams)	DWTINC (grams)	Successive day checked
Fishermans Island, 1976	SE	1	WTCAT 1	Gone	-	LH	WTCAT 1	Gone		15
	SE	2	Removed			LH	WTCAT 1	Gone		14
						LB	WTCAT 1	WTCAT 2		14
	SE	3	WTCAT 1	Gone		LB	WTCAT 1	WTCAT 2		5
						LB	WTCAT 1	Gone		5
	SE	4	WTCAT 1	Gone	-	LB	WTCAT 1	142		11
	SE	5	53	96	10.3	LB	60	62	0.5	4
			96	170	18.5		62	78	4.0	8
			170	Ran	-		78	Ran	-	16
				Gone				Gone		19
	SE	6	WTCAT 1	Gone		LB	82	117	2.5	14
	SE	7	Removed			LB	WTCAT 1	DEAD IN NEST		2

TABLE 10 (Continued)

Colony Year	Nest species	Case No.	Resident original weight (grams)	Resident final weight (grams)	DWTINC (grams)	Fostered species	Foster original weight (grams)	Foster final weight (grams)	DWTINC (grams)	Successive day checked
						LB	WTCAT 1	77	-	2
	SE	8	WTCAT 1	WTCAT 3		LB	WTCAT 1	WTCAT 2		13
	SE	9	53	Gone		LB	55	Gone		8
	SE	10	82	140	5.8	LB	82	154	7.2	10
			62	70	0.8					
	SE	11	Removed			LB	WTCAT 1	Gone		2
						CE	WTCAT 1	Gone		2
	SE	12	68	Gone		LH	112	WTCAT 3		8
	SE	13	Removed			CE	WTCAT 1	142	-	13
							142	DEAD IN NEST		15
	SE	14	108	Gone		LH	96	Gone	-	7
						CE	80	Gone	-	7
	SE	15	100	WTCAT 2		CE	128	DEAD IN NEST		7

TABLE 10 (Continued)

Colony Year	Nest species	Case No.	Resident original weight (grams)	Resident final weight (grams)	DWTINC (grams)	Fostered species	Foster original (grams)	Foster final weight (grams)	DWTINC (grams)	Succes-sive day checked
	SE	16	WTCAT 1	132	-	CE	WTCAT 1	97	-	7
	LB	1	WTCAT 1	DEAD IN NEST		SE	WTCAT 1	DEAD IN NEST		8
	LB	2	Removed			SE	WTCAT 1	Gone (nest fell)		8
	LB	3	WTCAT 1	WTCAT 3		SE	WTCAT 1	Gone		18
	LB	4	WTCAT 1	101		SE	WTCAT 1	>300 (ran)		12
			WTCAT 1	Gone						
	LB	5	WTCAT 1	WTCAT 2		SE	57	142	7.7	11
			WTCAT 2	Removed			142	150	4.0	13
							150	DEAD ON GROUND		21
						CE	152	142	-5.0	13
							142	DEAD IN NEST		21
	LB	9	WTCAT 1	Gone		SE	23	155	10.2	13
						SE	16	Gone		13

TABLE 10 (Continued)

Colony Year	Nest species	Case No.	Resident original weight (grams)	Resident final weight (grams)	DWTINC (grams)	Fostered species	Foster original weight (grams)	Foster final weight (grams)	DWTINC (grams)	Successive day checked
						CE	128	93	3.5	13
	LB	7	29	32	0.6	SE	18	61	8.6	5
			32	103	7.8		61	111	5.6	15
	LB	8	Removed			SE	WTCAT 1	DEAD IN NEST		10
						SE	WTCAT 1	DEAD IN NEST		10
						SE	WTCAT 1	WTCAT 2	-	10
							WTCAT 2	Gone		18
	LB	9	WTCAT 1	Gone		SE	WTCAT 1	Gone		2
						CE	WTCAT 1	Gone		2
						CE	Gone?	DEAD IN NEST		10
	LB	10	68	72	2.0	CE	152	142	-0.5	2
			Removed			CE	128	112	-5.33	3
	LH	1	WTCAT 1	WTCAT		SE	WTCAT 1	Gone		2

TABLE 10 (Continued)

Colony Year	Nest species	Case No.	Resident original weight (grams)	Resident final weight (grams)	DWTINC (grams)	Fostered species	Foster original weight (grams)	Foster final weight (grams)	DWTINC (grams)	Successive day checked
	LB	2	1 egg	36		SE	61	(o.k.)		7
			Removed			o.k.	125	-		10
						125	on limb			13
						on limb	on limb			15
	LH	3	Removed			SE	218	Gone		7
						CE	108	Gone		7
						LH	110	115	0.7	7
	LH	4	62	84	11.0	SE	84	113	14.5	2
			84	84	0.0		113	126	13.0	3
			84	on limb			126	on limb		10
	LH	5	25	45	6.7	SE	45	87	14.0	3
			45	Dead on Ground			87	Dead in Nest		16
	LH	6	Removed			SE	WTCAT 1	Pecked	-	2

TABLE 10 (Continued)

Colony Year	Nest species	Case No.	Resident original weight (grams)	Resident final weight (grams)	DWTINC (grams)	Fostered species	Foster original weight (grams)	Foster final weight (grams)	DWTINC (grams)	Succes-sive day checked
						SE	WTCAT 2	Gone		2
						CE	WTCAT 2	100	(negative)	2
	LH	7	185	on limb		LB	121	Pecked and hung		2
	LH	8	WTCAT 2	-		LH	155	o.k.		(same day)
						CE	130	Knocked to ground		
	LH	9	WTCAT 2	on limb		LH	150	on limb		10
			WTCAT 2	on limb						
	LH	10	225			CE	130	Pecked,on ground		(same day)
			243							
Walkers Marsh, 1976	LB	11	34	139	21.0	SE	41	150	21.8	5
	SE	17	24	Gone	-	LB	33	67	6.8	5
	SE	18	92	Gone		LB	159	Gone	-	5
	SE	19	85	95	2.0	LB	80	169	17.8	5

TABLE 10 (Continued)

Colony Year	Nest Species	Case No.	Resident original weight (grams)	Resident final weight (grams)	DWTINC (grams)	Fostered species	Foster original weight (grams)	Foster final weight (grams)	DWTINC (grams)	Successive day checked
	SE	20	Removed			LB	22	66	8.8	5
	SE	21	92	121	5.8	LH	34	77	8.6	5
	SE	22	164	Gone	-	LH	134	Gone	-	5
	SE	23	195	176	-3.8	LH	193	Gone	-	5
	LH	10	Removed			SE	21	94	14.6	5
Clubhouse Point, 1976	CE	24	46	239	19.3	LB	34	47	1.3	10
			46	140	9.4					10
	SE	25	Removed			LB	127	232	17.5	6
						LH	145	Ran	17.5	6
	SE	26	Removed			LH	69	Ran	-	7
	LH	11	215	Ran	-	SE	177	256	19.8	4
	LH	12	51	151	14.3	SE	70	150	11.4	7
			151	221	17.5		150	226	19.0	4

TABLE 10 (Continued)

Colony Year	Nest Species	Case No.	Resident original weight (grams)	Resident final weight (grams)	DWTINC (grams)	Fostered species	Foster original weight (grams)	Foster final weight (grams)	DWTINC (grams)	Successive day checked
Fishermans Island, 1977	LB	12	52	162	18.4	SE	139	283	24.0	6
	LB	13	34	89	5.5	LH	102	Gone	-	10
	LB	14	52	Gone	-	LH	130	Gone		4
						LH	109	Gone		6
	LB	15	Removed		-	LH	102	Gone		10
	LB	16	193	293	25.0	LH	176	Gone		4
	LB	17	Removed			LH	103	Gone		7
						LH	86	Gone		7
						LH	80	Gone		7
	LB	18	96	210	38.0	LH	95	Gone		3
			20	156	17.0				-	8
	LB	19	70	108.1	12.7	LH	157	102	-18.33	3
			108.1	209.7	12.7		102	Gone	-	8

TABLE 10 (Continued)

Colony Year	Nest species	Case No.	Resident original weight (grams)	Resident final weight (grams)	DWTINC (grams)	Fostered species	Foster original weight (grams)	Foster final weight (grams)	DWTINC (grams)	Successive day checked
	LB	20	56	55	-0.5	LH	154	Gone	-	2

TABLE 11

COMPARISON OF DAILY WEIGHT INCREASE (DWTINC), MEANS, STANDARD DEVIATIONS AND COEFFICIENT OF VARIATION BETWEEN CROSS FOSTER CHICK SAMPLES

	Cross Foster Exchange	N	Mean DWTINC	SD	CV
Fishermans Island, 1976	SE in LB nest	13	14.3	8.16	57.09
	SE in LB nest	5	7.4	8.37	113.07
	LH in SE nest	18	19.1	14.44	75.60
	LH in LB nest	25	14.2	8.90	62.53
	LB in SE nest	16	11.6	10.14	87.41
	LB in LH nest	13	27.1	25.29	93.28
Fishermans Island, 1977	SE in LH nest	3	16.7	4.93	29.60
	SE in LB nest	4	18.5	10.40	56.24
	LH in LB nest	10	15.1	4.49	29.79
	LB in SE nest	2	9.5	12.02	126.53
	LB in LH nest	17	17.5	9.97	57.06

TABLE 12

COMPARISON USING T-TESTS OF DAILY WEIGHT INCREASE (DWTINC) BETWEEN CROSS FOSTER AND CONTROL CHICK GROUP HAVING MEANS WITH HOMOGENEOUS VARIANCES. DATA COLLECTED AT FISHERMANS ISLAND, 1976

Species	Cross Foster Exchange	N	df	value	2 tailed P	Significance level[1]
SE	SE in LB nest	4	51	-3.08	0.003	**
LB	Hatch 1	49				
SE	SE in LB nest	4	45	-3.11	0.003	**
LB	Hatch 2	43				
SE	SE in LB nest	4	29	-2.44	0.021	*
SE	Hatch 1	27				
SE	SE in LB nest	4	26	-2.18	0.038	*
SE	SE Hatch 2	24				
LB	LB in SE nest	14	61	-2.31	0.024	*
LB	LB Hatch 1	49				
LB	LB in SE nest	14	55	-2.24	0.029	*
LB	LB Hatch 2	43				
LB	LB in SE nest	14	39	-0.78	0.442	NS
SE	SE Hatch 1	27				
LB	LB in SE nest	14	36	-0.47	0.638	NS
SE	SE Hatch 2	24				
SE	SE in LH nest	13	38	0.41	0.682	NS
SE	SE Hatch 1	27				
SE	SE in LH nest	13	35	0.70	0.489	NS
SE	SE Hatch 2	24				
SE	SE in LH nest	13	47	-2.56	0.014	**
LH	LH Hatch 1	36				

TABLE 12 (Continued)

Species	Cross Foster Exchange	N	df	value	2 tailed P	Significance level[1]
SE	SE in LH nest	13	47	-0.68	0.498	NS
LH	LH Hatch 2	36				
LH	LH in LB nest	25	72	1.51	0.135	NS
LB	LB Hatch 1	49				
LH	LH in LB nest	25	66	1.42	0.161	NS
LB	LB Hatch 2	43				
LH	LH in LB nest	25	59	3.15	0.003	**
LH	LH Hatch 1	36				
LH	LH in LB nest	25	59	0.91	0.364	NS
LH	LH Hatch 2	36				

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[1] P = probability values, * = P 0.05, ** = P 0.01, NS = not significant at the 0.05 level.

TABLE 13

COMPARISON USING MANN-WHITNEY TESTS OF DAILY WEIGHT INCREASE (DWTINC) BETWEEN CROSS FOSTER AND CONTROL CHICK GROUPS HAVING MEANS WITH HETEROGENEOUS VARIANCES FISHERMANS ISLAND, 1976

Species	Cross foster exchange	N	Z	2 tailed P[1]	Significance level[2]
LH SE	LH in SE nest SE Hatch 1	8 27	-0.9270	0.3539	NS
LH SE	LH in SE nest SE Hatch 2	18 24	-1.2461	0.2127	NS
LH LH	LH in SE nest LH Hatch 1	18 36	-1.3672	0.1716	NS
LH LH	LH in SE nest LH Hatch 2	18 36	-0.3395	0.7342	NS
LB LH	LB in LH nest LH Hatch 1	9 36	-0.4825	0.6295	NS
LB LH	LB in LH nest LH Hatch 2	9 36	-0.7665	0.4434	NS
LB LB	LB in LH nest LB Hatch 1	9 49	-0.5692	0.5692	NS
LB LB	LB in LH nest LB Hatch 2	9 43	-0.4113	0.6808	

[1] 2 tailed P corrected for ties.

[2] NS = not significant at the 0.05 level.

TABLE 14

ONE-WAY ANALYSIS OF VARIANCE FOR THE VARIABLE DWTINC AMONG TEST GROUPS OF CROSS FOSTERED CHICKS AND CONTROL GROUPS WITH HOMOGENEOUS VARIANCES FISHERMANS ISLAND, 1977

Test groups	MS Group	df	Ms Error	df	F	P	Significance level[1]
SE in LH nest SE, Hatch 1 + 2 LH, Hatch 1 + 2	0.6792	2	56.8198	155	0.012	0.9881	NS
SE in LB nest SE, Hatch 1 + 2 LB, Hatch 1 + 2	20.2275	2	78.4026	159	0.258	0.7728	NS
LB in SE nest	44.3429	2	78.4296	154	0.565	0.5689	NS

[1] NS = not significant at the 0.05 level

TABLE 15

MANN-WHITNEY TEST FOR THE VARIABLE DWTINC AMONG CROSS FOSTER AND CONTROL GROUPS WITH HETEROGENEOUS VARIANCE, 1977

Test groups	N	Mann-Whitney U Statistic	P	Significance level[1]
LH in LB nest	10	-0.2667	0.7897	NS
LH, Hatch 1	30			
LB in LH nest	17	-0.0102	0.9918	NS
LB, Hatch 1	33			

Note: Data from exchanges at Clubhouse Point was included in the test. A small control sample was also obtained in this colony. Statistics on controls were as follows: LH, Hatch 1; N = 5, $\bar{x}$ = 15.4, SD = 3.86, LB, Hatch 1; N = 7, $\bar{x}$ = 31.0, SD = 15.6

[1] NS = not significant at the 0.05 level

Snowy Egrets in Louisiana Heron Nests

Snowy Egret chicks placed in Louisiana Heron nests grew successfully with one exception in both years. Statistical analysis in 1977 indicated that fostered Snowy Egrets grew at a rate almost identical to both its own species and to the Louisiana Heron control group of first-hatched chicks (Table 14). In 1976, T-tests showed no significant difference between growth of the cross fostered Snowy Egrets and first and second-hatched Snowy control groups, nor with second-hatched Louisiana Herons, though the latter mean was slightly higher. These cross fostered chicks did grow at a significantly lower rate than first-hatched Louisiana Heron control group (Table 12). Because growth rate was high relative to its own species, cross fostered Snowy Egrets may have been growing at an optimal rate for that species and were satiated with a smaller amount of food than required by the faster growing, eventually larger, first-hatched Louisiana Herons.

Case LH-2, in Table 10, offers evidence that a parent Louisiana Heron with only eggs accepted a foster Snowy Egret even after its own chick hatched. The foster Snowy Egrets released a number of F. heteroclitus, demonstrating that it had been fed. There is, however, no absolute evidence that an adult Snowy Egret did not take over the nest. In two cases cross fostered Snowy Egrets were more successful than the resident nestmate. In cases LH-4 and LH-5, the fostered Snowy Egret grew at a faster rate than the resident Louisiana Heron chick. Death of both chicks was not considered due to nestling exchange but was considered representative of normal mortality observed in a portion of the control nests. Cases LH-3 and LH-1 were also considered normal occurrences in light of the larger number of successful nestling exchanges. LH-6 was an exceptional case. Because there were no other cases in which a foster Snowy Egret was pecked, it was suspected that the parent Louisiana Herons abandoned the nest and that the larger Cattle Egret chick pecked the Snowy Egret chick. It is of interest that of the three instances of failure, two involved adding a Cattle Egret to the nest. (Cattle Egret chicks were actively evicted from Louisiana Heron nests in several instances.)

Attempts were made to place larger Snowy Egrets into Louisiana Heron nests. Test exchanges at Walker's Marsh and Clubhouse Point were unsuccessful because vegetation was low enough that chick could escape from the foreign nest and run across the ground. One exchange, made at the latter colony, involved placing a Snowy Egret in a very distant Louisiana Heron nest. The foster chick grew at a rate slightly higher than controls indicating that it was fed and was not rejected by parent Louisiana Herons. Upon return to the four nests with larger Snowy Egret exchanges at Fishermans Island, all chicks were gone. At the time of the initial change, these nestlings were nearly large enough to begin climbing. Therefore, it was presumed that the chicks were still alive but not visible in the dense *Myrica* on the return visit. The nests still appeared active with a few dried fish and white-washing around the nest.

Louisiana Herons in Snowy Egret Nests

T-tests performed on 1976 data from Fishermans Island showed that cross fostered Louisiana Heron chicks grew at a rate not significantly different from first and second-hatched chicks of the same species, or from the foster control group (Table 13). Yet DWTINC did indicate that cross fostered Louisiana Heron chicks grew at a more rapid rate than the control group Snowy Egrets. Fostered Louisiana Herons must have competed successfully to achieve their species specific excess food requirements. Statistical analysis was not done of 1977 data as few exchanges between these species were made.

Cross foster cases in Table 10 complement statistical results. Cases SE-1 and SE-2 are considered as part of the normal nest failure experienced by this species. There was no evidence to determine what happened in case SE-14, as in seven days after the exchange, resident and foster chicks would have been large enough to leave the nest. Placement of a Cattle Egret chick in this nest may have interfered with the acceptance of foster chicks by parent Snowy Egrets. Other cases of Cattle Egret exchanges into Snowy Egret nests were unsuccessful.

Case SE-12 demonstrates one instance in which a larger Louisiana Heron was accepted into a Snowy Egret nest. It was expected that the larger exchanged Louisiana Heron chicks in cases SE-22 and SE-23 from Walker's Marsh returned to their own nests nearby. The Louisiana Heron chick in Case SE-25, Clubhouse Point, was recorded present and noticeably larger six days after the original exchange. This chick was placed in a Snowy Egret nest distant from the foster chick's original nest.

Little Blue Herons in Snowy Egret Nests

Comparative results on cross fostering tests between Little Blue Herons and Snowy Egrets offered more insight into the relative success in reciprocal exchanges. Placement of Little Blue Herons in Snowy Egret nests resulted in a generally lower rate of weight increase per day among the fostered Little Blue Heron chicks. T-tests in 1976 (Table 12) showed that the fostered Little Blue Herons grew at a significantly lower DWTINC than either first or second-hatched Little Blue Heron chicks in the control group. Although not significantly different, DWTINC among foster chicks was noticeably lower than that of control group first or second-hatched Snowy Egrets. Several more cases of slow growth were recorded in Table 10. Cases SE-2, SE-6 and SE-7 indicated slower growth, and SE-5 and SE-8 showed that cross fostered Little Blue Herons were growing at a slower rate than the resident Snowy Egret nestmates. Fostered Little Blue Herons also showed slow growth at Walker's Marsh (cases SE-17 and SE-20) and at Clubhouse Point (case SE-24). Contrary results only occurred in a few instances. At Clubhouse Point (case SE-25) and at Walker's Marsh (case SE-19) the introduced Little Blue Herons grew at a normal to high rate; in the latter case the fostered Little Blue Heron grew faster than its resident nestmate.

One exchange, not cited in the table of cases, was made between two nests containing, respectively, three Snowy Egret and three Little Blue Heron nestlings in very close proximity. The two broods contained chicks close in developmental stage. The two largest of each brood were exchanged. Two days later all fostered chicks were pecked and dead in branches between the nests and on the ground. The positioning of the chicks indicated that young were attempting to return to their own nest. The third-hatched chicks in each brood were intact, in their appropriate nest. This case is discussed later in the context of possible late developing recognition among species.

<u>Snowy Egrets in Little Blue Heron Nests</u>

Snowy Egrets placed in Little Blue Heron nests showed a significantly lower growth rate than first or second-hatched chicks of their own, or cross foster chick species at Fishermans Island, 1976. Table 11 shows a high coefficient of variation in the DWTINC statistic, and a low sampling size in this testing year. In 1977, the fostered Snowy Egret DWTINC was much greater, and not significantly different from first-hatched control group Snowy Egrets. In Table 10, cases LB-1, LB-2, and LB-8 were not considered as nests which failed due to testing. In case LB-2, the nest could have been abandoned after all Little Blue Heron chicks were removed, but LB-8 showed that at least one Snowy Egret chick was fed though the resident species chicks had been removed. Case LB-5 may have been disrupted by placement of a Cattle Egret chick in the nest. Growth of the Snowy Egret appeared slow. Growth was slightly retarded in the surviving Snowy Egret chick in Case LB-6. In case LB-7, growth again appeared retarded, but even though the foster chick was eleven grams lighter when placed in the nest, this Snowy Egret grew at a faster rate than the resident Little Blue Heron nestling. In case LB-10, Walker's Marsh, the fostered Snowy Egret grew at the same high rate as the Little Blue Heron, and in case LB-12, Clubhouse Point, the fostered Snowy Egret grew at a very high growth increment per day, exceeding that of its resident nestmate. This latter case indicated that a larger, older Snowy Egret was accepted and fed in the foster nest.

Louisiana Herons in Little Blue Heron Nests

Conflicting results also occurred in placing Louisiana Heron chicks into Little Blue Heron nests during 1976. Table 12 shows that DWTINC among cross fostered Louisiana Herons was not significantly different from first or second-hatched Little Blue Herons, nor from second-hatched Louisiana Heron chicks. However, growth was somewhat slower than any of the control groups with which it was tested and was significantly lower than that of first-hatched Louisiana Herons. No significant differences were found in 1977 (Table 15); growth in this year was slightly higher. Cross fostered Snowy Egrets usually lost weight in less successful exchanges into Little Blue Heron nests. A number of fostered Louisiana Heron chicks completely disappeared from Little Blue Heron nests in a short time period. Disappearances occurred at both Fishermans Island and

Clubhouse Point in 1977. During this year, the author attempted to make as many crosses as possible with foster chicks in WTCAT 2 (100 to 200 grams). In cases LB-14, LB-16, LB-18, and LB-20, Louisiana Heron chicks were noted missing within two to four days. Once I actually observed a 140 gram Louisiana Heron pecked and hanging below a Little Blue Heron nest one half hour after introduction. The two Little Blue Heron nestlings were perched in branches adjacent to the nest. This Louisiana Heron was removed and placed in another nest of its own species. It appeared cared for by the intraspecific foster parents for the duration of my visits to Clubhouse Point. In LB-19, Clubhouse Point, another Louisiana Heron decreased in weight from 157 grams to 102 grams in three days. In eight days it was gone while its nestmate Little Blue Heron chick increased during the first three days from 70 to 197 grams. It is not known whether older exchanged Louisiana Herons ran from the nest on their own initiative or whether they were chased by adult or nestling Little Blue Herons. Possibly, at these later ages, chick and/or adult recognition is beginning to develop. The conflicting results in the Louisiana Heron - Little Blue Heron exchange could have been due to differences in the adult experience in nesting or in actual learning ability. Learning may, in part, be reinforced by chick response. If the exchanged Louisiana Heron ran, or in some way did not elicit the appropriate food-begging response to the foster parent, perhaps it was either attacked or ignored. Unsuccessful exchanges of Cattle Egret chicks into Little Blue Heron nests also occurred and are discussed in a later section.

Little Blue Herons in Louisiana Heron Nests

The placement of Little Blue Heron chicks into Louisiana Heron nests yielded quite different results than the reciprocal. Table 13 shows that there were no significant differences between DWTINC of fostered Little Blue Heron chicks, and first and second-hatched Louisiana Heron or Little Blue Heron control chicks. Actual means show that fostered Little Blue Herons grew at a faster rate than any of the respective control groups. Statistical comparisons in 1977 did not show any significant differences (Table 15). Although DWTINC mean was 10 grams lower per day, control groups of Louisiana Herons and Little Blue Herons also grew at a slower rate of increase in weight per day in this year. Because Louisiana Heron nestlings were active defenders of their nest, especially at older ages, it is suspected that the case LH-7, in which a Little Blue Heron at 121 grams was placed with a Louisiana Heron chick at 185 grams, reflected active ejection of the foreign chick by the Louisiana Heron resident. In cases LH-8, and LH-10, the author returned to each Louisiana Heron nest within one hour to find the introduced Cattle Egret chick in each nest pecked and knocked to the ground. In both cases, the resident Louisiana Heron chicks were of WTCAT-3 (200-300 gram) size; they immediately began pecking at the foreign chicks. Case LH-8 suggested that the chicks could discriminate species, as a smaller, non-resident Louisiana Heron placed in the same nest was not attacked. This chick showed positive growth in subsequent visits. Most of the 1977 exchanges between Louisiana Herons and Little Blue Herons were made using nests in which the resident Louisiana Heron was between 100 to 150 grams, usually the second-hatched. It would appear that any introduced chick is accepted through this period. It was at later stages that chicks, and perhaps parent Louisiana Herons, rejected other species of chicks.

Extraspecific Cattle Egret Cross Foster Tests

Very few exchanges were made placing other species in Cattle Egret nests. Preliminary results confirmed an overall rejection of even small chicks of any species. In each case, the fostered chick was larger than the Cattle Egret left in the nest. Three Snowy Egret chicks were introduced. The first was found dead on the ground in three days; the other two were gone in three days. A fourth chick at 162 grams was placed in a nest with two newly hatched Cattle Egret chicks. It was not evicted, but after two more visits had not yet been fed. This Snowy Egret chick finally starved to death. A Little Blue Heron chick was pecked and found dead when checked on the third day, while the resident Cattle Egret nestlings had grown. Two Louisiana Heron chicks in the WTCAT 2 (100-200 gram) range were actively pecked out of Cattle Egret nests within one hour. After these results, no more crosses were made. Cattle Egrets nested later than the other three species so that peak hatching among the former coincided with the latest hatching other species. There were few available nests with appropriately sized chicks to introduce into Cattle Egret nests. Therefore, this type of cross was discontinued, and although no definite conclusions could be made, it would appear that Cattle Egrets do not as readily accept extraspecific chicks as do other species. They actively evicted dark-colored Louisiana Herons, and if they did not eject Snowy Egrets, they did not feed them. Only one Little Blue Heron was introduced and this chick was killed. Dusi (1968) found that when Cattle Egrets moved into a Little Blue Heron nesting colony the former species occasionally took over Little Blue Heron nests. Usually they would push eggs or chicks from the nest but in one instance the Cattle Egret raised a Little Blue Heron chick with its own brood. Thus, response may be individual rather than species specific.

At Fishermans Island, in both 1976 and 1977, a large percentage of the Little Blue Heron nests were marked and studied. There was no case in which Cattle Egrets usurped a Little Blue Heron nest, though they initiated nesting adjacent to Little Blue Herons rather than other species. This may have been because more Little Blue Herons were still nesting in one concentration.

Intraspecific Cattle Egret Cross Foster Tests

Because Cattle Egrets did not appear to accept even small extraspecific chicks in their nests, intraspecific exchanges were made at Fishermans Island in 1976 and 1977. Tables 16 and 17 show results from these exchanges. The small

TABLE 16

COMPARISON OF MEAN DAILY WEIGHT INCREASE (DWTINC) IN CATTLE EGRET CHICK TEST GROUPS, FISHERMANS ISLAND, 1976 AND 1977

Year	Nesting status	N	Mean DWTINC	SD
1976	Hatch 1	70	15.4	7.38
	Hatch 2	52	13.2	7.34
	Cross fostered chick	45	13.6	7.94
	Resident chicks in nest containing fostered chicks	15	14.5	8.22
1977	Hatch 1	31	18.2	6.95
	Hatch 2	30	13.0	8.01
	Cross fostered chick	50	16.2	7.83
	containing fostered chick	61	14.1	9.21

TABLE 17

ONE-WAY ANALYSIS OF VARIANCE FOR THE VARIABLE DWTINC AMONG TEST GROUPS OF CATTLE EGRET CHICKS FISHERMANS ISLAND, 1976 AND 1977

Year	Test groups	MS group	df	MS error	df	F	P	Significance level
1976	Hatch 1 Hatch 2 and cross fostered chicks	146.1070	2	62.0488	166	2.355	0.0981	NS
1977	Hatch 1, 1977 Group Hatch 1, 1976 cross foster chicks, 1977	82.9011	2	55.5007	148	1.494	0.2279	NS
	Hatch 2, 1977 Hatch 2, 1976 cross foster chicks, 1977	146.8798	2	59.0029	129	2.489	0.0869	NS

sample number of resident chicks receiving crosses resulted from my not initially weighing and measuring this group. However, in both years, the DWTINC reflected the fact that most chicks left in a nest were second-hatched chicks. Thus, the average DWTINC was intermediate in 1976 and was closer to the second-hatched chicks in 1977 because of the greater difference between first and second-hatched chick control groups in that year. Because the resident chicks grew at an explainable intermediate rate, this group was not tested against foster groups or control groups in Table 17. Both 1976 and 1977 statistical data indicated that there was not a significant difference in daily weight change, at least in the samples where weight change was a positive value (Table 17). The two years were tested separately because in 1977 there was a significant difference in DWTINC between the first and second-hatched chick. In all cross fostering tests except those in which surplus chicks had to be placed in a different nest, only the first-hatched chick was cross fostered. Therefore, one would expect DWTINC not to be significantly different from the first-hatched chick control sample. Table 17 shows that DWTINC of cross fostered chicks was neither significantly different from either the first or second-hatched chicks.

The highest means in Table 17 are those of first-hatched Cattle Egrets and cross fostered Cattle Egret chicks in 1977. Analysis of variance showed no significant difference in means among first-hatched (1977), second-hatched (1976), and cross fostered (1977) chicks. Second-hatched chicks were tested by year with the cross fostered (1977) chicks. As might be expected, the P value was close to the significant level ($P = 0.05$) due to the higher DWTINC of the cross foster chicks relative to both years' second-hatched control groups. The cross-foster group DWTINC for 1976 was close to significant and was more similar to the DWTINC of second-hatched than first-hatched control groups.

Most foster Cattle Egret chicks grew at a rate comparable to resident nestlings in both years. A number of exceptional cases are documented in Table 18. In cases CE-1 through CE-5, the cross fostered chick was missing in a period too short to have grown and run from the nest. In the first three cases, resident chicks showed a slow rate of growth comparable to the second-hatched chick control group. In cases CE-4 and CE-5 residents showed normal growth, while introductions disappeared. In cases CE-6 and CE-7, both residents and foster chicks disappeared in four days. In cases CE-8 through CE-11 both chicks disappeared after one interval of recorded growth, which was above average for the resident and closer to first-hatched sample mean growth for the foster chick in cases CE-8 and CE-9. Case CE-10 suggests that even if a very small introduced chick is placed with a large resident it can compete successfully with the resident (and in this case, do better). Cases CE-12 through CE-15 were instances in which fostered chicks were found dead. In cases CE-13 and CE-14, introduced chicks exhibited normal growth during the first six to ten days. Therefore, death was considered

TABLE 18

INFORMATION ON CROSS FOSTERING TESTS AMONG CATTLE EGRETS

FISHERMANS ISLAND

Case Number (Year)	Nest Member	Initial weight (grams)	Final weight (grams)	Successive day checked	DWTINC (grams)	Final fate	Successive day of final fate
CE - 1	cross	154		4		gone	
(1976)	resident	171	209	4	9.5		
CE - 2	cross	127		2		gone	
(1976)	resident	103	161	6	9.7		
CE - 3a	cross 1	161		4		gone	
CE - 3b	cross 2	142	78	2	-32.0	killed (pecked)	4
(1976)							
	resident	118	171	6	8.8		
CE - 4	cross	55		2		gone	
(1976)	resident	63	162	6	10.5	dead in nest	10
CE - 5	cross	143		2		gone	
(1976)	resident	99	211	10	11.2		
	resident	53	211	10	15.8		
CE - 6	cross	102		4		gone	
(1976)	resident	96		4		gone	

TABLE 18 (Continued)

Case Number (Year)	Nest Member	Initial weight (grams)	Final weight (grams)	Successive day checked	DWTINC (grams)	Final fate	Successive day of final fate
CE - 7	cross	103		4		gone	
(1976)	resident	134		4		gone	
CE - 8	cross	151	239	5	17.6	gone	
(1977)	resident	55	118	3	21.0	gone	
CE - 9	cross	118	152	2	17.0	gone	9
(1977)	resident	84	189	5	21.0	gone	15
CE - 10	cross	21	123	7	14.6	gone	14
(1977)	resident	206	229	7	3.3		
CE - 11	cross	156	246	7	12.8	gone	14
(1977)	resident	134	237	7	14.7	gone	14
CE - 12	cross	154				killed (pecked)	7
(1977)							
	resident	162				gone	7
	resident	80				(pecked)	
CE - 13	cross	113	206	6	15.5	dead in nest	10
(1976)	resident	80	93	6	2.2	dead on ground	10
CE - 14	cross	123	255	10	13.2	dead in nest	13
(1976)	resident	89	256	10	16.7	o.k.	13

TABLE 18 (Continued)

Case Number (Year)	Nest Member	Initial weight (grams)	Final weight (grams)	Successive day checked	DWTINC (grams)	Final fate	Successive day of final fate
CE - 15	cross	106	151	6	7.5	dead in nest	10
(1976)	resident	103	124	4	5.2	removed	5
CE - 16	cross	165	226	6	10.2	out of nest	10
(1976)	resident	53	77	10	2.4		
CE - 17	cross	159	188	4	7.2	out of nest	6
(1976)	resident	172	229	4	14.2	out of nest	6
CE - 18	cross	184	203	4	4.8	out of nest	10
(1976)	resident	217	253	4	9.0	out of nest	6
	resident	214	253	4	9.8	out of nest	6
CE - 19	cross	105	171	4	16.5	out of nest	10
(1976)	resident	92	160	4	17.0	out of nest	10
CE - 20	cross	129	231	5	20.4	out of nest	7
(1977)	resident	25	154	7	18.4	removed	7
CE - 21	cross a	162				out of nest	7
(1977)							

TABLE 18 (Continued)

Case Number (Year)	Nest Member	Initial weight (grams)	Final weight (grams)	Successive day checked	DWTINC (grams)	Final fate	Successive day of final fate
CE - 21 (1977)	cross b	165				out of nest	7
	cross c	145				out of nest	7

representative of the normal portion of nestling mortality. Cases CE-12 and CE-3(b) showed that the cross fostered chick (and in case CE-12, the resident) appeared to have been killed by pecking. It is possible that something other than the parent pecked at the chicks. Cases CE-16 through CE-21 indicated that the larger foster chicks survived in foreign nests, although growth rates were highly variable.

The diversity of growth rates and varying fates among specific case numbered nests were typical of the overall results in cross fostering and perhaps of the normal nesting pattern in Cattle Egrets. Very small exchanged chicks did not grow more successfully than larger chicks up to 150 grams. Cross foster tests among WTCAT 3 (200-300 gram) chicks were not possible because of the climbing adeptness in this age group. Since Cattle Egret parents consistently rejected small, extraspecific chicks, they may have better recognitive ability in discriminating their own chicks than do other species tested. Further tests among older Cattle Egret chicks would elucidate this species' recognition capabilities.

Discussion

In colonial nesting bird species, parental recognition of young ensures that parents feed their own young; therefore, perpetuate their own genotype. Recognition has been demonstrated in numerous ground nesting gull and tern species. If mixed-species nesting were more advantageous than nesting intraspecifically and has been selected among some ardeid species, then recognition would seem an adaptation of high priority. A parent would risk not only contributing to another genotype but would risk maintenance of species integrity.

Recognition at the level of species was tested in cross fostering experiments involving reciprocal exchanges among Snowy Egrets, Louisiana Herons, Little Blue Herons, and Cattle Egrets. A schedule of exchanges was planned according to age classes, sample size, and possible combinations. However, as previously discussed, hatching among species was asynchronous, so the number of chicks the same size or age were limited at any one time. Often additional chicks had to be redistributed in order to maintain original brood size. Numbers and types of cross fostering tests were in part controlled by brood availability. DWTINC of resident chicks in nests receiving extraspecific foster chicks were not compared statistically with control groups. For all species, resident chick growth fell in a range between the means of third and second-hatched chick groups. If there were cases in which an adult of the cross fostered species took over the nest, original residents grew, although at a slower rate because of the frequency with which third-hatched chicks were left as residents in these experiments. Species integrity was also considered in the number of tests performed. Harris (1970) found that cross fostering <u>Larus</u> <u>argentatus</u> and <u>L</u>. <u>fuscus</u> resulted in mixed-species pair bonding in two successive years. Reciprocal exchanges were discontinued. Tests that repeatedly caused mortality were also halted, as the fate of fostered chicks was considered more important than size of sample.

The cross fostering experiments produced varying results. Louisiana Herons and Snowy Egrets did not reject extraspecific chicks from one to approximately ten days old. After this time some introduced chicks returned to their own nests if nests were close together. Other older chicks remained in the foster nests. Snowy Egret chicks grew at a slower rate when placed in Little Blue Heron nests. Louisiana Heron chicks were occasionally accepted but often actively rejected or missing on the next visit. Little Blue Heron chicks placed in the aforementioned species nests appeared accepted to a greater degree than the reciprocal. Cattle Egrets did reject extraspecific chicks of all three species. However, all test groups of intraspecific foster chicks grew at rates comparable to control groups regardless of foster chick size (age). Intraspecific recognition was not evident in this species.

Among intraspecific, ground nesting species, the onset of parent recognition coincides with chick mobility (Miller and Emlen, 1975). Rodgers (1979) noted that when young Louisiana Herons begin being fed away from the nest, chicks food-beg from non-parents, but parents selectively feed their own chicks and refuse others. (Direct evidence would require marking individual parents and chicks.) Kittiwake (Rissa tridactyla) and Gannet (Morus bassanus) (Cullen, 1957; White, 1971 respectively) parents do not recognize young until fledging. Nest permanency ensures that adults feed their own young. Young Kittwakes, however, do recognize siblings and strangers soon after hatching (Cullen, 1957). I observed some discrimination by older Louisiana Heron nestlings which accepted introduced chicks of their own species and actively ejected Cattle Egret chicks.

Differences in development of parental recognition could be explained by degree of chick mobility in other colonial nesting species. Nests remained intact for appoximately two weeks among herons studied. After this time, chicks began wandering from the nest, and would have had to be identified individually by the parent. Cross fostering experiments were done within the first two weeks, so reported acceptance of foreign chicks was explainable. However, all four heron species studied had the same developmental schedule (see Intraspecific Growth) and similar degree of nest site permanence. Yet species displayed differential ability to identify extraspecific chicks. Some Little Blue Herons and all Cattle Egrets recognized introduced chicks by either ejecting them or refusing them food. Although Cattle Egrets demonstrated the greatest degree of recognition, they did not distinguish between their own and foster chicks of their species.

Both of the discriminating species nested in closer intraspecific groups in both seasons at Fishermans Island. Little Blue Herons nested slightly later than Snowy Egrets and Louisiana Herons. Cattle Egrets initiated nesting after the majority of Little Blue Heron chicks had hatched. On several occasions, I observed adult Cattle Egrets being chased from an area occupied by juvenile Louisiana Herons. Perhaps both later nesting species have developed recognitive ability as a defense mechanism. They must secure a nest site among already active nesting adults, defend their nest, and possibly defend access to the nest from the large number of nearly fledged young of earlier nesting species.

INTRASPECIFIC GROWTH

Methods

In 1976 and 1977, growth measurements were taken of chicks from nests of 9.55 Snowy Egrets, 10.27 Louisiana Herons, 13.32 Little Blue Herons, and 17.23 Cattle Egrets respectively. Each nest was tagged with numbered surveyors tape. Individual nestlings were identified by red or black indelible ink marks on the right or left side of the body. Markings lasted about one week. When chicks became large enough, Fish and Wildlife Service size number 6 or color bands were placed on the tibio-tarsus.

Weight was obtained by placing a nestling in a mesh hosiery washing bag suspended on a 300 gram pesola scale. Weight of bag and total weight were recorded to the nearest 1.0 gram. Age was also noted among chicks whose hatching date was known. Older nestlings often released food before being weighed. Samples were weighed and added to the chick weight when possible. Culmen length was measured from the point where the anterior feathers of the forehead ceased to overlie the culmen to the distal tip (Baldwin et. al., 1931). Measurements were taken with vernier calipers to the nearest 0.1 centimeter. Nests were visited at three day intervals, although inclement weather resulted in a few longer intervals between recordings.

The mean daily weight increase, DWTINC, was calculated for every two measurements of weight taken on an individual chick on two successive visits. The DWTINC was grouped by weight category for each species in each year. Weight categories, WTCATS, were partitioned as suggested by scattergrams of weight by DWTINC. Points were clustered such that a reasonable partition, consistent for all species, was between 1 to 99 grams (WTCAT 1), 100 to 199 grams (WTCAT 2), and from 200 to 299 grams (WTCAT 3). Weight increase per day growth curves were generated using the computed DWTINC within each WTCAT. A small sample of known one-day old chicks of each species was used as the initial weight. Additional known-aged chick measurements were used to compute average weight by age to be compared with the derived growth curves.

The variable DWTINC was tested for differences among WTCATS, among years, and hatching sequences for each species. This variable was also tested for differences within cross fostered chicks, the respective species control group, and the fostering species control group. Those means with homogeneous variances (Bartlett's test, $P < 0.05$) were tested by analysis of variance and a Student-Newman-Keuls _a posteriori_ test if there was a significant difference. For cases in which DWTINC showed heterogeneous variance, a Kruskal-Wallis analysis of variance or a Mann-Whitney nonparametric test was performed. Statistical package for the Social Sciences, 1977, was used for all aforementioned tests.

Results

Comparison of DWTINC among Hatching Sequences

Portions of this study required information on intraspecific growth rates. Sufficient samples of known-aged chicks beyond one day, and chicks at asymptotic weight were not obtainable. Therefore, the variable DWTINC was computed for all control test group chicks which has been weighed on at least two successive visits.

Review of actual DWTINC means indicated that in most cases third-hatched chick groups grew at a slower rate (mean increase per day) than earlier hatched nestmates (Table 19). Comparison of hatching sequences in DWTINC was most useful in depicting differential growth in the most extreme cases. First-hatched Louisiana Heron chicks grew at the highest increment per day among all species in all hatching sequences in both years (Table 19). This species showed a significant difference in DWTINC among all three hatching sequences in 1976 (Tables 20 and 21). The third-hatched control group was significantly different from the first and second-hatched chick groups in 1977 (Tables 20 and 21). All three hatching sequences among Cattle Egrets, 1977, were significantly different in DWTINC (Tables 20 and 21). Little Blue Herons grew at rates similar to the former species in 1976 (Table 19) but showed a closer similarity in growth among nestmates than in 1977 when growth was slower and hatching sequences exhibited a slightly larger magnitude of difference in growth rate (Table 19). All hatching sequences of Snowy Egrets grew at

TABLE 19

DAILY WEIGHT INCREASE (DWTINC) OF CHICKS OF FOUR HERON SPECIES AT FISHERMANS ISLAND, 1976 - 1977

Year	Hatching Sequence	Species	N	Mean DWTINC	SD
1976	1	SE	27	13.2	7.5
	2		24	12.3	7.6
	3		4	8.2	7.1
	1	LH	36	21.7	9.2
	2		36	16.3	9.5
	3		3	5.9	2.0
	1	LB	49	17.4	8.7
	2		43	17.2	8.5
	3		12	17.4	9.6
	1	CE	70	15.4	7.4
	2		52	13.2	7.3
1977	1	SE	60	15.3	9.2
	2		53	14.0	10.2
	3		27	11.2	7.8
	1	LH	25	16.1	7.4
	2		27	13.0	10.1
	3		8	6.0	6.4
	1	LB	26	14.9	6.9
	2		28	13.8	8.9
	3		18	19.6	8.8
	1	CE	31	18.2	7.0
	2		30	12.0	8.0
	3		13	9.1	10.1

TABLE 20

COMPARISON OF MEAN DAILY WEIGHT INCREASE BETWEEN HATCHING SEQUENCES OF EACH SPECIES USING ONE-WAY ANALYSIS OF VARIANCE

Year	Species	Hatching Sequence	MS Group	df	Ms Error	df	F	P	Significance level[1]
1977	SE	1-3	44.2606	2	56.6768	51	0.781	0.4633	NS
	LH	1-3	509.3862	2	85.2258	72	5.972	0.0040	**
	LB	1-3	0.3397	2	76.2695	101	0.004	0.9956	NS
1977	SE	1-3	153.0744	2	87.8074	137	1.743	0.1788	NS
	LH	1-3	309.3254	2	74.7719	57	4.137	0.0210	*
	LB	1-3	158.6735	2	67.2421	69	2.36	0.1020	NS
	CE	1-3	509.4971	2	73.3368	71	6.947	0.0018	**

[1] P = Probability values, * $P \leq 0.05$, ** $P \leq 0.01$, NS = not significant at the 0.05 level.

TABLE 21

COMPARISON USING STUDENT-NEWMAN-KEULS TEST OF MEAN DAILY WEIGHT INCREASE (DWTINC), FISHERMANS ISLAND

Year	Species	Hatching Sequence	Mean[1] DWTINC
1976	LH	1	21.7
		2	16.3
		3	5.9
1977	LH	1	16.1
		2	13.0
		3	6.0
	CE	1	18.2
		2	12.0
		3	9.1

---

[1] Vertical lines connect means that are not significantly different at $\alpha = 0.05$.

a more rapid rate in 1977, and the magnitudes of rates were more similar than in 1976 (Table 19). No significant differences in DWTINC by hatching sequence occurred in this species.

Comparison of DWTINC within Weight Categories

The computed variable, DWTINC, was not sensitive to changes in growth rate through time. Therefore, the variable was partitioned into weight categories, WTCATS, which represented age intervals among control group chicks. DWTINC within WTCATS were compared within hatching sequences by species and year. Generally DWTINC increased at each higher WTCAT among all species and hatching sequences (Tables 22 and 23). The mean increment in DWTINC was usually larger from WTCAT 1 to WTCAT 2 than from WTCAT 3 for all species. Cases in which DWTINC was greater for WTCAT 2 than WTCAT 3 occurred in 1976 among first, second and third-hatched Snowy Egrets and among first-hatched Louisiana Herons (Table 22). However, only among first and second-hatched Little Blue Herons did DWTINC means differ significantly between WTCAT 2 and WTCAT 3 (Tables 24 and 25). The rate of weight increase was high during WTCAT 2. Possibly chicks had attained a substantial portion of asymptotic weight and required less food during later stages of growth.

First and second-hatched Snowy Egrets exhibited a slow rate of growth in 1976 (Table 22). DWTINC among WTCATS were not significantly different (Tables 24 and 26), and during WTCAT 1 and WTCAT 2 increments, growth was very similar

TABLE 22

MEAN DAILY WEIGHT INCREASE (DWTINC) IN WEIGHT CATEGORIES FISHERMANS ISLAND, 1976

Species	Hatching Sequence	Weight Category[1]	N	Mean DWTINC	SD
SE	Hatch 1	1	7	10.3	4.4
		2	17	15.3	8.1
		3	3	7.8	5.5
	Hatch 2	1	8	8.2	3.5
		2	12	14.6	9.3
		3	4	3.6	5.7
LH	Hatch 1	1	8	13.6	5.6
		2	19	24.4	8.2
		3	9	23.3	10.2
	Hatch 2	1	14	9.4	7.5
		2	18	19.6	8.3
		3	4	25.6	4.5
LB	Hatch 1	1	15	12.0	5.8
		2	22	21.4	9.1
		3	12	16.7	7.5
	Hatch 2	1	16	12.7	6.5
		2	19	20.0	9.4
		3	8	19.5	6.5
	Hatch 3	1	8	13.1	5.5
		2	3	26.9	13.4
		3	1	23.0	-
CE	Hatch 1	1	22	12.5	5.8
		2	34	16.4	8.0
		3	14	17.8	7.0
	Hatch 2	1	30	10.5	6.4
		2	19	16.2	7.3
		3	3	21.0	3.0

---

[1] See text for weight category intervals.

TABLE 23

MEAN DAILY WEIGHT INCREASE (DWTINC) IN WEIGHT CATEGORIES FISHERMANS ISLAND, 1977

Species	Hatching Sequence	Weight Category	N	Mean DWTINC	SD
SE	1	1	7	9.5	4.0
		2	9	14.7	6.6
		3	9	21.0	6.9
	2	1	25	9.8	7.2
		2	26	17.1	9.7
		3	7	19.1	5.7
	3	1	16	9.3	8.7
		2	11	14.0	5.3
		3	0	-	-
LH	1	1	30	11.1	5.3
		2	44	18.1	6.9
		3	18	19.9	9.4
	2	1	6	7.7	5.2
		2	15	14.8	3.8
		3	5	20.9	2.6
	3	1	5	6.2	3.1
		2	2	13.3	7.5
		3	0	-	-
LB	1	1	9	9.0	6.1
		2	10	15.4	3.6
		3	6	21.5	4.8
	2	1	12	6.8	3.4
		2	14	15.5	3.8
		3	4	28.5	10.7
	3	1	9	8.2	2.5
		2	4	14.6	3.3
		3	2	26.5	1.8
CE	1	1	13	15.8	4.0
		2	15	18.4	9.1
		3	3	19.9	6.2
	2	1	15	10.2	5.1
		2	12	16.4	10.2
		3	3	13.7	6.4

TABLE 23 (Continued)

Species	Hatching Sequence	Weight Category	N	Mean DWTINC	SD
CE	3	1	7	6.8	6.7
		2	4	24.5	12.8
		3	2	14.9	0.1

[1] See text for weight category intervals.

TABLE 24

COMPARISON USING ONE-WAY ANALYSIS OF VARIANCE OF DAILY WEIGHT INCREASE AMONG WEIGHT CATEGORIES (WTCATS) WITHIN HATCHING SEQUENCES FOR MEANS WITH HOMOGENEOUS VARIANCES

FISHERMANS ISLAND

Test	Species	Hatching Sequence	Ms Groups	df	Ms Error	df	F	P	Significance level[1]
Among WTCATS 1976	SE	1	109.8963	2	51.6201	24	2.129	0.1409	NS
	LH	1	344.1169	2	68.3935	33	5.031	0.0124	*
	LH	2	603.7429	2	59.8561	33	10.087	0.0004	***
	LB	1	397.3645	2	62.0063	46	6.408	0.0035	**
	LB	2	262.5010	2	62.7102	40	4.186	0.0224	*
	LB	3	266.7741	2	63.2511	9	3.585	0.0716	NS
	CA	1	146.3289	2	51.6023	67	2.894	0.0623	NS
	CA	2	287.6079	2	44.2672	49	6.497	0.0031	*
Among WTCATS 1977	SE	1	263.1899	2	37.6345	24	6.993	0.0045	*
	SE	2	437.5327	2	69.0040	55	6.341	0.0033	*
	SE	3	143.6626	1	56.9837	25	2.252	0.1249	NS
	LH	2	240.6876	2	15.6109	23	15.418	0.0001	***
	LH	3	73.0321	1	18.9344	5	3.857	0.1067	NS
	LB	1	285.3611	2	23.9492	22	11.915	0.0003	***
	LB	3	289.3330	2	7.2698	12	39.799	0.0000	***
	CE	1	34.3342	2	49.3572	28	0.696	0.5072	NS
	CE	2	128.4793	2	59.3583	27	2.164	0.1343	NS

---

[1] P = probability values, $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$, NS = not significant at the 0.05 level.

TABLE 25

COMPARISON USING STUDENT-NEWMAN-KEULS TEST OF MEAN DAILY WEIGHT INCREASE AMONG WEIGHT CATEGORIES (WTCATS), FISHERMANS ISLAND

Test	Species	Hatching Sequence	Weight Category	Means
Among WTCATS 1976	LH	1	1	13.6
			2	24.4│
			3	23.3│
	LH	2	1	9.4
			2	19.6│
			3	25.6│
	LB	1	1	12.0│
			3	16.7│
			2	21.4
	LB	2	1	12.7│
			3	19.5│
			2	20.0
	CE	2	1	10.5
			2	16.2│
			3	21.0│
Among WTCATS 1977	SE	1	1	9.5│
			2	14.7│
			3	21.0
	SE	2	1	9.8
			2	17.1│
			3	19.1│
	LH	1	1	11.1│
			2	18.1│
			3	19.1
	LH	2	1	7.7
			2	14.8
			3	20.9
	LB	1	1	9.0
			2	15.4
			3	21.5
	LB	3	1	8.2
			2	14.6
			3	26.5

TABLE 25 (Continued)

Test	Species	Hatching Sequence	Weight Category	Means
Among WTCATS 1977	CE	3	1	6.8
			3	14.9
			2	24.5

---

[1] Vertical lines connect means are not significantly different at $\alpha = 0.05$.

TABLE 26

COMPARISON USING KRUSKAL-WALLIS TEST OF DAILY WEIGHT INCREASE AMONG WEIGHT CATEGORIES (WTCATS) FOR MEANS HAVING HETEROGENEOUS VARIANCES FISHERMANS ISLAND

Test	Species	Hatching Seqence	$\chi 2$	P	Significance level
Among WTCATS 1976	SE	2	3.169	0.205	NS
Among WTCATS 1977	LH	1	9.980	0.007	**
	LB	2	20.580	0.000	***
	CE	2	5.025	0.081	NS
	CE	3	6.267	0.044	*

Note: χ^2 corrected for ties.

[1] P = Probability values, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, NS = not significant at the 0.05 level.

to that of Little Blue Herons in 1977 (Table 25). However, at higher weights in WTCAT 3, growth was extremely low relative to growth in this species in 1977 and relative to other species (Tables 22 and 23). Because growth was not rapid during either WTCAT 1 or WTCAT 2, it is assumed that chicks were not near asymptote. Low rate of weight increase during WTCAT 3 represented overall poor growth for Snowy Egrets.

Within the Louisiana Heron control groups, each hatching sequence generally grew at an increased rate at each higher WTCAT. The magnitude of increase was greater in several WTCAT cases in this species than in other species (Table 22). First and second-hatched Louisiana Herons showed a significant difference in DWTINC among WTCATS during both years. Generally WTCAT 1 was significantly lower than WTCATS 2 and 3.

Significantly differences in WTCAT growth rates occurred among second-hatched Cattle Egrets in 1976 and among third-hatched chicks in 1977 (Tables 23 and 24). Both hatching sequences represented the smallest (youngest) chick in the brood, as in 1976 not enough third-hatched chicks survived to be analyzed. In both years, significant differences resulted from extreme DWTINC values in two WTCATS. These data suggest that an especially low stage of growth could be compensated at some later stage by relatively rapid growth.

All factors considered in DWTINC comparisons influenced rates. Weight category, hatching sequence, and year contributed to DWTINC differences within the same species.

In the same nesting season growth rate variations were not common to all species. To better understand patterns of species specific growth, rates were depicted in growth curves during the first three weeks of age.

Construction of Growth Curves

Rate of growth in feather development or in hard parts may be less variable among nestlings, but for that reason, they are poor indicators in an analysis of comparative growth. Measurements and weights from control groups and additional measurements and weights gathered from random chicks of each species were pooled without regard to hatching sequence, or year of nesting. The resulting regressions in Table 27 show a strong relationship between culmen and weight. Because culmen grows at a consistent increment per day despite loss of weight, culmen is considered the independent variable upon which the dependent variable, weight, was regressed. In a large enough sample size, it should be possible to correlate an average weight with culmen length, and therefore with age.

The DWTINC from each WTCAT was used to construct growth curves for each species according to hatching sequence and year. The resulting curves allowed a more integrated interpretation of species specific growth patterns within broods and among different years. Weight at day one was the average known weight among a known-aged sample of each chick species. The same mean weight was used for both years, as intraspecific age-one chick weight is quite constant geo-

TABLE 27

REGRESSION OF CULMEN LENGTH AGAINST WEIGHT IN A SAMPLE OF CHICKS FROM ONE TO TWENTY-ONE DAYS OF AGE

Species	Coefficient of determination r^2	N	df	P
SE	0.83348	300	1,298	<0.001
LH	0.92880	136	1,134	<0.001
LB	0.90372	166	1,164	<0.001
CE	0.84524	189	1,187	<0.001

Note: Data pooled from Fishermans Island in 1976 and 1977.

graphically and temporally (Shanholtzer, 1972; McVaugh, 1972; personal observation).

Snowy Egret Growth

Comparison of Snowy Egret growth rates during the 1976 and 1977 seasons indicated that in both years, broods grew at a slower rate than broods of other species. There was not much discrepancy in weight among first and second-hatched chicks. During 1976, the gains made by the first-hatched chicks from days 9 to 16 were balanced by increased growth rate in second-hatched chicks from days 12 to 20, while first-hatched chick growth declined from day 16 onward (Figure 11). According to the 1976 growth curve, both hatching sequences would have taken a longer period of time to reach asymptotic weight. In 1977, third-hatched chicks survived long enough to be represented through WTCAT 2. During the time the third-hatched chicks grew, growth rates of the first and second-hatched chicks were slower than in 1976, and quite similar to each other (Figure 12). After the third-hatched chicks expired or disappeared, growth rates of the first and second-hatched chicks became more rapid than 1976 growth during the same time intervals. These data suggested that parent Snowy Egrets attempted to feed all three chicks, possibly inhibiting potential growth rates among older nestlings. Alternatively, the slower rates in these chicks may have been due to some local change in feeding conditions and/or weather. A considerable amount of mortality was noted, particularly within this size and larger sized chicks in 1976.

Figure 11. Derived Growth Curves for
Snowy Egrets in 1976.

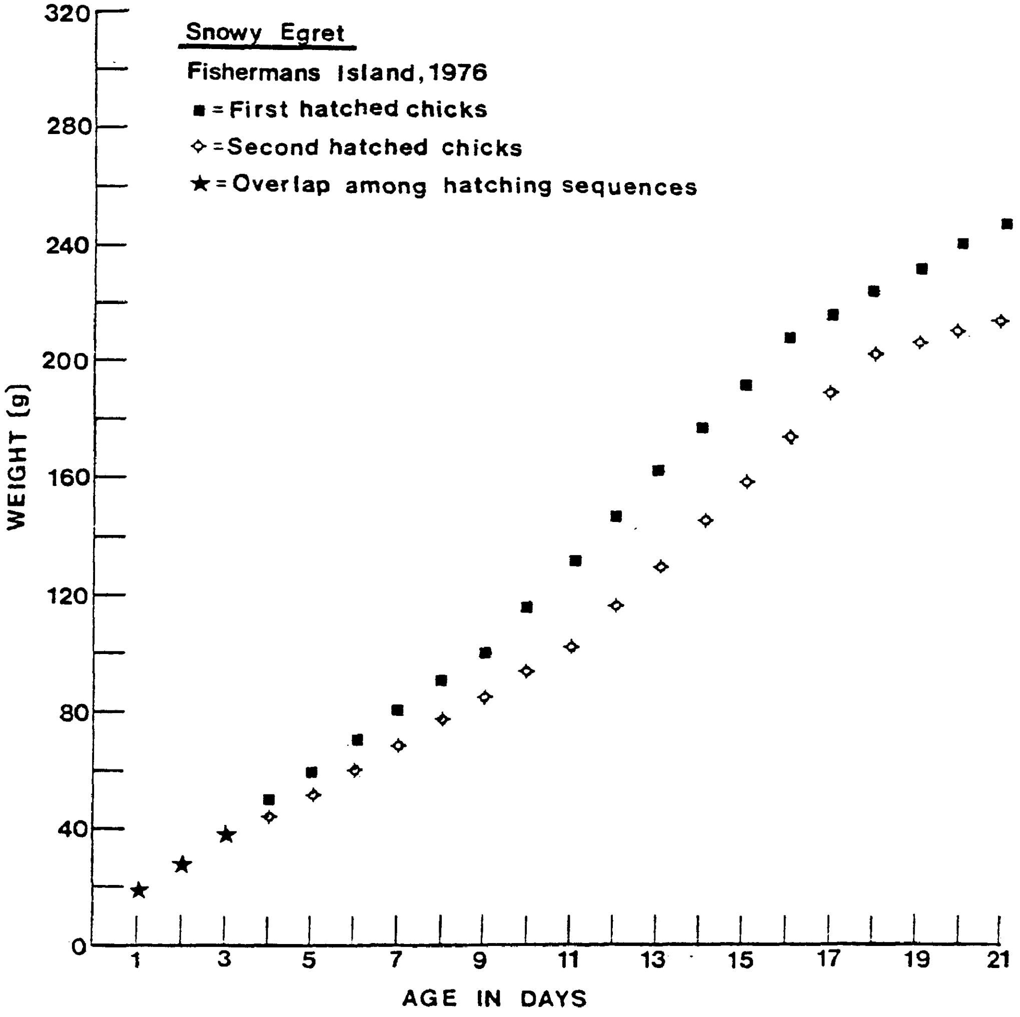
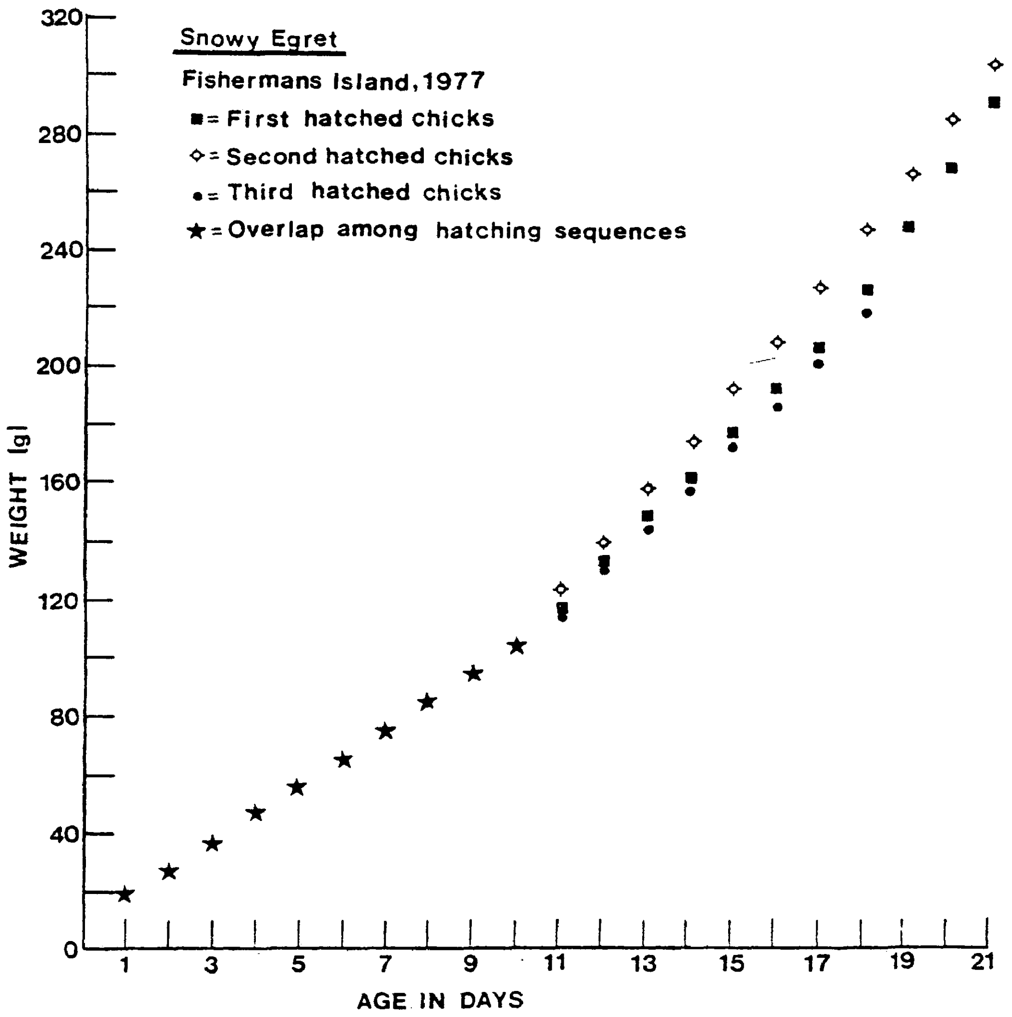

Snowy Egret
Fishermans Island, 1976
■ = First hatched chicks
◇ = Second hatched chicks
★ = Overlap among hatching sequences
WEIGHT (g)
320
280
240
200
160
120
80
40
0
1
3
5
7
9
11
13
15
17
19
21
AGE IN DAYS

Figure 12. Derived Growth Curves for Snowy Egrets in 1977.


Snowy Egret
Fishermans Island, 1977
■ = First hatched chicks
◇ = Second hatched chicks
● = Third hatched chicks
★ = Overlap among hatching sequences
WEIGHT [g]
0
40
80
120
160
200
240
280
320
AGE IN DAYS
1
3
5
7
9
11
13
15
17
19
21

Heavy winds and rain may have affected growth and mortality in Snowy Egrets. Perhaps parents did not offer sufficient protection to this aged group chicks. Much later in the season many small-sized Snowy Egret chicks were standing in limbs within early nesting subzones. It was suspected that these chicks were retarded in growth rather than young from later nesting birds.

Little Blue Heron Growth

Growth rates in 1976 and 1977 showed that among all hatching sequences, Little Blue Heron chicks grew at a faster rate in 1976 (Figures 13 and 14). The magnitude of difference in weight by age was larger in the poorer growth year between first and second-hatched chicks. The very rapid growth rate in the third-hatched chicks during 1976 may have been distorted because of the small sample size. In 1977, third-hatched chicks grew more rapidly (even with a larger sample size), than second-hatched chicks. In both years, many of the Little Blue Heron nests contained four eggs and in many cases, it was the fourth-hatched chick that either died or grew slowly.

Characteristically, the smallest chick in the clutch among all species studied would vocalize more than its nestmates. Perhaps parent Little Blue Herons responded to the increased calling by feeding the most active vocalizer. Perhaps older Little Blue Heron nestlings were more passive than older nestlings of other species in obtaining food, and so the youngest vocalizing chick in this species might gain an

Figure 13. Derived Growth Curves for Little Blue Herons in 1976.

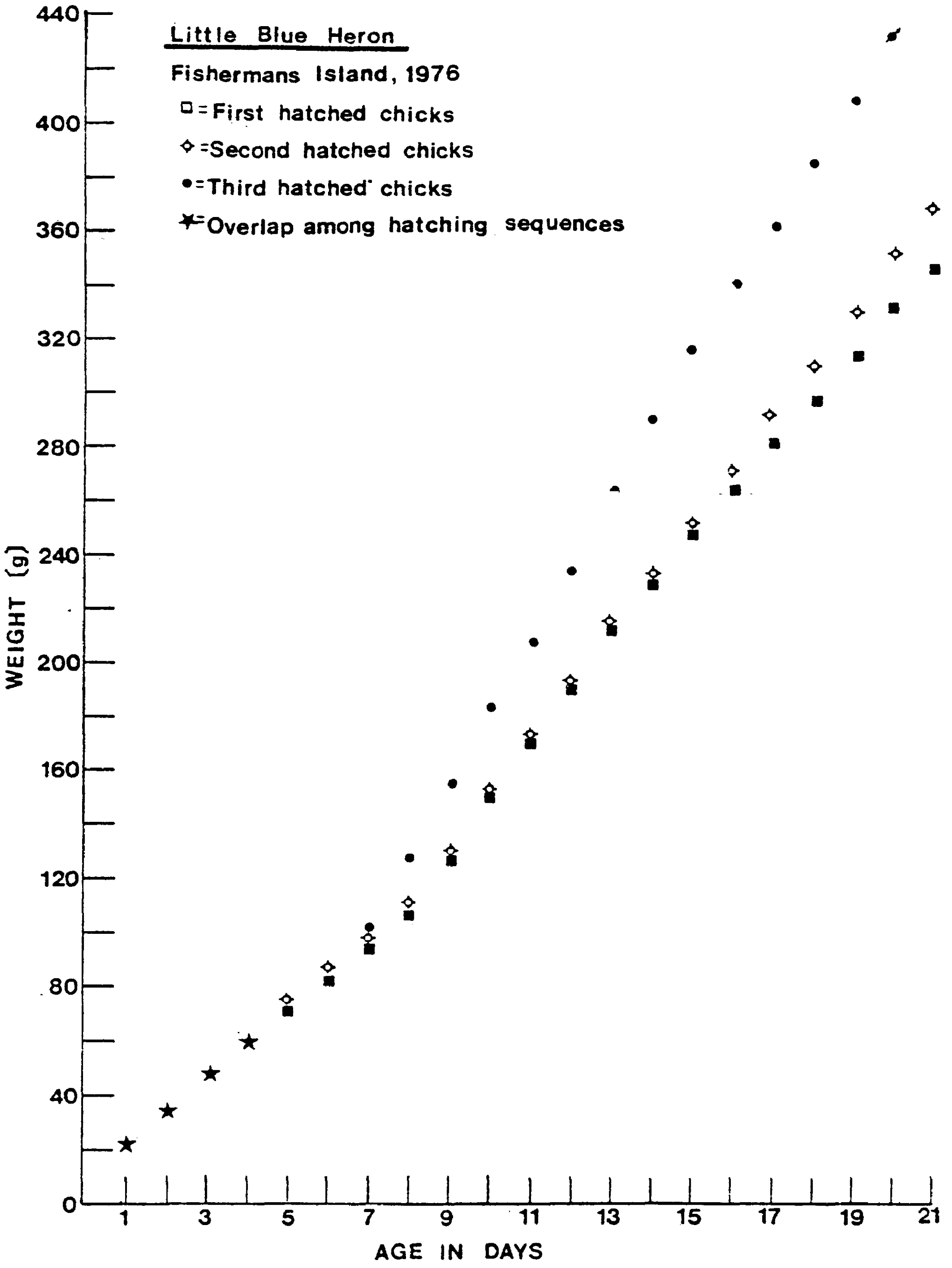
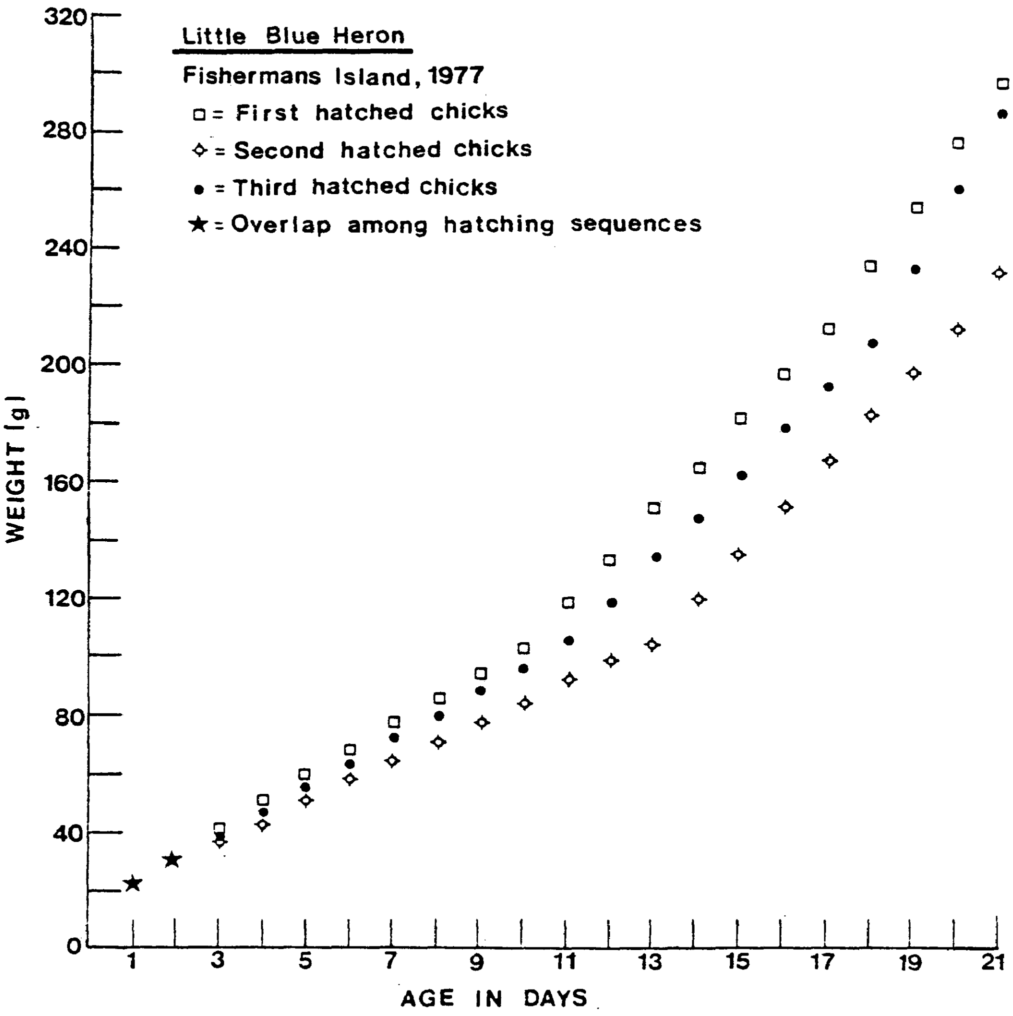

Little Blue Heron
Fishermans Island, 1976
□=First hatched chicks
◇=Second hatched chicks
●=Third hatched chicks
★=Overlap among hatching sequences
WEIGHT (g)
0
40
80
120
160
200
240
280
320
360
400
440
1
3
5
7
9
11
13
15
17
19
21
AGE IN DAYS

Figure 14. Derived Growth Curves for Little Blue Herons in 1977.


Little Blue Heron
Fishermans Island, 1977
□ = First hatched chicks
◇ = Second hatched chicks
● = Third hatched chicks
★ = Overlap among hatching sequences
WEIGHT (g)
0
40
80
120
160
200
240
280
320
1
3
5
7
9
11
13
15
17
19
21
AGE IN DAYS

advantage over its nestmates.

Louisiana Heron Growth

Third-hatched Louisiana Herons were also quite vocal, but to no avail because both years, within the sampled population and among numerous observed nests, the third-hatched chick seldom survived through day 14 after hatching. There was also a size difference between the first and second-hatched chicks within the brood. Figures 15 and 16 show that weight differences between first and second-hatched chicks continued in both years through the third week after hatching. First-hatched Louisiana Herons grew at the higher rate during 1976 than the first-hatched species. In both years the difference in DWTINC between first and second-hatched Louisiana Heron chicks was similar and was greater than that of any other species of the same age. Possibly the lower magnitude of the increase per day in 1977 was due to initial survival of the third-hatched chick in many sampled broods.

It may be that this species' strategy is to put more effort into feeding one chick so that it might grow and fledge in a shorter time period. Alternatively, Louisiana Heron chicks may be more aggressive at obtaining food and need only a slight head start over a nestmate to perpetuate their advantage in competing for food. The author has noted a discrepancy in size between nestmates and chick aggressiveness in several colonies in both Virginia and South Florida.

Figure 15. Derived Growth Curves for Louisiana Herons in 1976.

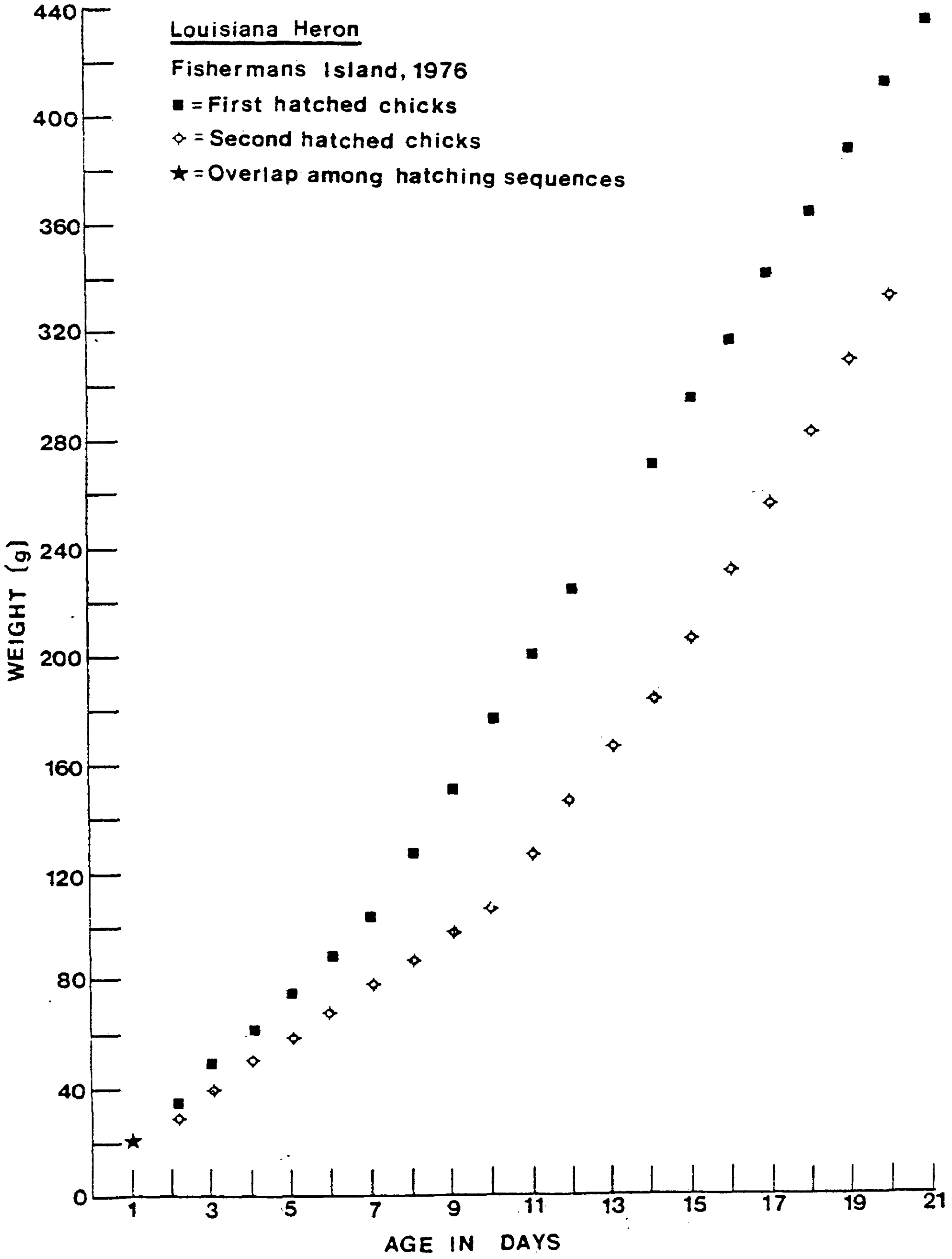
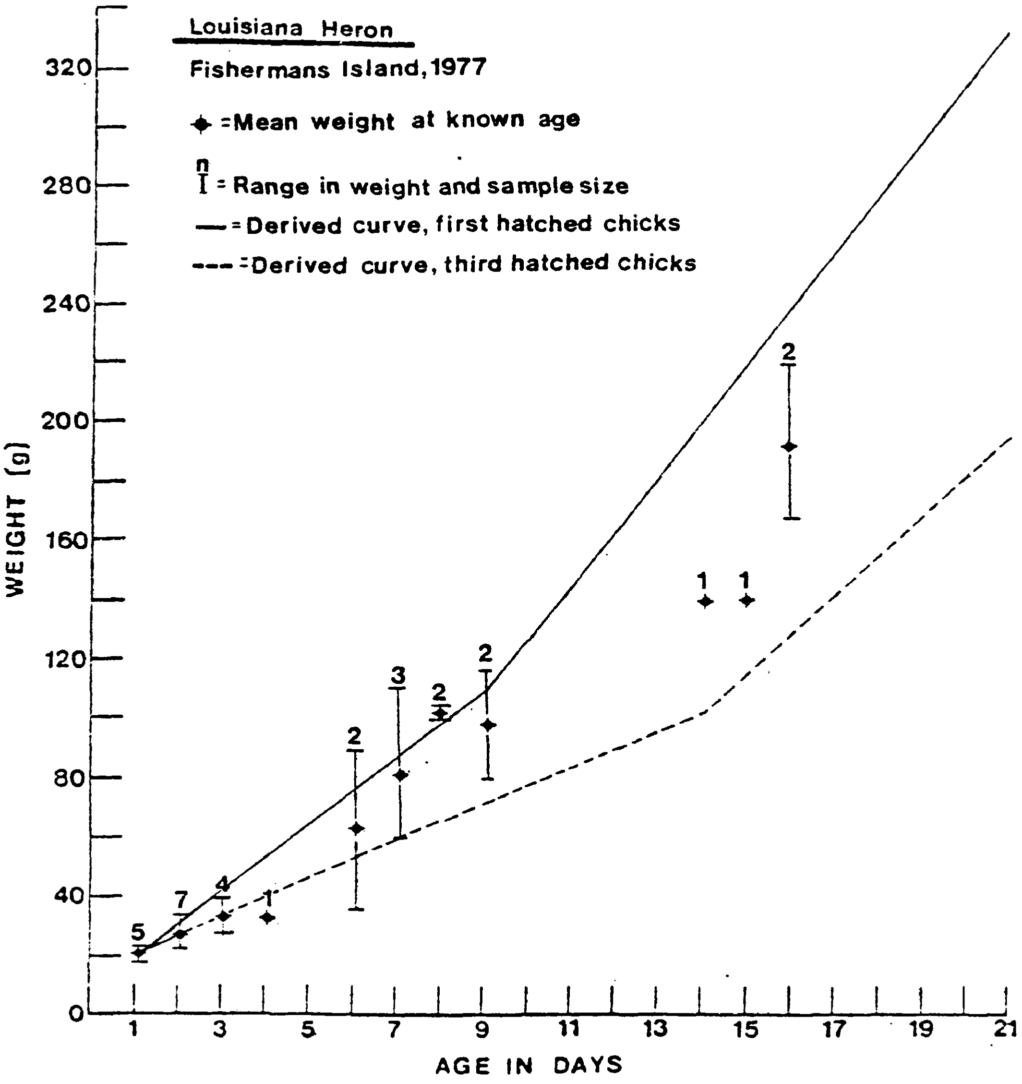

Louisiana Heron
Fishermans Island, 1976
■ = First hatched chicks
◇ = Second hatched chicks
★ = Overlap among hatching sequences
WEIGHT (g)
0
40
80
120
160
200
240
280
320
360
400
440
AGE IN DAYS
1
3
5
7
9
11
13
15
17
19
21

Figure 16. Derived Growth Curves for Lousiana Herons in 1977.


Louisiana Heron
Fishermans Island, 1977
= Mean weight at known age
n I = Range in weight and sample size
— = Derived curve, first hatched chicks
--- = Derived curve, third hatched chicks
WEIGHT (g)
0
40
80
120
160
200
240
280
320
AGE IN DAYS
1
3
5
7
9
11
13
15
17
19
21
5
7
4
1
2
3
2
2
1
1
2

It would be informative to follow growth rates of first and second-hatched chicks in a sample of Louisiana Heron nests in which the third-hatched chick survives over a longer period.

Cattle Egret Growth

First-hatched Cattle Egret chicks grew at a higher rate during the 1977 season (Figures 17 and 18). In the same year, there was more of a difference between the first and second-hatched chicks' growth rate, with the latter growing at a slower rate than in 1976. In 1977, sampled broods indicated that Cattle Egret adults were able to support a third-hatched, slow-growing chick as well as a first-hatched chick at slight expense to the growth rate of the second-hatched chick. Yet overall growth was higher for Cattle Egret broods in 1977.

Measurements of Known Aged Chicks

To test the validity of the derived growth curves, the author attempted to obtain a sample of measurements from known-aged chicks among the three species. In view of the small sample size obtained, no attempt was made to separate chicks according to hatching sequence (Tables 28 and 29). However, data from third-hatched chicks having very low weights were eliminated from the sample. The information was graphed in comparison with the alternate method, which represents growth rate using only average weight at day one (Figures 19, 20 and 21). Days on the axis of the graph coincide with known ages. For the derived curves, the actual number

Figure 17. Derived Growth Curves for Cattle Egrets in 1976.

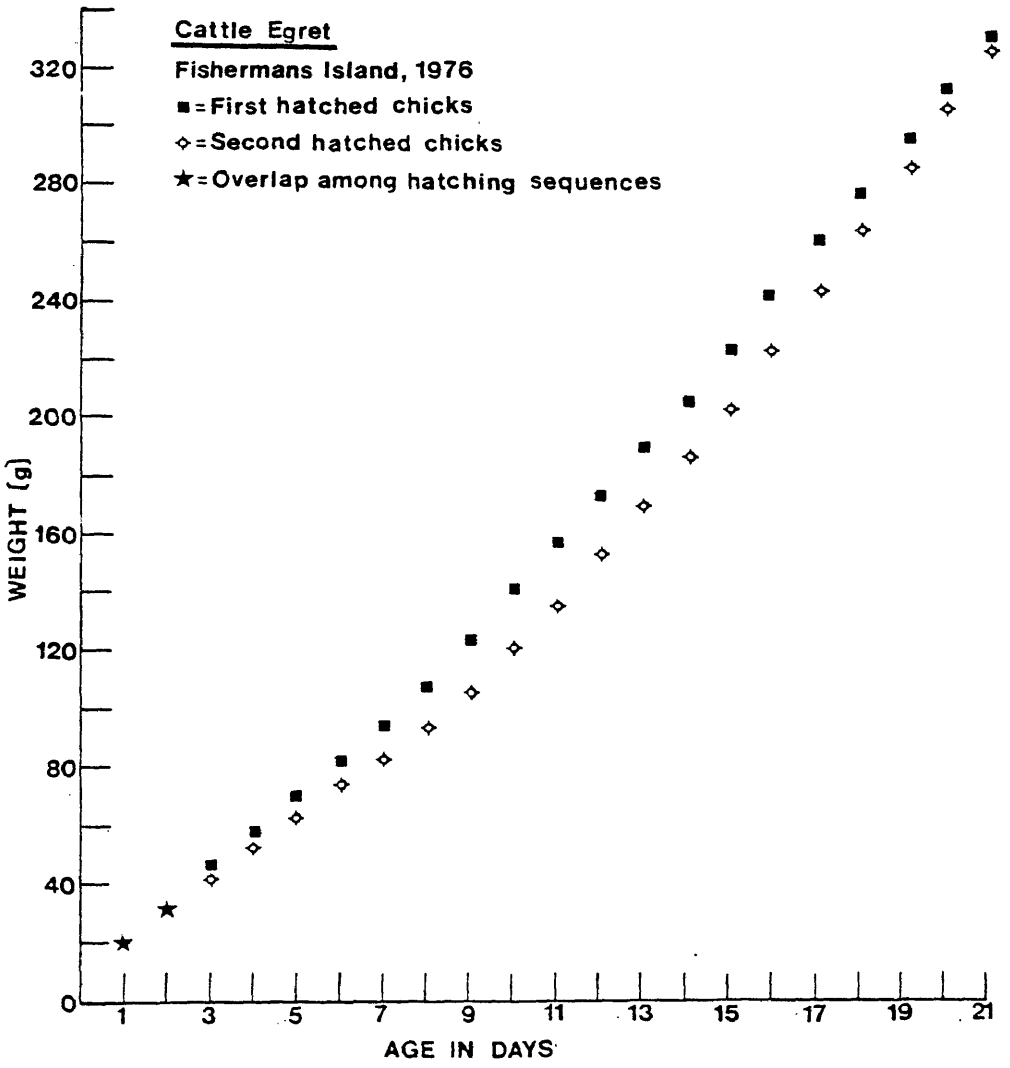

Cattle Egret
Fishermans Island, 1976
■ = First hatched chicks
◇ = Second hatched chicks
★ = Overlap among hatching sequences
WEIGHT (g)
0
40
80
120
160
200
240
280
320
1
3
5
7
9
11
13
15
17
19
21
AGE IN DAYS

Figure 18. Derived Growth Curves for Cattle Egrets in 1977.

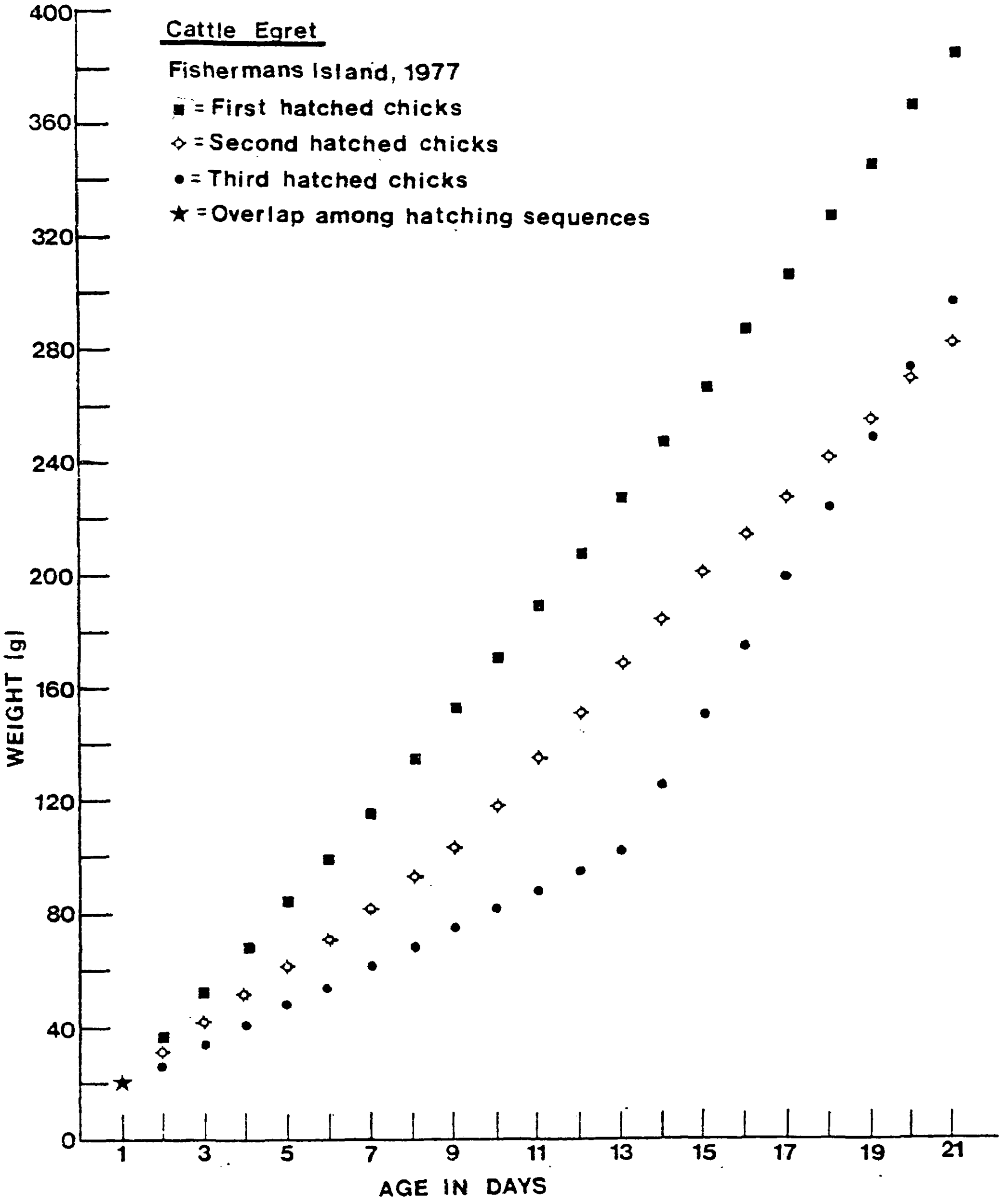

Cattle Egret
Fishermans Island, 1977
■ = First hatched chicks
◇ = Second hatched chicks
● = Third hatched chicks
★ = Overlap among hatching sequences
WEIGHT (g)
0
40
80
120
160
200
240
280
320
360
400
AGE IN DAYS
1
3
5
7
9
11
13
15
17
19
21

TABLE 28

MEAN, MINIMUM AND MAXIMUM WEIGHT OF SNOWY EGRETS, LOUISIANA HERONS, AND LITTLE BLUE HERONS OF KNOWN AGE, FISHERMANS ISLAND, 1977

Species	N	Age (days)	Mean Weight (grams)	SD	Minimum weight (grams)	Maximum weight (grams)
SE	13	1	18.1	1.3	16.0	21.0
	13	2	22.6	4.7	16.0	29.0
	13	3	29.5	6.4	21.0	38.0
	11	4	40.9	12.5	24.0	64.0
	3	5	39.3	18.6	20.0	56.0
	3	6	60.0	17.8	46.0	80.0
	5	7	52.4	24.5	18.0	81.0
	5	8	75.0	28.1	39.0	102.0
	10	9	90.2	29.6	50.0	146.0
	3	10	116.0	6.08	112.0	123.0
	5	11	121.6	53.2	64.0	197.0
	7	12	157.0	25.5	107.0	186.0
	1	13	146.0	-		
	3	14	164.0	25.5	139.0	190.0
	4	15	149.2	49.3	78.0	191.0
	2	16	228.0	24.0	211.0	245.0
	1	19	242.0	-		
LH	5	1	20.4	2.5	17.0	24.0
	7	2	26.1	4.6	22.0	33.0
	4	3	32.2	4.8	27.0	38.0
	1	4	31.0			
	2	6	61.5	38.9	34.0	89.0
	3	7	80.0	26.7	59.0	110.0
	2	8	101.5	2.1	100.0	103.0
	2	9	97.0	26.9	78.0	116.0
	1	14	139.0			
	1	15	140.0			
LB	6	1	22.2	2.2	20.0	25.0
	7	2	23.3	2.4	21.0	27.0
	4	3	26.5	5.8	18.0	31.0
	2	4	32.0	5.7	28.0	36.0

TABLE 28 (Continued)

Species	N	Age (days)	Mean weight (grams)	SD	Minimum weight (grams)	Maximum weight (grams)
	4	5	45.0	16.1	23.0	60.0
	4	6	46.8	13.9	26.0	55.0
	2	7	71.5	14.8	61.0	82.0
	1	9	148.0	-	-	-
	1	10	153.0	-	-	-
	3	12	179.3	50.0	149.0	237.0
	2	16	237.0	56.6	197.0	277.0
	1	17	241.0	-	-	-
	1	19	252.0	-	-	-

TABLE 29

MEAN, MINIMUM AND MAXIMUM CULMEN LENGTH OF SNOWY EGRETS, LOUISIANA HERONS, AND LITTLE BLUE HERONS OF KNOWN AGE AT FISHERMANS ISLAND, 1977

Species	N	Age (days)	Mean culmen (mm)	SD	Minimum length (mm)	Maximum length (mm)
SE	13	1	10.5	0.78	10	12
		2				
	13	3	12.9	1.12	11	15
	11	4	14.5	1.63	12	17
	3	5	14.3	1.53	14	16
	3	6	17.0	2.00	15	19
	5	7	14.8	2.78	12	18
	5	8	20.2	2.68	16	23
	10	9	22.3	2.75	18	28
	3	10	22.7	1.15	22	24
	5	11	26.2	3.83	23	32
	7	12	28.4	3.60	24	32
	1	13	29.0	-		
	3	14	32.0	-	32	32
	4	15	32.2	3.40	28	35
	2	16	34.5	2.12	33	36
	1	19	38.0	-		
LH	5	1	11.4	0.89	10	12
	7	2	12.7	0.76	12	14
	4	3	13.5	1.00	13	15
	1	4	15.0	-		
	2	6	21.5	4.95	18	25
	3	7	22.0	1.73	20	23
	2	8	23.0	1.41	22	24
	2	9	25.5	0.71	25	26
	1	14	34.0	-	-	-
	1	15	37.0	-	-	-
	2	16	36.5	0.71	36	37

TABLE 29 (Continued)

Species	N	Age (days)	Mean Culmen (mm)	SD	Minimum length (mm)	Maximum length (mm)
LB	6	1	10.7	0.82	10	12
	7	2	11.9	0.90	10	13
	4	3	13.0	0.82	13	14
	2	4	13.5	0.71	13	14
	4	5	15.0	1.55	14	16
	4	6	16.0	1.55	15	17
	2	7	20.5	2.12	19	22
	1	9	27.0	-	-	-
	1	10	33.0	-	-	-
	3	12	31.0	5.30	25	33
	1	13	-	-	-	-
	1	14	37.0	-	-	-
	2	16	37.0	-	37	37
	2	17	37.0	1.41	36	38

Figure 19. Comparison of Mean and Range of Weight of Known Aged Chicks with Derived Growth Curves for the Most Rapidly and Least Rapidly Growing Hatching Sequences among Snowy Egrets at Fishermans Island, 1977.

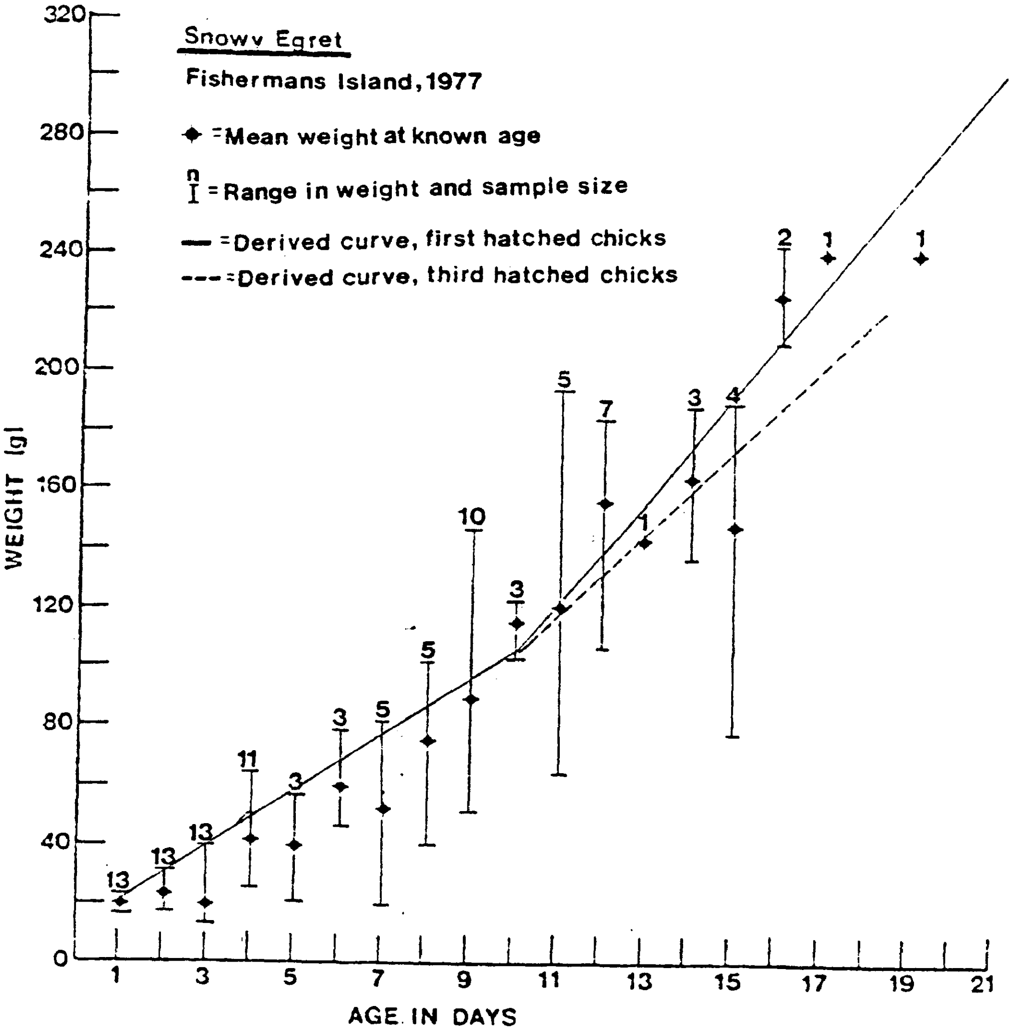

Snowy Egret
Fishermans Island, 1977
✦ =Mean weight at known age
n I =Range in weight and sample size
— =Derived curve, first hatched chicks
--- =Derived curve, third hatched chicks
WEIGHT (g)
0
40
80
120
160
200
240
280
320
AGE IN DAYS
1
3
5
7
9
11
13
15
17
19
21
13
13
13
11
3
3
5
5
10
3
5
7
1
3
4
2
1
1

Figure 20. Comparison of Weight and Range of Weight of Known Aged Chicks with Derived Growth Curves for the Most Rapidly and Least Rapidly Growing Hatching Sequences among Louisiana Herons at Fishermans Island, 1977.

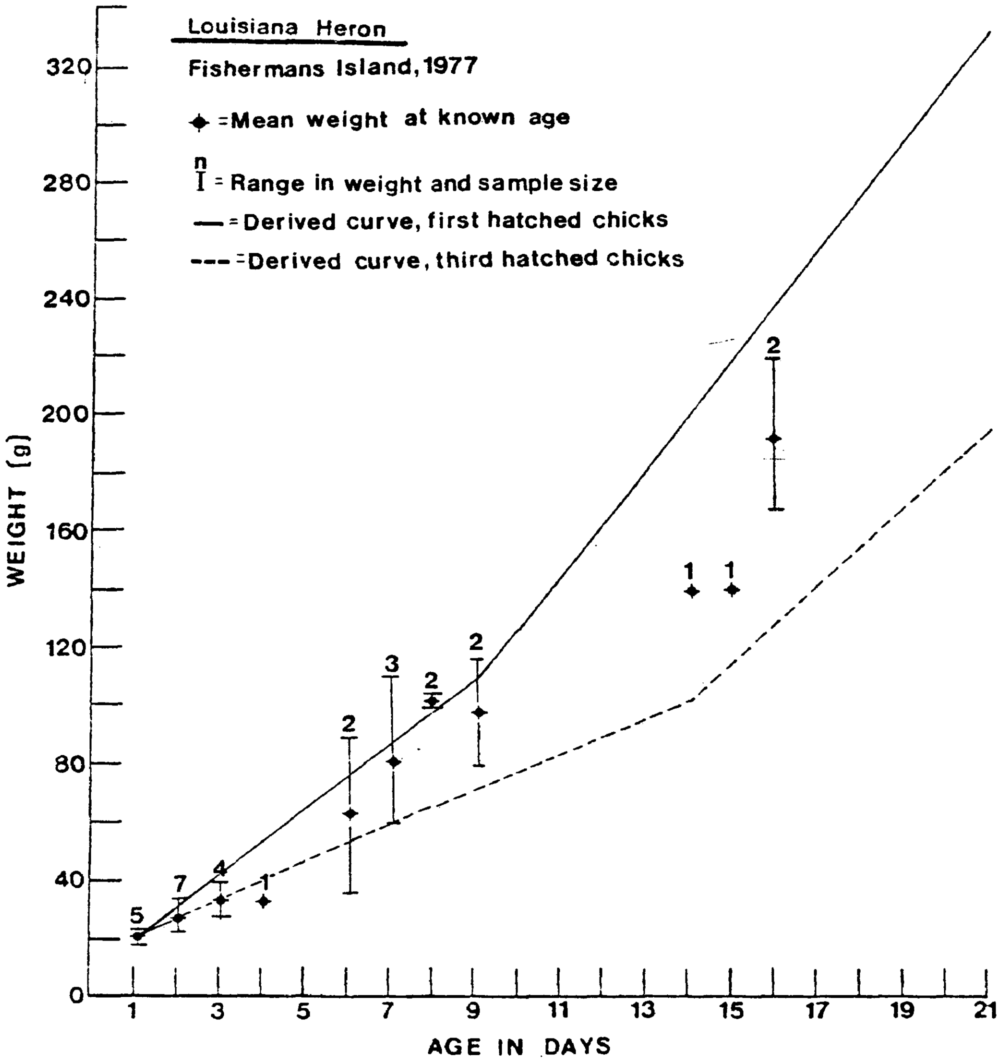
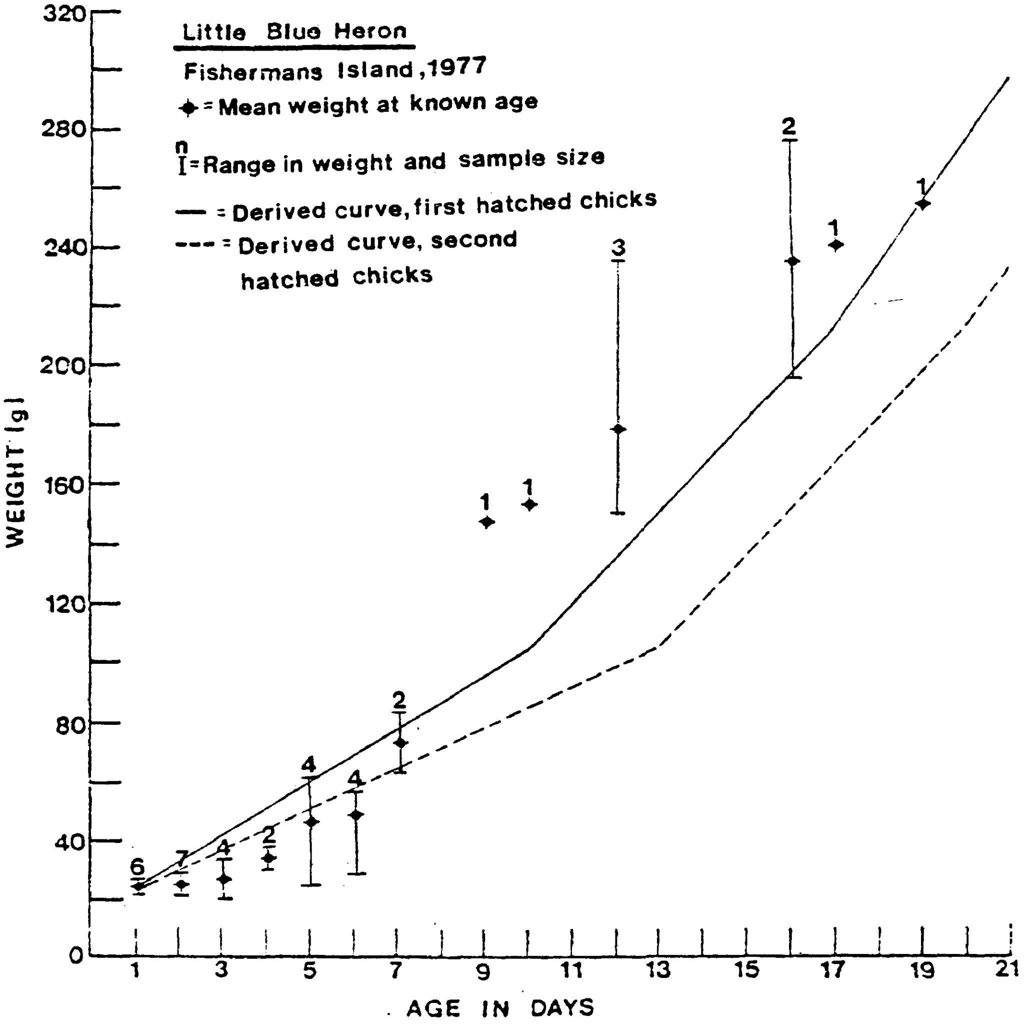

Louisiana Heron
Fishermans Island, 1977
◆ = Mean weight at known age
n I = Range in weight and sample size
— = Derived curve, first hatched chicks
--- = Derived curve, third hatched chicks
WEIGHT (g)
0
40
80
120
160
200
240
280
320
AGE IN DAYS
1
3
5
7
9
11
13
15
17
19
21
5
7
4
1
2
3
2
2
1
1
2

Figure 21. Comparison of Mean and Range of Weight of Known Aged Chicks with Derived Growth Curves for the Most Rapidly and Least Rapidly Growing Hatching Sequences among Little Blue Herons at Fishermans Island, 1977.


Little Blue Heron
Fishermans Island, 1977
◆ = Mean weight at known age
n
I = Range in weight and sample size
— = Derived curve, first hatched chicks
--- = Derived curve, second hatched chicks
WEIGHT (g)
0
40
80
120
160
200
240
280
320
AGE IN DAYS
1
3
5
7
9
11
13
15
17
19
21
6
7
4
2
4
4
2
1
1
3
2
1
1

of days taken to reach a given weight were based solely on WTCAT information. Although the resulting derived curves coincide well with points of known age, the day on which chicks began growing at a different rate were arbitrary. Most marked nests originally contained broods with chicks from one to three or four days old. Therefore, the computed rates of weight increase and the general range within which chicks begin increasing in DWTINC were close to the day designated on the axis; it would take that long growing at that average rate to attain the weight at which DWTINC increased. The point of inflection between WTCAT 2 and WTCAT 3 was more arbitrary because of the small sample size, especially in WTCAT 3.

Chick measurements in weight category 3 (200 to 300 grams) should be approaching asymptote. A substantial sample of adult and nearly fledged chick weights and measurements of each species would be necessary to determine accurately points of inflection along the curve and to decide what portion of the growth curve best shows differences in growth indicative of relative success in producing fully fledged young. There are few data on adult weights of the species studied. I obtained information from the reference collection of Dr. Oscar T. Owre at University of Miami, Coral Gables, Florida. Five specimens of Snowy Egrets weighed 213.7, 347.5, 201.7, 287.5, and 340.5 grams; five Louisiana Heron specimens weighed 380.0, 392, 378.8, 265.5 and 299.3 grams. First year Little Blue Heron specimens weighed 512, 333, and 398 grams; all-white Little Blue Heron specimens weighed 374, 240, 367.6 and 394.4 grams; and adult Little Blue Heron specimens weighed 448, 425, 490, 331, and 382.2 grams. (Presumably the birds of lower weight were not in good condition or died before being collected). From these weights and a few field samples (personal observation), it is anticipated that the 21 day growth curves generated in this study represent a significant proportion of adult weight. There is presently little information pertaining to the actual length of time each species of chick is fed by its parents or to whether fledged chicks attain adult weight while still in the colony.

Discussion

Intraspecific growth was used as an index by which to compare growth of cross fostered chicks. Success was defined as the ability of a cross fostered chick group to be fed by an extraspecific parent and to increase in weight at a daily rate not signficantly different from that of resident control chick group of the same hatching sequence and species. Intraspecific growth rates were also used to derive mean brood ages in studies of synchrony.

Measurements such as wing length, culmen, or tarsus had low variable among individual chicks of the same age. For this reason, growth in weight over time was selected as the measurement that would best reflect potential growth differences among chick groups. Variation in weight change per day, DWTINC, was attributed to several factors. Among individual chicks, recent feeding or loss of meal at time of weighing or genetic differences could cause within-group variation. Review of sample frequencies showed that, once samples were partitioned according to known effects, differences were not unidirectional and that DWTINC means were calculated from a relatively normal distribution. Differential competitive ability among hatching sequences and developmental stage were known to affect DWTINC and were considered in comparisons. Among-brood distinctions could be due to foraging ability of parents, as well as due to aforementioned considerations. Sampling method could also affect results.

Several methods have been proposed for comparing growth rates. Ricklefs' (1967, 1968, 1969) methods required the age of chick to be known generating asymptote from data requiring knowing age, and fitting data to existing growth curves. There was no reason that the data accumulated in this study should necessarily conform to a specified growth curve. Furthermore, very little known age data could be collected. Ricklefs and White (1975) presented methods for constructing growth curves without knowledge of ages by using a large sample of known day old chick measurements, then constructing a curve based on measurements of less variable body parts. By correlating age with hard parts, age to weight was extrapolated using hard part to weight correlations. Measured heron chicks showed some variation in both culmen and in wing length. Both of these body parts changed in very small increments per day. It was concluded that the errors introduced by correlations and best fit curves might outweigh the more direct approach of speculating age/weight relationships using a large sample size.

A preliminary inspection of scatter diagrams, with change in weight per day as the abcissa and weight as the ordinate, indicated that among all species, there was a clustering of points within the weight categories subsequently compared in results. By using the mean change in weight per day, DWTINC, within each weight category, WTCAT, a curve was generated. The point of origin was day one, determined by mean weight of a sample of known day old chicks. These derived curves were similar to curves constructed from data on a small sample of known-aged chicks. However, because sample sizes of the former type curves were much larger, growth in separate hatching sequences could be represented.

Growth curves for each species in two different years showed discernible species specific patterns of brood growth over time. Snowy Egret chicks grew at a slower rate than other species, and this may be correlated with the apparent attempt by parents to raise all chicks in a brood at a comparable rate. When the third chick survived, the first and second-hatched chicks grew at a slower rate. Increases in the growth of the second-hatched chicks were compensated by a decline in growth of the first-hatched chicks. Similarly, when the third-hatched chicks expired in 1976, the first and second-hatched chick groups began growing at a more rapid rate. By overlaying the curves from 1976 and 1977, one could see that all three hatching sequences were raised between the range of the first and second-hatched chicks of the 1976 sample. At later stages, however, 1977 growth rates increased rather than tapered off as they did in 1976. Possibly change in food availability altered later rates in the two years.

Cattle Egrets also raised only the first two hatched chicks in 1976 sampled broods. Overlaying the 1976 on 1977 curves indicated that their growth strategy was different from that of Snowy Egrets. Raising a third-hatched chick in 1977 did not inhibit the growth of the first-hatched chick. Second-hatched chicks grew at a slower rate than the first in the better growth season, 1977. Thus survival of the third chick may have been at the detriment of only the second-hatched chick groups.

Whereas the magnitude of difference in growth of the first and second-hatched chick was greater in the better growth season for Cattle Egrets, the magnitude was greater during the poorer growth season for Little Blue Herons. Differences between 1977 and 1976 indicated that 1976 was a better growth year for all three hatching sequences and that the rate of growth in this year was not matched by any one hatching sequence from the alternate year. Comparison of growth in the two years for this species suggested that external factors can mask any intrinsic rate of growth and that species specific growth should be considered only in relative terms. The high rate of growth in third-hatched chicks during both years indicated that some factor other than small sample size influenced results. Typically, the youngest chicks were most vocal. Perhaps they do not initially compete as well for food and vocalize due to hunger. They may also be at a different stage in ability to thermoregulate and may suffer from lack of protection. Vocalizing from any type of distress may stimulate the parents to attend them preferentially. Thus, the "squeaky wheel" may obtain more food.

Louisiana Heron growth strategy appeared different from other species in that the slight head start provided the first-hatched chick was perpetuated and amplified with age in both years. Growth of the first and second-hatched chicks was of equivalent difference both years, and higher in the year in which only two chicks were supported. For this species it would be misleading to conclude that higher growth rates reflected a better growth year. In 1977, broods of three instead of two chicks were raised at the expense of a more rapid growth rate in the first and second-hatched chicks.

Growth curves showed that for all species and hatching sequences the most rapid and most variable increases in weight occurred after 4 to 7 days and continued to day 21. In some instances the sampled species group would have exceeded adult weight at the WTCAT 3 rate. Chicks may, in fact, reach weights in excess of adult weight as a safety margin for the period of time during which they learn to find their own food. If increased success in feeding efficiency with age is common among these species (Kushlan, 1978), it would be of advantage to have surplus weight while wandering and learning to capture prey.

High growth rates create an overall rapid growth or could offset a relatively lower rate during a separate growth stage. However, any very low DWTINC in any WTCAT affected overall growth by greatly prolonging the duration of time necessary to reach weights comparable to those attained by other species in much shorter periods of time.

There is no reason to conclude that most rapid growth rate is necessarily the most successful. In the same species, broods of three in one year grew more slowly than broods of one or two, but slower growth was compensated by the ability to raise more chicks in another year. This indicated that parents may select alternate strategies in different years. Growth rate would be determined by parental care rather than physiological maximum (Ricklefs, 1969).

The assumption was made that if species were nesting colonially, there was selective advantage in doing so. If colonial nesting was advantageous, each member would only benefit if young were raised during a relatively short, equal period of time. Similarities even in separate WTCATS among hatching sequences and species in two different years showed that there was a common range in magnitude of DWTINC among all species during each stage of growth. Interspecific similarity in overall growth rates was further evidenced in testing the statistic DWTINC among two species and a cross foster group. Magnitude of relatively high or low rates were also similar, independent of species and year.

Intraspecific growth rates are useful in comparing species specific success within one nesting season in the same colony and in comparing apparent strategies in raising broods. Further information on older nestlings and fledgling rates will be necessary to determine the predictive value of information obtained during the first three weeks of growth. It will also be important to compare growth rates of chicks in different geographical locations or in colonies with dissimilar local feeding habitats. Yearly changes in the same colonies would offer further insight into the influence that external factors, such as weather and food availability, have on species specific growth patterns.

CONCLUSIONS

All four heron species showed some intraspecific synchrony in that they initiated nesting in already active, mixed-species nesting areas. The sequence of nesting within the same subzones was repeated during 1976 and 1977. Little Blue Herons and Snowy Egrets nested synchronously throughout the colony, although at separate times from each other. Louisiana Heron broods differed in age and location according to subzone. Interspecific social stimulation is proposed as to be an important factor in nest site selection. Dense packing of nests possibly was facilitated by differing behavioral stages among nearest extra and intraspecific neighbors. Asynchrony of nesting on a shorter time scale was considered equally advantageous within the nesting season.

Asynchronous nesting would be selective in reducing predation by Fish Crows, the primary predators at Fishermans Island. These aerial predators increased in number during the second year of study but appeared to be selecting only eggs as food. Predation pressure would be reduced if eggs were available for only a short time during which the predator might have limited ability to find eggs amidst the massive movement of adults and chicks in a given area.

The possibility that the colony acts as an information center for several species was explored. Interspecific colonial nesting would be advantageous if individuals increased their probability of finding food by nesting with other species. Observations of feeding flight movements indicated that Fishermans Island colony itself was not important as a center for information exchange. Although Snowy Egrets, Little Blue Herons, and to a lesser degree Louisiana Herons were observed moving in and out of the colony in intraspecific and extraspecific groups, individuals joined and departed flight groups en route to or from the colony. As a rule, flight groups were composed of individuals nesting in separate nesting locations within the colony. It was suggested that the continuous presence of flight movement and of nearby feeding aggregations increased the probability of any individual among the three species finding food.

A requisite of information exchange was that similar prey items were being taken by these species, and that the items were locally abundant but patchy in occurrence. Food analysis showed a high degree of overlap in prey selection and a relatively low diversity in food types captured by the three heron species. Individual species selected different proportions of the same prey item in separate years indicating that prey availability was temporally variable. Results of trapping and seining collections in 1977 showed that Snowy Egrets, Louisiana Herons and Little Blue Herons were collecting the most locally abundant prey types. Availability studies also indicated that size classes and types of food were temporally and locally abundant. Cattle Egrets fed young different types of prey, which were not analyzed for availability.

It was expected that parents would distinguish at least young of their own species, for if recognition did not occur, parents would risk contributing both to another genotype and to another species by feeding other herons' broods. Studies of intraspecific, ground nesting species showed that differences in development of recognition may be correlated with nest permanency and chick mobility. Nest site recognition is sufficient to ensure parents feed appropriate young in species whose chicks remain in the nest until fledging. In other species, chicks begin to wander from the nest at an early age, and recognition by parents appears at this time.

Cross fostering tests at Fishermans Island showed that up to 10 days, Louisiana Herons and Snowy Egrets did not recognize young of other species. Many chicks between 10 and 20 days were also accepted. If recognition did develop, it was possibly coincident with the stage at which young perched outside the nest and actively pursued food. Some Little Blue Heron parents rejected extraspecific chicks, while others accepted foster young. Cattle Egrets rejected all extraspecific chicks, but showed no recognition of foster young of the same species. All four heron species had the same degree of nest permanency and the same developmental schedule; yet species showed differential recognitive abilities. It is hypothesized that the response of Little

Blue Herons and Cattle Egrets might be related to their nesting more intrapsecifically and later in the season. Recognition may develop earlier as a defense mechanism to ensure that the parents secure a nest site and can defend access to the nest by recognizing aggressive, extraspecific juveniles near their nest.

Initially, intraspecific growth rates were analyzed for use in other studies. The results offered informative species specific growth patterns and insight into colonial nesting. The greatest amount of intraspecific variation was found in growth rate within a hatching sequence through a three week period. In most cases, chicks grew at an increasing rate per day through twenty-one days. Variation was also found among hatching sequence groups. The species specific differences suggested that heron parents used different strategies in raising a brood size that was initially equal. Disparities were related to differential growth rates among hatching sequences and to survival. Each species showed different growth rates among hatching sequences in two different years indicating that the intrinsic rate of growth may be masked by external factors such as food availability and weather. In some instances relative success in two years could not be determined by growth rate alone. Slower growth rates were sometimes correlated with raising larger broods. For the cases in which relative success could be determined, comparative species curves showed that not all species experienced better growth in the same year. Some curves were steep enough to predict that within one month of age chicks may exceed adult weight. Excess weight may be important during the period in which young expend excess energy in learning to feed efficiently.

It was hypothesized that if mixed-species nesting was selectively adaptive, members would only benefit if chicks were raised in a relatively equal period of time. Although growth rate differences were found, a common minimum and maximum range could also be detected among all species. Similarity of interspecific growth rates implied that if egg-laying was synchronous, all species of chicks would fledge within a short time period.

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VITA

Paula Christine Frohring

Born in Chagrin Falls, Ohio, January 16, 1950. Graduated from Hathaway Brown School, Shaker Heights, Ohio, June, 1968. Attended Wheaton College, Norton, Massachusetts, 1968 - 1970. Received Bachelor of Science Degree in Biology, University of Miami, June, 1972. Employed as Assistant to Director of Hiram College Biological Station, Hiram, Ohio, 1972 - 1974. Candidate for Master of Arts Degree, College of William and Mary, 1974 - 1981. Biologist with U. S. National Park Service, South Florida Research Center, Homestead, Florida, studying heron ecology in the Everglades from 1978 to present.