1984

Aspects of Breeding Behavior of the Royal Tern (Sterna maxima) with Particular Emphasis on Prey Size Selectivity

William James Ihle
College of William & Mary - Arts & Sciences

ASPECTS OF BREEDING BEHAVIOR OF THE ROYAL TERN (*STERNA MAXIMA*) WITH PARTICULAR EMPHASIS ON PREY SIZE SELECTIVITY

A Thesis

Presented to

The Faculty of the Department of Biology

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

---

by

William J. Ihle

1984

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

the requirements for the degree of

Master of Arts

Bill Hale
Author

Approved, April 1984

Mitchell A. Byrd

Norman J. Fashing

Stewart A. Ware

R. Michael Erwin

DEDICATION

To Mom, for without her love and encouragement

this thesis would not have been completed.

FRONTISPIECE. Begging royal tern chick and its parent in the creche are surrounded by conspecific food parasites immediately after a feeding. Gackering and other aggressive postures were evident among those royal terns which stole food from chicks.

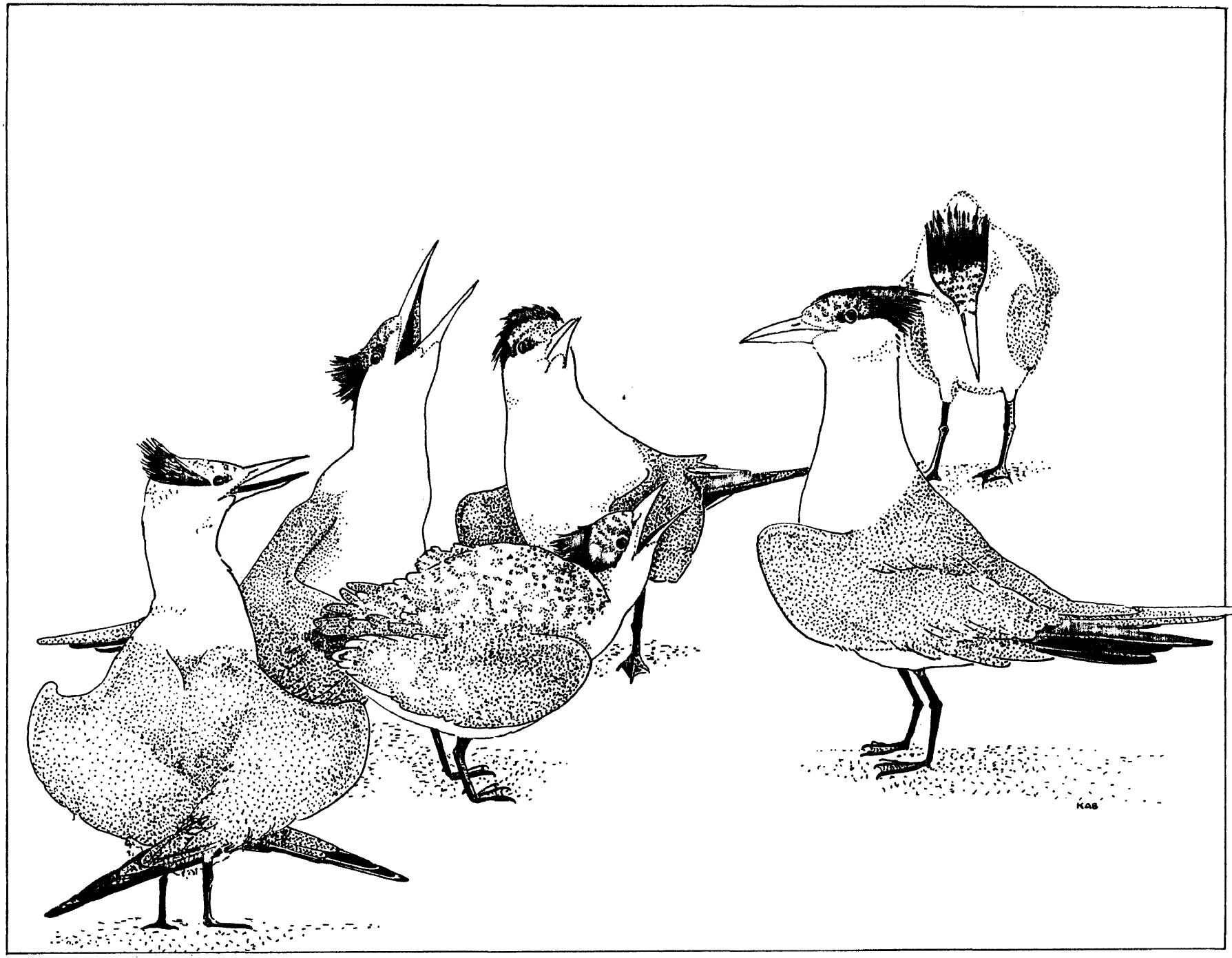


TABLE OF CONTENTS

ACKNOWLEDGMENTS

I would like to extend my sincere thanks to each member of my graduate committee: Dr. Mitchell Byrd, for giving me the opportunity to study royal terns in Virginia; Dr. Norman Fashing, for his assistance with the statistical design and analysis of the project; Dr. Stewart Ware for his expert advice on reorganization and rewording of various portions of the thesis, and Dr. R. Michael Erwin for his sincere interest, criticism, and overall guidance throughout all phases of the project. I wish to express particular appreciation to Dr. Ware for his tireless assistance in the arduous task of making the thesis more readable and understandable. I also thank Dr. Gus Hall who gave freely of his time while helping me find solutions to the various problems I encountered in the early stages of the project. I wish to thank the Virginia Society of Ornithology and the Virginia Commission of Game and Inland Fisheries Non-Game Program for financial assistance.

Others who offered their assistance during my study include, Dean Ahrenholtz (National Marine Fisheries Service), Jimmy Hoff (VIMS), John Weske, Bill Williams, Fenton Day, Anna Vascott, Jewel Thomas, Dave Ribar, Rebecca Kinkead, Donna Middleton, and Kathy Born.

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

APSTRACT

Aspects of the breeding behavior of the royal tern were studied at a colony on Metomkin Island, Virginia during May, June, and July of 1983. The relationship between prey size and chick body size was examined and discussed in detail. Other aspects investigated included kleptoparasitism (or food parasitism) and its effect on food choice, courtship feeding as a predictor of male breeding behavior, the elapsed time period between hatching and scrape egression, creche feeding behavior, and territorial and predatory behavior of herring gulls among a colony of royal terns.

The fates of 1226 fish and 201 soft-shelled blue crabs were noted and sizes of the chicks for which the food was brought were recorded during 103 hours of observation. Observations on creche behavior were taken from a blind as well as during approach and departure from the colony.

Prey size was found to have a highly significant positive association to chick body size in royal terns. Creche kleptoparasitisms were both intra- and interspecific in nature, and were influenced by both food size and chick body size. Royal tern food parasites were determined to consist of breeders as well as birds involved in ground courtship (i.e., potential breeders). Intermediate sizes comprised the majority (78%) of fish sizes seen fed to chicks. A high degree of similarity exists between fish sizes documented in courtship feeding and fish sizes seen being fed to chicks. Chicks were observed leaving their nest scrapes at widely varying time intervals (3-10 days). After creche formation, royal tern chicks up to two weeks old, were preyed upon by herring gulls which also nested in the vicinity of the royal tern colony.

Some conclusions of the study are as follows: 1) Intermediate fish sizes fed to young maximize the feeding efficiency ratio for parent royal terns. 2) Courtship feeding may act as a predictor of the males' performance in feeding young. 3) The creche-joining age is influenced by human disturbance and is older than 2-3 days. 4) Royal terns may benefit from delayed creche formation. 5) Royal terns have evolved several behavioral adaptations towards reducing food parasitism in the creche. 6) On Metomkin Island, due to their predatory behavior and competitive interaction, herring gulls are a serious threat to the diversity of smaller seabird species which share the nesting island with the large aggressive gulls.

ASPECTS OF BREEDING BEHAVIOR OF THE ROYAL TERN (*STERNA MAXIMA*) WITH PARTICULAR EMPHASIS ON PREY SIZE SELECTIVITY

INTRODUCTION

The royal tern (Sterna maxima) is a relatively large, crested, obligate creche-forming tern which breeds on isolated coastal barrier islands or spoil banks which are free of quadruped predators. Its present North American range extends from the Gulf Coast of Mexico through Texas, north to Maryland, and in southern California. It nests in dense, tightly packed colonies, sometimes in great numbers. Often nesting in its midst is a smaller closely related congener, the sandwich tern (S. sandvicensis). A single egg is laid (about 97% of the nests in a given colony contain only one egg, [Buckley and Buckley 1972b]) and at some point after hatching the chicks gather in a creche where they are located, recognized, and fed by their own parents. Royals are consistent inshore feeders, seeming to prefer large shallow bays (e.g., Chesapeake Bay) and obtain their food by plunge-diving, in the same manner as most other terns. The royal has a strong tendency to desert en masse well-established colony sites which are invaded by mammalian predators and relocate elsewhere. However, from observations taken over four breeding seasons (1967-1970) in Virginia and North Carolina, Buckley & Buckley (1972a) found that there the royal tern had no critical predation problems beyond the egg stage. Instead of the adults

removing the eggshells as soon as the eggs hatch (a common anti-mammalian predator device), the young royals leave the nest to join the creche. Most writers (Buckley & Buckley 1972a; Smith 1975) agree that recently hatched crested tern chicks leave the nest scrape after three days. However, others claim that the period before this egression is longer (1 week) (Dragesco 1961) or unknown (Ansingh et. al., 1960).

The Buckleys noted that terns carrying fish were often harried by laughing gulls (Larus atricilla) and herring gulls (L. argentatus), but in all observed encounters the terns outmaneuvered and outdistanced the pursuing gulls. Hatch (1970) observed herring and great black-backed gulls (L. marinus) eating live chicks of both common and arctic terns (S. paradisaea) on Petit Manan Island, Maine, and noted that increasing populations of gulls threatened nesting terns on North America's Atlantic coast. However, until this study, such predation has not been reported for royal terns.

Feeding strategies should evolve to maximize the yield of usable energy in relation to the energy invested in locating, capturing, and digesting food items. In this regard, Hopkins & Wiley (1972) state that intermediate food sizes fed to chicks would probably maximize the efficiency ratio, i.e., amount of food/parental cost. Royal terns capture a wide array of prey sizes and species (Erwin 1975, 1977) so it would be interesting to see if this tern makes an attempt to match the size of the prey to the size of its chick. In their study, Buckley & Buckley (1972a) found that most of the fish caught and fed to the young were about 5-10 cm in length and their size often seemed unrelated to the size of the chick being fed. They also stated that chicks in the creche ate any fishes offered by adults and were usually so eager to

grab fish from incoming adults that they regularly saw what appeared to be instances of the wrong chick being fed because it grabbed the fish from the landing adult.

Regarding the theory of optimal central place foraging (Orians & Pearson 1979), the royal tern is defined as a piscivorous single-prey loading species (i.e., those that carry only one prey item each trip). For single-prey loading species, a few studies have shown that the mean size of prey carried to nestlings was greater than that eaten by foraging adults (Royama 1970; Hartwick 1976; Hegner 1982).

Kilham (1981) noticed that during royal tern courtship feeding the size of the fish offered by the male appeared to be important to selection of a mate by the female. Nisbet (1973) speculated that one function of courtship feeding may be to give females a chance to assess potential mates as future providers for chicks, so the degree of similarity of fish sizes in courtship feeding and in feeding of chicks is of interest.

Food parasitism, or kleptoparasitism, has been suggested as a possible influence on food choice in breeding arctic terns (Hopkins & Wiley 1972). Kleptoparasitism originally referred to the interspecific stealing of already procured food, but Brockmann & Barnard (1979) showed that intraspecific food stealing effectively is the same behavior. Brockmann & Barnard state that although kleptoparasitism is a term that is generally reserved for interspecific stealing of food, other terms such as "piracy", "food parasitism", "pilfering", and "robbery" are also used for intraspecific food theft, emphasizing the close relationship between intra- and interspecific feeding patterns. Kleptoparasitism is particularly associated with certain ecological conditions, such as the

availability of hosts feeding on large visible food items periods of food shortage, and crowded conditions (e g., nesting colonies). Adult common terns (S. hirundo) steal from other adults and from chicks as they are being fed (Hays 1970, Hopkins & Wiley 1972). In mixed colonies of terns, the birds begin stealing from each other early in the season when they are carrying fish for mating displays. The attacks continue while they are feeding the chicks (Hopkins & Wiley 1972; Dunn 1973a; Fuchs 1977). Gulls also nest in close proximity to tern colonies and they steal from terns as well as from one another (Hatch 1970,1975; Veen 1977).

The major questions to be examined in my study are these: 1) Is prey size related to chick body size in royal terns? 2) Is kleptoparasitism in the creche inter- or intraspecific in nature? 3) Is kleptoparasitism's occurrence influenced by: a) food size, b) chick body size, c) social environment, and d) other factors. 4) Are royal tern food parasites non-breeders or breeders with young to feed?

In addition, I have made an attempt to analyze the effects of food parasitism as well as the role of courtship feeding on food choice by breeding royal terns. The elapsed time period between hatching and scrape egression in royal terns is examined and discussed. Also investigated is royal tern creche feeding behavior in addition to territorial and predatory behavior of herring gulls among a colony of royal terns.

METHODS

During June and July of 1983 I collected data on the nesting and feeding behavior of royal terns on Metomkin Island, Virginia (Figures 1 & 2). I recorded my observations while out in the open, concealed behind beach vegetation, or sitting within a blind which was erected in the vicinity of the colony. The fates of 1226 fish and 201 soft-shelled blue crabs (Callinectes sapidus) were noted and sizes of the chicks for which the food was brought were recorded during 103 hours of observation. During observations at the colony site, individual fish-carrying terns were selected as randomly as possible (by taking the first I happened to see) and followed with binoculars (7 X 35). When a tern arrived carrying a fish, it was watched until a chick was fed or until it flew away with the fish. In each case I recorded the length of the fish, the size of the chick to which it was fed, and the social feeding environment. A feeding was considered "successful" when the chick managed to swallow the fish. If the chick was robbed of its food, I registered which species stole the food and any events connected with the robbery. Observations were taken at all times of day (dawn, morning, afternoon, and twilight) during the feeding period.

For the purposes of this study, I defined social environment in two ways. "Alone" referred to those chicks which were fed at a certain distance (> 2.0 meters) from other chicks or adults, while "among" meant those fed in proximity to others of their kind (e.g., the first week

Figure 1. Map showing the general location of Metomkin and Cedar Islands on the Eastern Shore of Virginia.

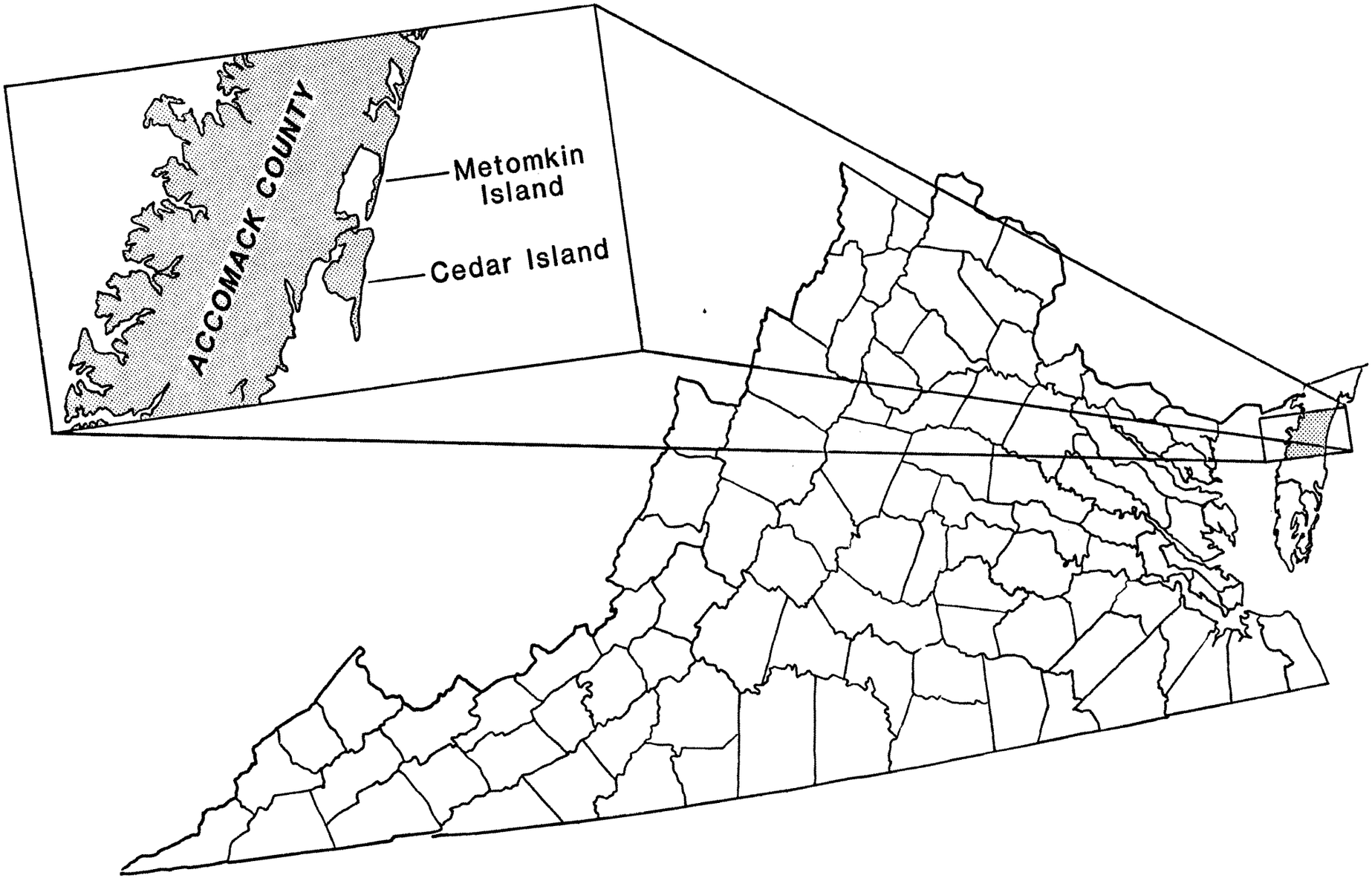
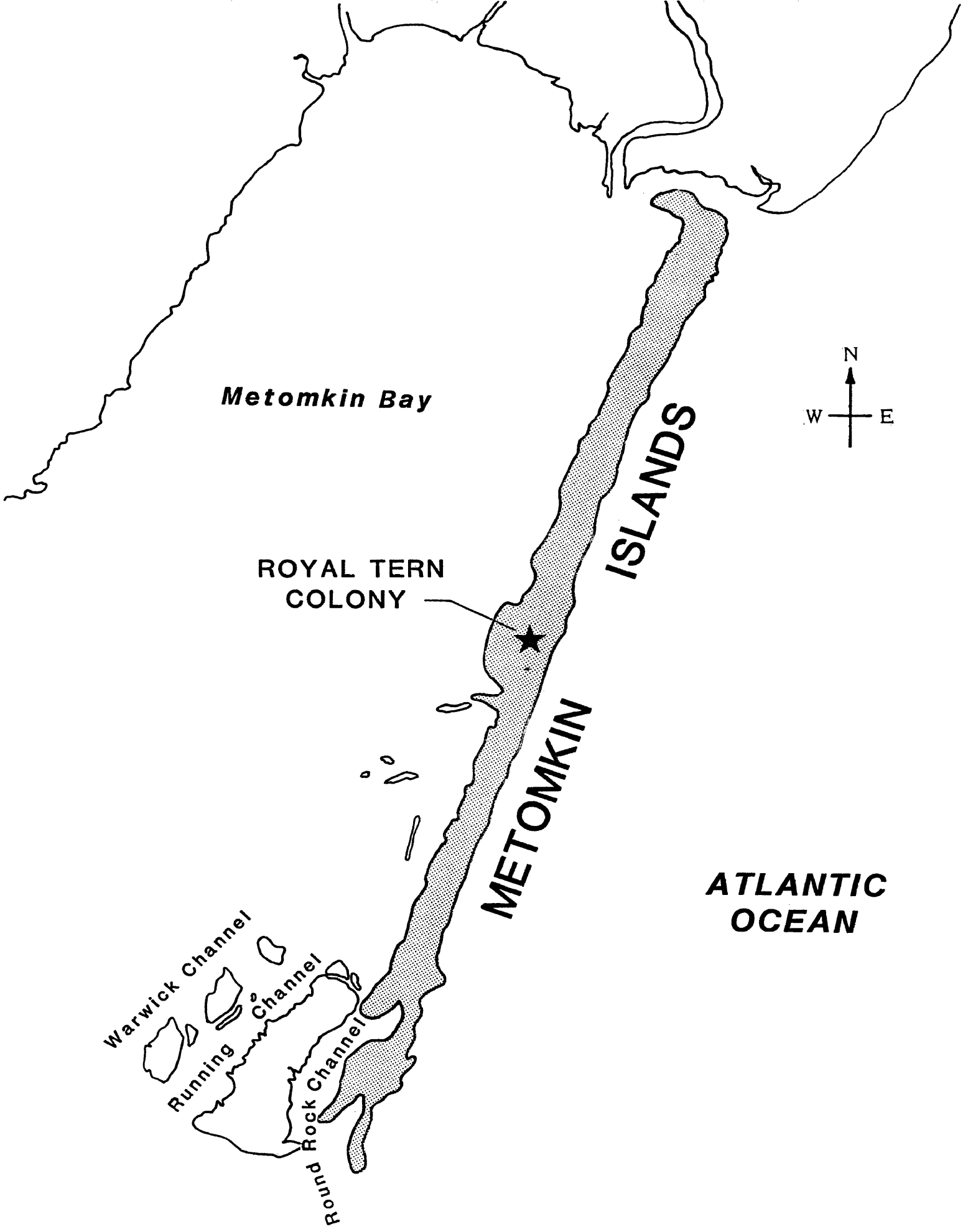

ACCOMACK COUNTY
Metomkin Island
Cedar Island

Figure 2. Map of the study site, Metomkin Island. Approximate location of the main royal tern colony in 1983 is indicated.


Metomkin Bay
N
W
E
ROYAL TERN
COLONY
METOMKIN ISLANDS
ATLANTIC
OCEAN
Warwick Channel
Running Channel
Round Rock Channel

after hatching where small downy chicks were seen being fed in the nest scrape).

Food items were divided into four size categories in relation to the length of the adult terns' bill and recorded as 0 through 4 (Hopkins & Wiley 1972). These size classes included fish whose lengths were: (0) respectively less than, (1) roughly equal to, (2) greater than but < 2X, and (3) at least twice the length of the adult terns' bill. I used a fifth food category (4) for soft-shelled blue crabs (soft-shells) because they were of a different texture and shape from the fish.

Chick sizes were determined based on age differences by one week time increments. There is a high degree of breeding synchrony in royal tern colonies, so it can be expected that a high percentage of chicks will be quite close in age (and therefore size). Whenever I observed an unusually small or large chick in a feeding, the age of the chick was estimated based on a size comparison with the average-sized chick in the creche at that time. Observations of very small chicks (1 week old or less) were taken at a subcolony located roughly 80 yards from, and hatching about a week earlier than the main colony. Later observations (chicks 2 weeks old and older) were taken at a certain portion of the main creche for several consecutive weeks. Collecting most of the data at the same creche locale largely reduced the job of estimating chick age to simply recording the date of each observation.

During the study, I noticed that different-sized food items tended to be carried differently by the terns relative to both: a) the bill axis and b) distance from the bill tip. Size 0 fish were often seen being held perpendicular to the bill axis and very close to the tip.

Size 1 fish were often held in a similiar fashion to size 0 but slightly further back from the tip. Sizes 2 and 3 fish were often held well back from the tip and more parallel to the bill axis. In those instances where assigning a specific size to a fish being carried by a tern was more difficult, I used these position guides as a partial indicator of the size of the fish.

Observations on creche behavior (e.g., nest egression, predation by herring gulls, etc.) were taken from the blind as well as during approach and departure from the colony.

FUNCAT and chi square contingency tests were used to treat categorical data on food/chick sizes and to allow testing of subsidiary hypotheses. (The FUNCAT statistical package models FUNctions of CATegorical responses as a linear model (Sall et. al. 1979). It uses generalized least squares to produce minimum chi square estimates. FUNCAT assumes a multinomial response. Data to be analyzed by FUNCAT can be either raw data or summary data with frequency counts. The FUNCAT procedure is most often used in experimental situations where there are clearly defined discrete response and design effects.)

RESULTS

Overall Diet

Fish and soft-shelled blue crabs appeared to make up the bulk of the royal terns' diet with fish comprising 86% and soft-shells 14% of the total. The overall percent of each food size category fed to royal tern chicks breaks down as follows: Size 0 = 13.05%, Size 1 = 23.12%, Size 2 = 43.45%, Size 3 = 6.30%, and Size 4 = 14.08%. Fish of sizes 1 and 2 made up the bulk of the food seen being fed to royal chicks, particularly those fish whose lengths corresponded to modal size category 2 (7-9 cm).

Food Size Data

A chi-square contingency analysis shows a highly significant positive association between prey size and chick age (Table 1). The differences between observed and expected frequencies in Table 1 shows that small chicks received more small items from their parents than was expected and larger chicks received more large food items than was expected.

A possibility exists that fish size and chick size are correlated only because, as the season progresses, growth influences both groups.

I tested for a seasonal effect by conducting two seperate chi square analyses testing for systematic changes in fish size during the season for both one and two week old royal tern chicks. One week old chicks received three different food sizes in the same proportions over a three week period (Table 2). A similiar result was obtained for two week old chicks (Table 2).

As expected, the modal food size being fed to chicks from one to six weeks old increases (Figure 3). The smaller food size seen for six week old chicks is probably due to a smaller sample size.

Those food items in size category 0 and 1 showed very sharp declines in frequency after the first week and a gradual decline after the second week relative to larger fish sizes. The larger intermediate fish size (2) showed a gradual increase in frequency up to week three, then remained fairly stable from weeks three to five. The frequency of fish of size 3 remained low throughout the feeding period. Feedings involving soft-shell crabs became noticeable only after the chicks reached three weeks of age then increased in frequency in the fourth and fifth weeks (Figure 3).

TABLE 1

EFFECT OF CHICK AGE ON FOOD SIZE FREQUENCIES

		FOOD SIZE*					
		0	1	2	3	4**	TOTALS
CHICK AGE (Weeks)	1	112 [44.3] (33.0%)	140 [78.6] (41.2%)	80 [147.7] (23.5%)	5 [21.4] (1.5%)	3 [47.9] (0.9%)	340
	2	24 [14.5] (21.6%)	45 [25.7] (40.5%)	36 [48.2] (32.4%)	5 [7.0] (4.5%)	1 [15.6] (0.9%)	111
	3	10 [17.3] (7.5%)	34 [30.8] (25.5%)	62 [57.8] (46.6%)	10 [8.4] (7.5%)	17 [18.7] (12.8%)	133
	4	18 [45.2] (5.2%)	63 [80.2] (18.2%)	170 [150.8] (49.0%)	24 [21.9] (6.9%)	72 [48.9] (20.7%)	347
	5	17 [54.2] (4.1%)	36 [96.2] (8.6%)	229 [180.7] (55.0%)	40 [26.2] (9.6%)	94 [58.6] (22.6%)	416
	6	5 [10.4] (6.3%)	12 [18.5] (15.0%)	43 [34.8] (53.8%)	6 [5.0] (7.5%)	14 [11.3] (17.5%)	80
	TOTALS	186	330	620	90	201	1427

$X^2 = 425.8$, $P < 0.001$

Absolute abundance of each food type listed with percentage in parentheses. Expected cell frequencies are given in brackets.

*See text (page 6) for food size categories

** Callinectes sapidus

TABLE 2

EFFECT OF SEASON ON FISH SIZES FED TO ROYAL TERN CHICKS

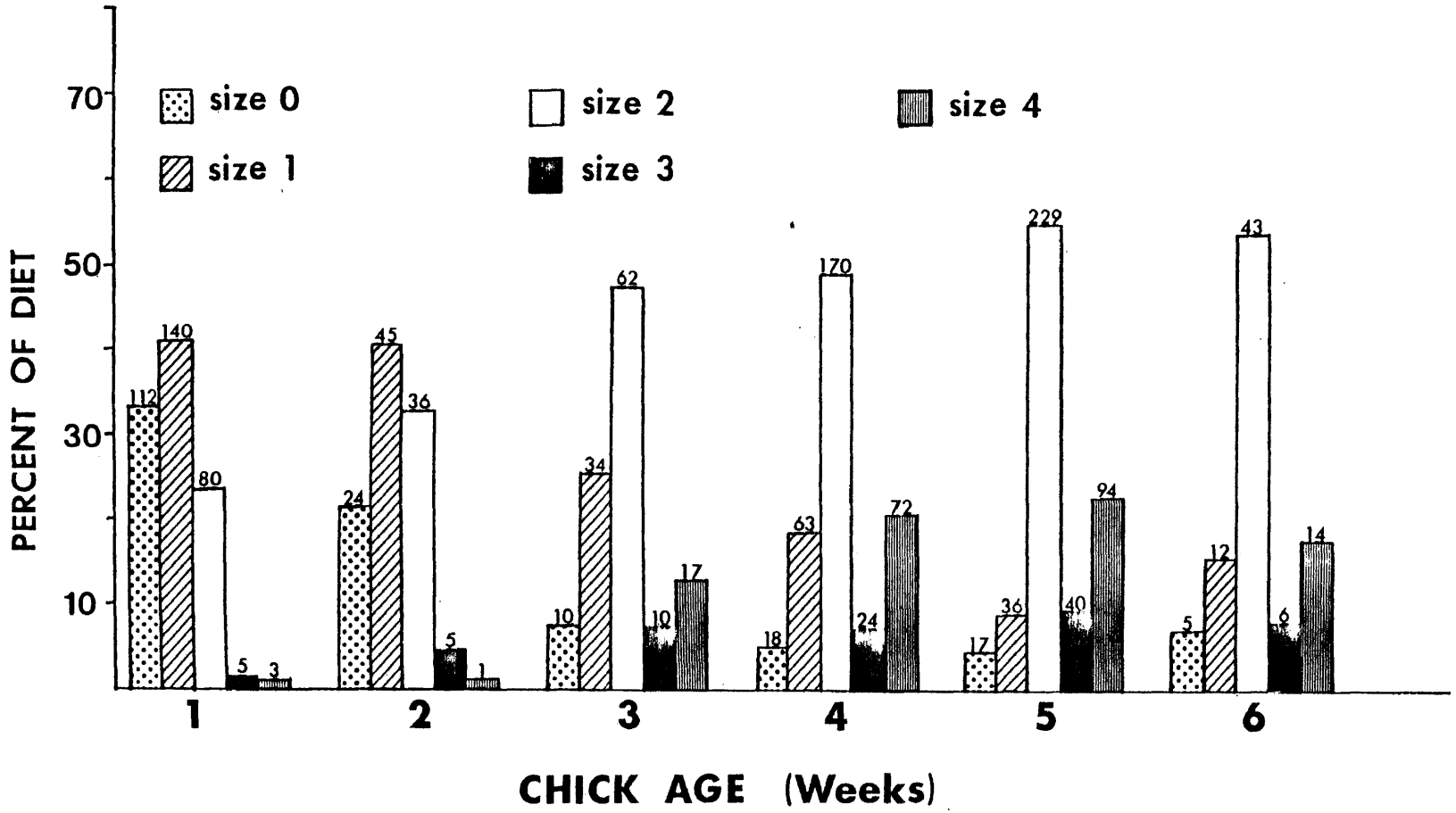
	FISH SIZE	DATE JUNE 2-8	JUNE 9-15	JUNE 16-22	TOTALS
1-week old	0	54 [58.3]	22 [17.8]	34 [33.9]	110
	1	80 [72.6]	15 [22.2]	42 [42.3]	137
	2	36 [39.2]	15 [12.0]	23 [22.8]	74
	TOTALS	170	52	99	321

[X^2 = 5.41, 0.20 < P < 0.30, Expected frequencies are in brackets]

	FISH SIZE	DATE JUNE 9-15	JUNE 16-22	JUNE 23-30	TOTALS
2-week old	0	15 [11.1]	3 [7.5]	4 [3.4]	22
	1	22 [23.7]	18 [16.0]	7 [7.3]	47
	2	18 [20.2]	16 [13.6]	6 [6.2]	40
	TOTALS	55	37	17	109

(X^2 = 5.22, 0.20 < P < 0.30, Expected frequencies are in brackets)

Figure 3. Percentage of each food category in the diets of six sizes of royal tern chicks.


size 0
size 1
size 2
size 3
size 4
PERCENT OF DIET
70
50
30
10
112
140
80
5
3
24
45
36
5
1
10
34
62
10
17
18
63
170
24
72
17
36
229
40
94
5
12
43
6
14
1
2
3
4
5
6
CHICK AGE (Weeks)

Kleptoparasitism of Royal Tern Chicks on the Ground

I observed both intra- and interspecific kleptoparasitism occurring on the ground in the royal tern creche. Crabs were stolen by other terns and gulls twice as often as were fish (Table 3).

A test of independence of all four fish sizes versus kleptoparasitism occurrence showed that the probability of a kleptoparasitism occurring was positively associated with the size of the fish (Table 4). Fish of sizes 0 and 1 were stolen at extremely low percentages (< 1%) while the largest fish size was stolen almost 17% of the time. Size 2 fish were observed being fed to chicks at very high frequencies but were stolen with a relatively low percentage (although higher than that for sizes 0 and 1). The chi square values listed for each cell beneath Table 4 reveal that the cell containing kleptoparasitisms for size 3 fish was a major contributor to the overall significant chi square value. This indicates that large fish are stolen with a high frequency and therefore, for all food size categories, represent the highest risk of kleptoparasitism for parents (Figure 4).

TABLE 3

PROBABILITY OF KLEPTOPARASITISM ON CHICKS WHICH ARE FED CRABS OR FISH

FOOD	NUMBER OBSERVED	NUMBER STOLEN	PERCENTAGE STOLEN	CHI SQUARE	P
CRABS	201	17	8.5%	5.58	< 0.02
ALL FISH	1226	53	4.3%		
TOTALS	1427	70	4.9%		

TABLE 4

EFFECT OF FISH SIZE ON THE PROBABILITY OF KLEPTOPARASITISM IN ROYAL TERNS

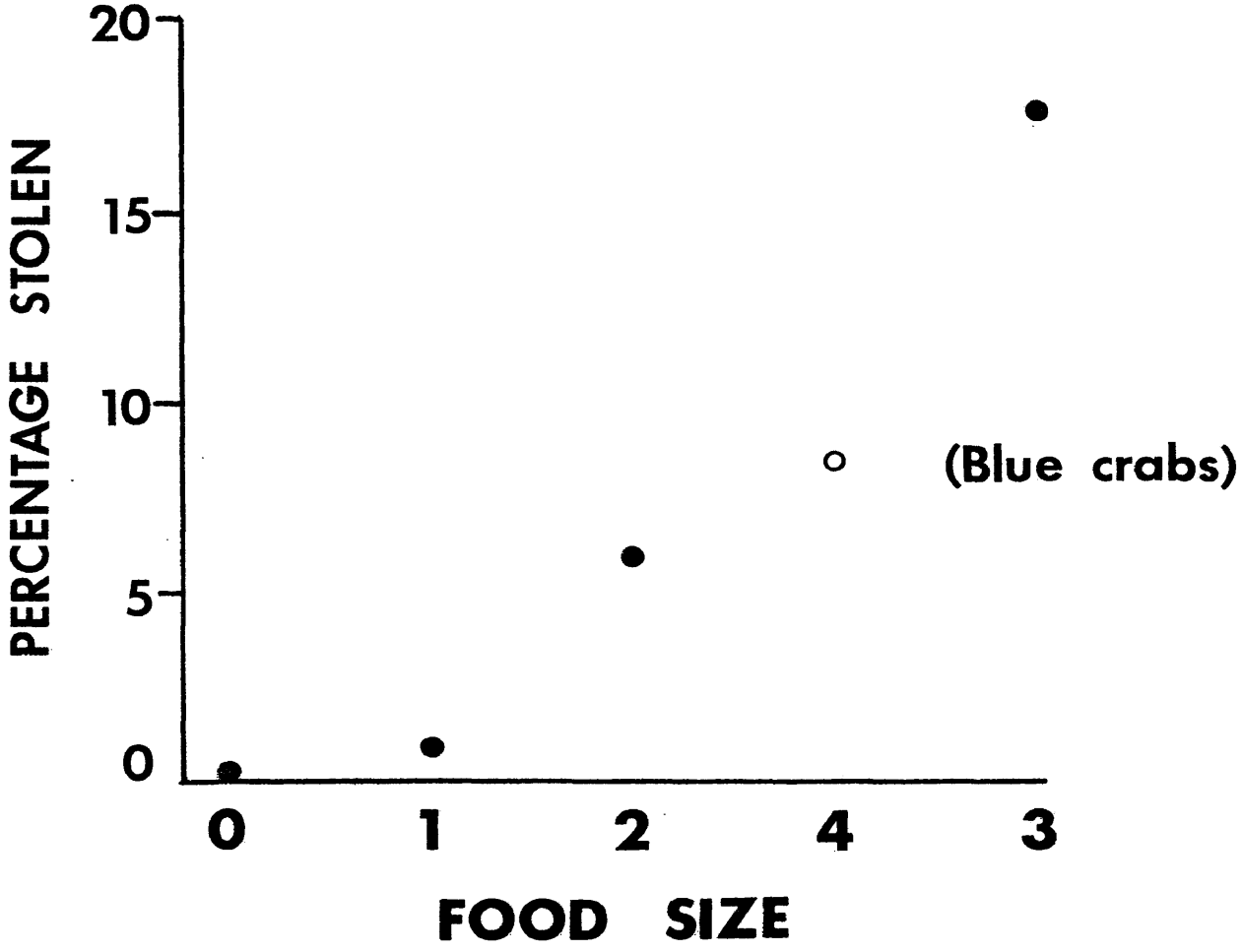
FISH SIZE	NUMBER OBSERVED	NUMBER STOLEN	PERCENTAGE STOLEN	CHI SQUARE	P
0	186	1	0.5%		
1	330	3	0.9%		
				43.97	< 0.001
2	620	34	5.5%		
3	90	15	16.6%		
TOTALS	1226	53	4.3%		

TOTAL X^2 (BY CELL) =

0.25 + 5.88 +
0.37 + 8.45 +
0.08 + 1.76 +
1.13 + 26.06* = 43.97

* X^2 Value for cell containing frequency of stolen fish of size 3

Figure 4. Kleptoparasitism risk factor for five food sizes.


20
15
10
5
0
PERCENTAGE STOLEN
(Blue crabs)
0
1
2
4
3
FOOD SIZE

All the food I observed being stolen on the ground was stolen from royal tern chicks which were either in the process of taking food from a parent or had just received food from a parent. Therefore, royal tern chicks acted as food hosts to all kleptoparasites in the study (including other royal tern chicks). Out of 70 food robberies observed, 46 (65.7%) were intraspecific, while the remaining instances of food theft (34.3%) were by laughing gulls (15 instances) and herring gulls (9 instances) (Table 5).

Royal tern chicks swallow their prey head first and a large prey item would often remain tail-end out of a chicks' mouth for a brief period after feeding. In several observations where laughing gulls (9 instances) and herring gulls (3 instances) stole food from tern chicks, a neighboring chick had grabbed the tail-end part of the host chicks' prey and started pulling on it, thus preventing the recipient from fully ingesting its food. Such interference from nearby chicks in the creche made it quite easy for parasitic laughing gulls and herring gulls to swoop down quickly and steal the food from the struggling chicks. At times these interfering chicks were successful in stealing food from other chicks in the creche and supplemented their own diet by doing so. (25 instances of food parasitism were observed among creching chicks.)

Any chick which adopted the begging posture was seen to quickly draw several "gackering" adults to its immediate vicinity. (The term "gackering" refers to a series of rapidly given, hoarse

TABLE 5

FREQUENCY OF PARASITISM OF ROYAL TERN CHICKS*

KLEPTOPARASITE					
ROYAL TERN CHICK	ROYAL TERN ADULT	LAUGHING GULL	HERRING GULL		
25	21	15**	9**	70	ROBBED TOTAL

*royal tern chicks served as hosts for all food robberies listed and also stole food from each other.

**interference by royal terns or chicks with chicks during feeding led to additional kleptoparasitisms by laughing gulls (9 instances) and herring gulls (3 instances)

"ack-ack-ack-ack" calls indicating threat and performed in aggressive encounters on the ground in sitting or standing position. This call is given in concert with lunging, gaping, and bickering displays when dueling with neighbors [Buckley & Buckley et. al., in press].) It is possible that such gackering behavior on the part of the adults served to confuse the aural portion of the recognition between parent and young, thereby increasing the liklihood of an unsuccessful food transfer between the two. Quite often, I observed chicks immediately after a feeding being surrounded by loudly gackering adults with apparent food stealing intentions. Parents invariably responded aggressively to these intruders with threat displays accompanied by gackering and pecking.

Adult royal terns were observed stealing food from tern chicks on 21 occasions. Royal tern chicks on the ground lost food to adults in two different ways: 1) Right at or immediately after the transfer of food from parent to chick, a strange adult would rush in and steal the morsel from the chick (17 instances, some prompted by robbing attempts of other chicks), and 2) Chicks dropped their food which was quickly snatched off the ground (4 instances). In some food parasitisms, chicks receiving food were interfered with by nearby chicks and while struggling to maintain possession, lost the prey to an adult (see above). On four occasions, I observed royal terns feeding fish to their chicks which they had just stolen from another chick. Royal terns engaged in courtship on the ground (i.e., potential breeders) were also observed pirating food from creching chicks. Such birds would suddenly break away from their courtship partners and snatch a fish from a nearby chick which had just been fed. These terns showed the solid black

forehead and pileum and were easy to distinguish from other terns which had young. (The breeding royal terns' black forehead fades rapidly to mottled white when incubation begins.)

In many instances I watched adults violently attacking stray chicks with vicious pecks in addition to stealing food from other chicks. Royal tern chicks in the process of being robbed were often assaulted by several adults simultaneously and appeared to run the risk of potential injury from their larger, stronger attackers. The adults seemed to exhibit an "all-or-none" response in their food robbing behavior. Once a robbing attempt was initiated, targeted chicks were pecked and thrown about wildly until their food was taken. Food parasitisms were always initiated at the point of food transfer between parent and chick or immediately afterwards. Once begun, such struggles quickly attracted other tern adults as well as gulls. For example, one feeding incident involving a three week-old chick in the creche (which was fed a size 2 fish) immediately attracted several royal terns, laughing gulls, and a nearby herring gull which all contested for the food item. In this specific robbery, the action was typically fast and involved so many birds that I was unable to determine the exact fate of the food, except to note that it was stolen.

In other incidents, I observed adult royals vigorously pulling large fish (9-12 cm) directly from the mouths of chicks which were unable to swallow their food quickly enough to prevent this from happening.

One particularly interesting event I observed involved a royal tern feeding its creching chick a large flounder. Due to their bulky nature, flounder were often difficult for the chicks to ingest and as this

particular chick struggled with the awkward prey, three adult terns quickly landed near it. The first of these adults to land already carried a small, slender fish in its bill. Based on its behavior, I feel this tern was intent on stealing the flounder from the then struggling chick and abandoning its own smaller catch. Finally, the chick managed to swallow its fish and only then did this adult leave, still carrying its small slender fish. This observation suggests that terns foraging for chicks may indeed select certain sized food items, when and where a choice is possible.

Interspecific Kleptoparasitism of Royal Tern Adults in the Air.

Royal terns carrying large food items (soft-shell crabs, flounder, and other large fish) were harassed considerably more and attracted more birds upon feeding chicks than terns carrying smaller items. A royal tern with a large conspicuous prey item was frequently pursued by other royal terns, and such chases often continued for several hundred yards away from the colony site. A tern chasing another tern carrying a large bulky food item has a clear advantage in flight and persistently dives at and harasses the potential victim from behind and below. However, I was not able to determine the outcome of these chases as inevitably the terns flew past my visual range before the chase ended. Such spirited chases were quite easy to distinguish from courtship flights.

Laughing gulls also chased fish-carrying royal terns but employed different tactics in doing so. They attempted to steal from airborne terns only in the immediate airspace over the creche. Piratical chases

by laughing gulls of royal terns were shortlived and usually terminated a short distance out of the colony, whether or not the laughing gull had succeeded in stealing the prey. On no occasions were laughing gulls observed in lengthy food chases with royal terns.

Laughing gulls were often seen kleptoparasitizing royal terns, (9 instances of this were observed in 1982 on four different days) sometimes singly but most often while in groups. Such robberies usually began with a single laughing gull securing a hold on a food item held by a royal tern which was flying over the creche. The two birds, struggling for possession, would fall to the ground where one or more additional laughing gulls would quickly join the fracas and invariably succeed in taking the food from the bill of the tern, after which all birds involved would quickly disperse.

Temporal Changes In Food Size Category Frequencies

FUNCAT analysis of the data in Table 1 indicates that fish sizes 0 (X^2= 91.34, $P < 0.0001$) and 1 (X^2= 86.43, $P < 0.0001$) underwent highly significant changes in frequency throughout the six chick age classes. Fish size 2 also underwent significant frequency changes throughout the six chick age classes (X^2= 25.15, $P < 0.0001$) but as indicated by the lower chi square estimate, these frequency changes were not nearly as drastic as those seen for fish sizes 0 and 1. Fish size 3 underwent insignificant frequency changes among the different chick ages (X^2= 10.08, $P < 0.0731$). The insignificant P value for this portion of the test probably reflects insufficient data for fish in size category 3.

The null hypothesis that there was no difference among chick age classes for each fish size category was tested using FUNCAT analysis and rejected for all fish sizes except size 3.

Fish in size category 0 were important in the diet of freshly hatched chicks. Size 0 fish showed a 12% decrease after the first week (one week-old chicks received 60% of the total number of size 0 fish seen fed) and were probably not important in the diet after chicks reached two weeks of age. Size 1 fish appeared in high numbers for five chick age groups but were probably less important in the diets of four and five week-old chicks than in 1,2, and 3 week-old chicks. Size 2 fish were plentiful in the food of ALL chick age groups, especially for those chicks aged three weeks and older (Size 2 fish comprised roughly 50% of the diets of chicks three weeks and older; Figure 3). Size 3 fish were not plentiful in the diet of any chick age group. Soft-shell crabs were virtually non-existent in the diets of 1 and 2 week-old chicks. Soft-shells began to appear in the chicks' diet at three weeks of age, then became more numerous as chicks reached four and five weeks of age. Chicks younger than three weeks had extra difficulty handling the large, bulky soft-shells which were stolen at a relatively high percentage in the creche (Figure 4).

In summary, intermediate fish sizes appeared to be abundant dietary items in every chick age class; however, larger intermediates were fed at higher frequencies to older chicks. Fish in the smallest size class were most important to hatchlings, while very large fish are important perhaps only to chicks which are about to fledge. Soft-shell crabs were important dietary items for chicks which were three weeks or older.

Spatial Changes in the Social Feeding Environment Over Time.

Table 6 shows that the social feeding environment changed as the chicks grew older and more mobile. As the chicks grew older they were observed being fed more frequently at a greater distance from other birds in the creche (= alone, Table 6). This was in contrast to the social feeding environment seen in the scrape and pre-creche stages (see Discussion, Nest Scrape Egression and Creche Formation) where royal chicks were fed while adjacent to other young which were being closely guarded by a single parent (= among, Table 6). Early feedings (chicks up to two weeks old) were characterized by chicks being crowded together as when still in the nest scrapes or immediately after leaving the scrapes, in both cases being closely guarded by the female. Later feedings (chicks > 3 weeks) revealed more isolated chicks in the open when approached by parents with food. The analysis in Table 7 indicates that the large X^2 value for chicks 1-6 weeks old may reflect the chicks' presence in the colony during the first week. The value obtained for chicks 2-6 weeks old (Table 7) is not nearly as large, but still indicates a significant trend towards isolation during feeding.

Royal Tern Feeding Behavior

In those feedings which occurred shortly after hatching, adults brought mostly small fish (sizes 0 and 1) back to the hatchlings still in the scrape and being brooded by the mate. Upon landing, parents would gently lower the fish until it almost touched the breast of the

TABLE 6

EFFECT OF AGE ON THE SOCIAL FEEDING ENVIRONMENT OF ROYAL TERN CHICKS

	CHICK AGE (Weeks)						
	1	2	3	4	5	6	TOTALS
FED AMONG	304 [175.7] (95.6%)	78 [61.5] (70.3%)	55 [73.2] (41.7%)	161 [184.6] (48.3%)	139 [227.3] (33.9%)	39 [53.8] (40.2%)	776 (55.4%)
FED ALONE	13 [141.3] (4.1%)	33 [49.5] (29.7%)	77 [58.8] (58.3%)	172 [148.4] (51.7%)	271 [182.7] (66.1%)	58 [43.2] (59.8%)	624 (44.6%)
TOTALS	317	111	132	333	410	97	1400

X^2 = 322.93, $P < 0.001$, Expected cell frequencies are in brackets, actual percentages for each age class given in parentheses.

TABLE 7

EFFECT OF AGE ON THE SOCIAL FEEDING ENVIRONMENT OF ROYAL TERN CHICKS (WEEKS 2-6 ONLY)

	CHICK AGE					TOTALS
	2	3	4	5	6	
FED AMONG	78 [48.4] (70.3%)	55 [57.5] (41.7%)	161 [145.1] (48.3%)	139 [178.7] (33.9%)	39 [42.3] (40.2%)	472 (43.6%)
FED ALONE	33 [62.6] (29.7%)	77 [74.5] (58.3%)	172 [187.9] (51.7%)	271 [231.3] (66.1%)	58 [54.7] (59.8%)	611 (56.4%)
TOTALS	111	132	333	410	97	1083

($X^2 = 51.50$, $P < 0.001$)

brooding bird. Shortly after, the chick would emerge from beneath the mate and take the fish from the bill of the feeding parent. Very small chicks experienced handling problems when presented a size 2 fish, and in two instances either declined to eat or dropped the fish after repeated attempts to swallow it. Later feedings (after creche formation) involved larger fish which were delivered much more rapidly to the chicks by their parents.

Royal terns, upon returning to the colony to feed older chicks, recognize their young in the creche (Buckley & Buckley 1972a), land in front of them and deliver the prey item very quickly, often seeming to force the food into the gaping mouth of the chick. Very likely, the parent-chick recognition is achieved before the adult ever touches the ground, and this often required numerous passes over the creche by food-laden adults before they located their chick. After several passes over the creche without locating the chick, royal terns were frequently seen flying out to the surf and dipping the prey in the water, as if drinking. The chicks in the creche which heard their parents calling overhead were observed to leave the crowded part of the creche and move into the open where they could readily be seen and recognized by their airborne parents. The royal tern chick responds to the approach of the food-laden adult by assuming the exaggerated begging posture seen in other crested tern species (Smith 1975).

Rejected Food Items

Not all food brought back to the creche by parents was readily consumed by the young. Certain prey taxa (e.g., Pleuronectidae (flounder), Syngnathidae (seahorses, pipefishes)) were ultimately rejected by the chicks because either the food was too large and bulky to swallow or the behavior of the chicks after handling the food indicated that it was unpalatable to them. For example, in certain feedings, chicks outright rejected food items of a size which they were quite capable of ingesting. All three cases of this sort which I observed (2 pipefish, 1 seahorse)involved prey items which belonged to the family Syngnathidae. Such prey items were only briefly handled by the chicks before being rejected.

Nest Scrape Egression and Early Creche Formation.

During the early stages of the study, the royal tern chicks I observed showed a strong tendency to remain within the nest scrape for periods exceeding one week, as long as I refrained from physically approaching the nesting area too closely. Any direct intrusion into the nesting colony at hatching (e.g., walking up to or among the nests, cannon netting, etc.) impels a rapid movement of the chicks away from their individual scrapes.

In those portions of the colony where intrusion was the greatest, large numbers of very small chicks were observed to flee and form a rudimentary creche at some distance from the scrapes. However, at other

undisturbed parts of the nesting colony, later visits during a hatching success study revealed noticeably larger chicks (one week and older) crouching motionless in their respective scrapes. Upon leaving the nesting area, I watched these large chicks suddenly jump up and flee the nest area with surprising rapidity; this was taken as another indication that they were significantly older than 2-3 days. These chicks appeared to be quite capable of creching behavior but had not formed a creche.

Territorial Clashes Between Royal Terns and Two Species of Gulls.

Herring gulls and laughing gulls nested in abundance in the vicinity of the royal tern colony and subcolony. Both species of gull were involved in territorial disputes with royal terns and their creching chicks. The nature of the outcomes of these territorial infringements by royal tern chicks were starkly contrasting and depended upon which species of gull held the territory being violated. When downy tern chicks, just out of the scrape and accompanied by a parent, trespassed onto a laughing gull nesting territory, the result was a confrontation between the adult tern and the incubating gull. The tern would eventually prevail and the gull would surrender to it the nest territory until the tern chick moved on.

At a small subcolony located approximately 80 yards from the main colony, I observed territorial clashes between royal terns and laughing gulls. In the subcolony, roughly 100 pairs of terns nested in proximity to six laughing gull nests. The gull nests were located in grass and

were scattered along the periphery of the royal tern subcolony.

In the early stages after leaving the scrape, downy royal chicks were closely accompanied by a single parent (presumably the female) which defended them from ALL other birds. The adult royal terns did not always appear to guide the movements of their chicks (although at times this was seen) which roamed the nest area, but instead closely followed their movements and defended them wherever they happened to move. Thus,during this "pre-creche" stage,the adults seemed to defend a "mobile" territory, which had dimensions coinciding with the size and location of their chicks.

As the chicks left the scrapes and began to wander about (accompanied by the parent) they often strayed close to the perimeter of the nest colony and consequently into the territory of a nesting laughing gull. Such trespasses would bring into juxtaposition a laughing gull intent on defending its nest and eggs and a royal tern equally intent on defending its roaming chick, just out of the scrape. Fierce territorial battles would ensue between the gull and tern, beginning with vocal and visual threat displays and followed by violent pecks and bill clasping. Some of these encounters I witnessed between royal terns and laughing gulls endured for longer than five minutes with the end result inevitably being one of two things: (1) the tern chick would move away from the gull nest followed by its parent, or (2) the unfortunate laughing gull would be forcibly repelled from its nest (exposing eggs) by the parent tern, and would remain in vocal protest a short distance away until the tern chick and its parent moved on. In this manner, several incubating laughing gulls in the immediate vicinity of the royal tern subcolony were seen temporarily abandoning their nests for

intervals lasting up to ten minutes.

Near nesting territories of the herring gull, responses were quite different. Adjacent to the main royal tern nest colony, several pairs of herring gulls held and defended nesting territories. After the chicks had left the main nest area to form a creche they strayed unavoidably into these herring gull territories. During a visit to the creche in early July, 1983, I found six royal tern chicks lying dead on the sand in a rough horseshoe pattern. On another day I collected eight additional chick carcasses at the same location. These chicks were in an early stage of putrefaction, had multiple head and neck wounds, and appeared too large to serve as prey for herring gulls. All 14 birds appeared to have been victims of territorial aggression by a herring gull which held a territory containing two gull chicks nearby.

Predation By Herring Gulls.

Predation by herring gulls upon royal tern chicks was observed after the chicks left the nest scrapes. Such predation was observed on eight different days in 1982 and 1983. Following a disturbance, very young chicks (2-3 days) forced out of the scrape, seemed particularly vulnerable to herring gulls. After its formation, herring gulls were observed to enter and exit the creche almost at will, appearing to ignore the threat displays of the relatively few adult terns present in the creche. At least two individual herring gulls would regularly enter the creche and capture any downy royal chicks, devouring them whole (Appendix I). These sought-after chicks were found: a) among the

larger chicks present in the creche, b) being guarded closely by a single parent in the open, or c) hiding in the Spartina. Successful defense of downy chicks by royal terns against predatory herring gulls in the creche was seen only sporadically and had no lasting impact on the behavior of the gulls.

Herring gulls which specialized in preying on chicks (probably only two gulls were actually involved) would land at the edge of the colony and remain stationary for periods ranging from 15 to 90 minutes. This was usually ample time for the creche to " relax" (colony life returned to normal) and for small downy chicks to venture out into view. Then, with a sudden rush, the herring gull would enter the creche, head for the smallest chick in view, capture it, and often eat it immediately. Often the gulls would be unsuccessful in catching a chick, in which case they would fly out of the creche, circle it once or twice, land and repeat the cycle. Aggressive retaliation by royal terns was seen; in some instances even causing the attacking gull to drop the chick which (if able) would quickly scurry back into the creche. Retaliating adult royals used short dives and rapid ground approaches with open bill and intense gackering. Herring gulls responded to ground-charging terns by backing away for a short distance, and with upward pecks at aerial harassers. However, such defensive attempts by royal terns were successful only for very brief periods and never resulted in permanently displacing the herring gulls from the creche. Once in the grasp of a herring gull, downy royal chicks weakened very quickly, and even if they managed to escape with assistance from a parent, they often limped back to the creche. Thereafter, these injured chicks were easy targets for future attacks by predatory gulls. During the first week in July, 1983,

all downy royal chicks were removed from the creche area I observed and consumed by herring gulls. (This involved approximately 15 chicks, as most chicks in the creche at this time were larger.)

DISCUSSION

Prey Size Availability and Selectivity

Killifishes (Fundulus), anchovies (Anchoviella), and menhaden (Brevoortia) were listed as major food items in the royal terns' diet in North Carolina and Virginia (Buckley and Buckley 1972a). Erwin (1975) also listed as common prey items, silversides (Menidia), spot (Leiostomus xanthurus), striped mullet (Mugil cephalus),and butterfish (Poronotus triacanthus). In the months of chick feeding (June & July), there is quite a selective range in fish sizes, particularly for Brevoortia and Fundulus spp. Menhaden spawned in March will be about 3 cm in length, while those spawned in October are close to 8 cm. In addition, there are 1, 2 , and 3 year old age classes of menhaden available to foraging seabirds at this time.

The growth rate for juvenile menhaden is reported to be about 0.7 mm per day for the months June-September (Kroger et. al., 1974). This means an increase in length of close to 3 cm in a six week period. However, another report claims the growth rate of juvenile menhaden to be only 0.5 - 1.0 cm per month (Dean Ahrenholtz, pers. comm.). Killifish (Fundulus heteroclitus) are reported to grow from 6.3 mm to

26.0 mm in their first growing season (Kneib & Stiven 1978), an increase of 1.97 cm in three months. Such slow growth rates for menhaden and killifish probably cannot account for the dramatic increase in frequency of larger fish observed being carried in to growing royal tern chicks over a five week period (Figure 3, Table 1).

The wide array of prey sizes (Table 1) taken by royal terns probably reflects their tendency to forage both close to and at considerable distance from their nesting area (Erwin 1977). Foraging terns can capture different sizes of menhaden simply by fishing in different areas. Small menhaden prefer low salinity areas (e.g., tidal streams) while larger menhaden frequent higher salinity environments, such as are found in shallow waters near inlets and just beyond the breakers off barrier beaches (Dean Ahrenholtz, pers. comm.).

Erwin (1975) found that out of 203 total fish fed to pre-creche and creche age chicks, 76% were of intermediate size (38% for both small and large intermediate fish sizes). My data indicate that out of 1226 total fish fed to pre-fledge royal tern chicks, 78% were of intermediate size, 27% and 51% for small and large intermediate fish sizes, respectively. This is not an unequivocal comparison, however, since the size categories used in the two studies were not defined in exactly the same manner.

The results in Tables 1 and 2, as well as the presence during breeding months of several year age classes of at least three genera of fish known to be important taxa in the diet of North Carolina and Virginia royal terns indicate that royals may exhibit some prey size selectivity over time while foraging for a growing chick. Taylor (1974) found that among breeding sandwich terns, both changes in identity and

in size of prey are explicable partly in terms of availability and partly by the terns' selective behavior.

Wetting Food Items

The periodical prey-dipping behavior of parent royal terns after several passes over the creche indicates that keeping the food wet may in some way be important to their chicks. Quite possibly, by keeping the food moist, parent terns greatly facilitate the swallowing ability of their chicks. A dry prey item would be more difficult to swallow quickly than a wet one. Also, feedings are very likely a major source of seawater for the chicks so it is essential to keep the food moist.

Rejected Food Items

Buckley and Buckley (1972a) stated that chicks in the creche ate any fishes offered by adults. My limited observations refute this. Certain large flounder (Pleuronectidae) were manipulated in the bill for extended periods by young in the creche before they aborted swallowing attempts and abandoned the food. All Syngnathids (seahorses, pipefishes) have jointed bony exterior plates arranged in rings, quite possibly rendering them unpalatable to young royal terns which handled them briefly before dropping them onto the sand. Possibly, some negative tactile cue involving the "exoskeleton" of these particular prey caused the rejection. Usually a laughing or herring gull would

swoop down and pick the food up off the ground. Hatch (1970) observed a similiar occurrence in common tern colonies.

Kleptoparasitism Of Royal Tern Adults By Laughing Gulls

Buckley & Buckley et. al. (in press) have noted that kleptoparasitism of young or adult royal terns by other larids and magnificent frigatebirds (Fregata magnificens) have not been observed to be successful, "the S. maxima always outflying the kleptoparasite." At the time of the Buckleys' Virginia royal tern study (1967-1970), both laughing gulls and herring gulls nested on Virginia beaches in vastly reduced numbers in comparison to those seen at present (M. Byrd, pers. comm.). With increased numbers of gulls coming into contact with food-carrying royal terns at the colony site, the potential for kleptoparasitisms is consequently increased. In my study, laughing gulls were often seen stealing food from royal terns in the airspace over the creche. Possibly, while royal terns are searching the creche below for their chicks, they are momentarily vulnerable to piracy.

Food Parasitism and "Trade-offs" in Royal Tern Foraging

The relaxed creche of a royal tern colony appears to present numerous opportunities for kleptoparasitism to birds in and near the creche. For several weeks, large numbers of chicks are very close together and feedings occur almost constantly during the daylight hours

(although peak feeding times are seen at dawn and dusk [Erwin 1975]).

Food parasitisms rarely occurred while chicks were small and receiving small fish. Only later, when large numbers of larger fish and soft-shell crabs were brought back, did food robberies become noticeable.

The amplified begging posture I observed in royal tern chicks just before feeding has been described for other species of crested terns. Smith (1975) reports adult sandwich terns feeding juveniles which adopted an exaggerated form of the food begging posture. He notes that this posture is often adopted in species where adults have to make a very fast delivery to avoid fish predators such as gulls, skuas, and other terns.

The spatial changes observed in the creche during feedings as chicks grew older (Tables 6 & 7) may be influenced by the threat of food parasitism from nearby chicks. As chicks grow larger, the trend toward temporary isolation during feedings, the appearance of excessive begging behavior, and the rapid food delivery by the parent may all reflect adaptations by the species to minimize food parasitism.

A royal tern with a hungry chick has a great need to procure sufficient quantities of suitable prey to feed to that chick so it will continue to grow and develop at a rate which is equal to that of its creche mates. At the same time, the foraging parent must manage to catch enough food for its own maintainence as obviously a weakened or unhealthy tern will not be capable of foraging sufficiently for its chick. Possibly, for these reasons, parent terns will seize any opportunity to steal food from other tern chicks in order to feed their own. The food stealing behavior of adult royal terns fits the "walk

across grab" strategy seen by Hulsman (1976) among black-naped terns (S. sumatrana), roseate terns (S. dougalli) and crested terns (S. bergii) which robbed members of their own species. Intraspecific food robbing has been observed among common terns and roseate terns by other researchers. Dunn (1973a) reports that food parasitism by roseate terns was a means of providing food for growing chicks rather than for self-maintainence. Hays (1970) observed young common terns with fish being lifted 8-10 feet into the air by adults which were intent on stealing their food. She watched these chicks fall to the sand without their food during such interactions. Hopkins & Wiley (1972) observed common terns stealing fish from arctic terns and presenting the "loot" to their own young.

Apparently, a food-laden royal tern returning to the creche must overcome several obstacles before its chick can ingest the procured food. First of these obstacles is the ubiquitous laughing gull which is very capable of pirating the food directly from the mandibles of the adult as it reaches the creche and begins to scan the ground for its chick. Second, it must locate its own chick within the creche. Finally, upon achieving recognition, the tern must deliver the food to the chick quickly and effectively. The size of the food item has a direct influence on the amount of energy expended by parents in overcoming these obstacles -- the larger the food the more energy needed.

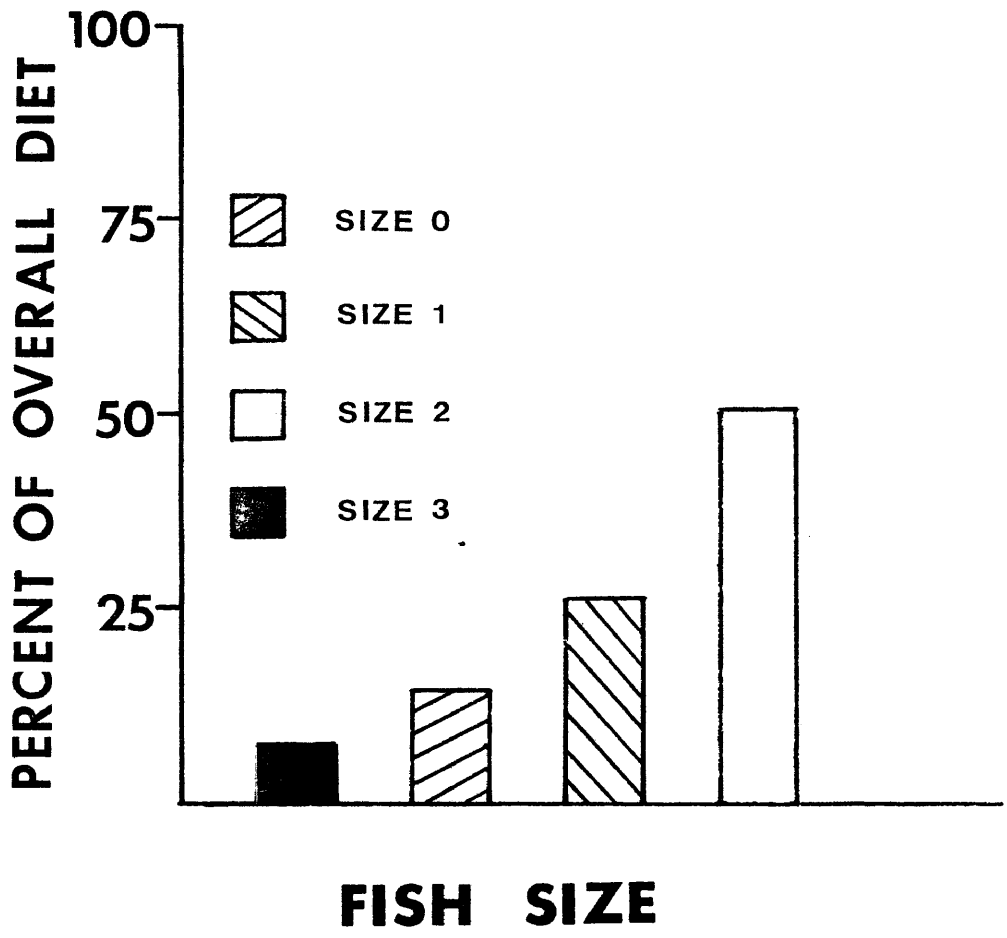
Food procuring appears to present a problem for an adult royal tern which is foraging for its chick. Hopkins & Wiley (1972) have listed the disadvantages to parent terns of feeding their chicks either too large or small a fish. The disadvantages to feeding large fish are: 1) they

are cumbersome to carry 2) they attract piratic pursuits in the air; 3) they are more difficult for chicks to swallow quickly. Hopkins & Wiley claim that due to these factors a chick which is fed a large fish stands a greater risk of losing that fish to adults and other chicks through piracy. A tern feeding its chick small fish will minimize these hazards; however, it will expend more energy by making more trips to provide the same amount of food. I came to the same conclusions based upon my observations of royal tern chick feeding behavior. The ideal food size would be the largest possible prey which the chick could ingest quickly enough and still nourish the bird sufficiently until its next feeding. Obviously this "ideal size" would vary as a function of time for as chicks get larger they are capable of handling larger prey. Hopkins & Wiley end their discussion by speculating that intermediate fish sizes would probably maximize the efficiency ratio, i.e., amount of food/parental cost. A bar diagram of the percentages of fish size categories for the royal tern (Figure 5) strongly supports this speculation since intermediate fish sizes (size categories 1 and 2) comprised 78% of the overall total number of fish fed to royal tern chicks. It is quite possible, that in the absence of fish pirates larger fish (size 3) would be taken more often.

Courtship Feeding As A Predictor Of Future Performance Of Royal Tern Males In Feeding Chicks

Nisbet (1973) speculated that the performance of the male common tern in courtship feeding is a predictor of his future performance in

Figure 5. Percent of overall total of each fish size fed to royal tern chicks.


100
75
50
25
PERCENT OF OVERALL DIET
SIZE 0
SIZE 1
SIZE 2
SIZE 3
FISH SIZE

feeding the chicks. In order to test Nisbet's theory for royal terns, one must have some idea of which food types/sizes are involved in successful courtship feeding and which food types/sizes the parents are bringing back to the colony to feed their chicks.

Kilham (1981) noticed that in royal tern courtship feeding the size of the fish appeared to be important to female selection. On 23 occasions in which the female accepted, the fish was about 7 cm in length. Of seven refusals observed, the fish was 5 cm in length or less and slender. Kilham concluded that female royal terns demanded an offering of a definite type before continuing in the courtship, this being a fish about 7 cm long. (In a study of the pre-nesting behavior of the swallow-tailed kite (Elanoides forficatus), Kilham (1980) noticed that during courtship feeding, females accepted only anoles (Anolis carolinensis) which were of a specific size.)

A comparison of the percentages of each fish length category brought to young during the pre-fledge period revealed that intermediate fish sizes made up 78% of the chicks' fish diet (Figure 5). In addition, Figure 5 shows the modal size category (2) comprising 51% of the total number of fish seen fed to chicks. This particular category included those fish which were 7 cm in length.

For single-prey loading species, (such as the royal tern), a few studies have shown that the mean size of prey carried to nestlings was greater than that eaten by foraging adults (Royama 1970; Hartwick 1976; Hegner 1982). In addition, Hopkins & Wiley (1972) have suggested that in terns, intermediate fish sizes would maximize the efficiency ratio for foraging parents with chicl in terms of amount of food/parental

cost. If this is true, females would maximize their breeding success by choosing as mates those males which brought them intermediate fish sizes (i.e., about 7 cm) during courtship feeding. Quite possibly, such males would tend towards maximizing their feeding efficiency ratio later in the breeding cycle (while feeding the chick) by bringing back intermediate fish sizes. It should be mentioned that this interpretation of the relationship between Nisbet's speculation, Kilham's observations, and my chick-feeding data is not unequivocal, and that a different explanation for the prey size similarity in courtship and chick feeding may exist. Possibly, more data is needed before the question can be fully resolved.

Nest Scrape Egression And Creche Formation

At what age do royal, sandwich, and creche-forming terns in general leave the nest and join the creche? This particular question recurs with high frequency in the ornithological literature on terns. Downy royal tern chicks were observed leaving their individual sand nest scrapes at widely varying elapsed time intervals from the time of hatching. The difference in elapsed time between hatching and nest exodus appears to be strongly influenced by human intrusion and disturbance levels (Smith 1975). Based upon my observations of breeding behavior in royal terns, the time at which the chick leaves the scrape to join the creche varies from 3 to 10 days and is dependent on such disturbance levels (i.e., human intrusion, dogs, etc.). My observations coincide closely with those of Smith (1975) who noted that at sandwich

tern subcolonies which he visited daily, chicks left within three days of hatching, while at others in the same colony which were undisturbed, the exodus was much slower. Veen (1977) felt that in reaction to human disturbance sandwich terns tended to lure their chicks away from the nest. He concluded that human disturbance seemed to accelerate nest desertion. Chestney (1970) observed young sandwich terns fledging where they had hatched at a colony in Scotland which had been completely undisturbed that season. Dragesco (1961) indicates that S. maxima albidorsalis (African race) do not move about until one week of age and, although they may group at this time, a creche is not formed (or joined) until 15 days of age.

I feel that creche formation in royal terns may be a gradual process involving several phases. I observed three phases during my study, all leading to the formation of a creche: (1) after hatching, chicks remain in the scrapes and are fed and protected there by parents (7 days or longer); (2) pre-creche stage where chicks initially leave the scrape and are closely accompanied by a parent (7-14 days); (3) creche stage where chicks are large enough not to be eaten by large predatory gulls and are left unattended while not being fed (14-21 days). In sandwich tern colonies, Veen (1977) noted that early nest departure had a disadvantage in that it increased the chances of predation by black-headed gulls (L. ridibundus).

The ability of adult crested terns and royal terns to distinguish their young and eggs from those of others has been well documented (Davies et. al. 1962, Buckley & Buckley 1972b). In particular, the individual egg and chick variation among royal terns has been shown to be extremely high and is used very effectively by adult royal terns as a

powerful aid in locating their nests and young (Buckley & Buckley 1972b). However, much energy appears wasted by the parents which, upon returning from distant foraging sites, fly repeatedly over the creche with food while attempting to locate their own chick among the many spread out on the sand below. In many instances, food-laden terns would circle the creche in the general vicinity of the chick up to 15 times before landing and feeding their chicks. During each pass the parent birds risked losing their catch to piratical laughing gulls. Buckley & Buckley (1972a) also noted food-stealing by creching chicks on those royal tern adults which flew too close to other chicks while attempting to find their own.

When the large distances which royal terns cover during foraging (> 21 km) are taken into account (Buckley & Buckley 1972a, Erwin 1977), a kleptoparasitism occurring before or during actual food transfer to a chick may represent a significant loss in terms of energy for both parent and chick. Particularly during stormy weather, kleptoparasitisms may be highly detrimental to the survival chances of the chick since the plunge-diving method of catching fish is known to be highly sensitive to adverse weather conditions (Hawksley 1957, Dunn 1973b).

Kruuk (1964) showed that birds in large breeding colonies may effectively reduce avian predation either because many individuals jointly mob an intruding predator or because nests in the center of the colony are relatively invulnerable to predators ("selfish herd" phenomenon of Hamilton 1971). Erwin (1977, 1978) reported that tern species which fed at greater distances from the colony site also nested in larger colonies and were more gregarious (larger groups) than the more solitary, small colony, inshore feeding terns. Royal terns feed

more often at distant sites than other tern species and also nest in the largest colonies of any of the Atlantic coast species (Erwin 1977, 1978). Erwin concluded that colonial nesting may not only deter predators but also increase searching efficiency ("information center" hypothesis) over a range of foraging areas where the distribution of food is patchy and unpredictable.

Such observations help to delineate the potentially tremendous benefits accrued by breeding royal terns if all disturbance at hatching and in the days following is minimized, thereby allowing the young to remain in the nest scrape for as long as possible. These major advantages might be: (1) Greatly reduced search time required of food-laden parents returning from distant foraging sites to find their young; (2) Eliminates the threat of predation by herring gulls, which I never observed entering the dense nesting aggregations of royal terns during incubation and after hatching. (3) The smallest chicks in the creche often have difficulty keeping up with the pace set by the larger chicks, and therefore run a very real risk of being trampled by larger chicks (Buckley and Buckley 1972a). Delayed creche-joining would reduce this risk. Buckley & Buckley (1972a) noted that freshly hatched royal tern chicks, while still in the nest with the eggshells, would normally be susceptible to predation, but were not bothered by any diurnal predators. They continue by suggesting that (except laughing gulls) other avian egg-predators are probably intimidated by the sheer numbers and noise of an active colony, this possibly being the most important factor for the success of large colonies of royal and sandwich terns. To defend successfully their brood from predatory herring and great black-backed gulls, sandwich terns were observed to sit down on the

nest, threatening from a sitting position thus hiding eggs and chicks from the view of the predator (Veen 1977). I feel that the effectiveness of such an anti-predator behavior mechanism is greatly diminished if small vulnerable chicks do not remain in the nest depression where they can be hidden by their parents.

Territorial Encounters: Gulls Versus Royal Terns

The fierce encounters seen between royal terns with chicks and laughing gulls at laughing gull nests indicate that the intensity of protective behavior of the terns toward their offspring had peaked. Such observations are consistent with those of Buckley & Buckley (1972a) who note: "Approximately at the chicks' creche-joining age, parental aggression -- manifested by dive bombing assaults, aerial defecation, and accompanying shrill attack calls -- reaches its peak."

Trespassing onto the breeding territory of a herring gull (unlike that involving laughing gulls) appeared to be a significant source of mortality for royal tern chicks. While parents are at distant foraging sites, chicks in a relaxed creche may unintentionally wander too near the active territory of a herring gull and become severely injured or killed as a result. At least 14 chicks were probably killed by a herring gull in defense of its territory. Such mortality seems especially high when compared with reports from previous investigators (Buckley & Buckley 1972a) who noted that in four breeding seasons a total of 15 dead young were found in all royal tern colonies studied.

Predation By Herring Gulls

The current increase in the numbers of large gulls (Drury 1965; Kadlec and Drury 1968) concomitant with an explosive range expansion to the south has engendered much concern and speculation about its consequences for other seabirds. Many researchers believe that the abundance of food on garbage dumps has decreased winter mortality and increased reproductive success in herring gulls (Drury & Kadlec 1974, Burger 1977). With rapid population increases, herring gulls require considerable nesting space -- that presently used by several other gull and tern species (Burger 1979). Burger and Lesser (1979) found predation rates on common tern nests were much higher on islands with nesting herring gulls than those without gulls. Palmer (1941) observed that herring gulls returned to New England coastal nesting areas in late February or early March while terns did not appear in the area until mid-May. Burger (1979) noted the large, dominant herring gulls displacing and outcompeting the smaller, later-nesting laughing gulls in direct aggressive encounters on nesting islands in New Jersey. Such discrepancies in spring arrival time on the breeding grounds heavily favor the large gulls, which are territorially well-established before the smaller terns and gulls ever appear to claim nest sites.

The population of nesting herring gulls in Virginia has increased dramatically since their appearance about fifteen years ago (B. Williams, pers. comm.). Royal terns do not first appear in Virginia until late March, long after herring gulls have arrived on nesting beaches of the Eastern Shore barrier island chain. At present, royals appear to have no problem establishing their sizeable, dense, nesting

aggregations on beaches which also contain nesting colonies of herring gulls. The problems begin later, after the chicks have hatched and joined the creche.

Among all vertebrate predators, only the brown pelican (Pelecanus occidentalis) has been reported in the literature to prey on chicks of the royal tern (Blus et. al., 1979). In the summers of 1982 and 1983 I observed herring gulls preying upon royal tern chicks in the creche (Appendix I). On Metomkin Island, these predatory herring gulls removed not only very small chicks but several which were significantly larger as well. All predations occurred after the chicks had left the nest scrapes and joined the creche. Chicks up to two weeks of age appeared to be quite susceptible to herring gull predation. Great black-backed gulls were also present on Metomkin in 1983, but no predation by this species was observed.

Buckley and Buckley (1972a) feel that creche behavior must be a highly efficient method of protecting well-developed chicks from predators (although against what they are uncertain) while minimizing the amount of time the parents have to spend guarding the young from various predators. My observations indicate that creche behavior is ineffective, at best, against predatory herring gulls, which essentially behaved as ground predators.

At present, herring gulls appear to nest along most of Metomkin Island in large numbers and show no sign of declining. This places them in close and prolonged contact not only with breeding royal terns but with many smaller seabird species as well, such as common terns, least terns (S. albifrons), gull-billed terns (Gelochilodon nilotica), piping plovers (Charadrius melodus), and American oystercatchers (Hoematopus

palliatus). Very likely these smaller species (albeit, some more aggressive) also suffer from herring gulls preying upon their offspring. Erwin (1980) has suggested that other ground-nesting marsh dwellers such as the Forster's tern (S. forsteri), and clapper rail (Rallus longirostris) may soon have to compete for nest sites with the larger aggressive gull. In light of the present burgeoning population of this destructive avian predator on seabird nesting islands, such as Metomkin, it appears that herring gulls are and will continue to be, a serious threat to the diversity of smaller seabird species.

Conclusions

Royal terns apparently make an effort to match the prey size to the body size of their chicks during the pre-fledge feeding period. Mostly smaller fish sizes were seen at first, with intermediate and larger sizes predominating later on. While foraging for chicks, royal terns appear to select intermediate fish sizes most (78%) of the time. Food parasitism appears to influence food choice by royal terns feeding chicks because large food items are relatively low in frequency (6.3%) and are fed with a high risk of kleptoparasitism (almost 17%).

Kleptoparasitism in the creche is both intraspecific and interspecific. Laughing gulls are quite capable of stealing food from adult royal terns which fly over the creche in search of their chicks. On the ground, attempts at intraspecific food robbery appeared to increase the likelihood of interspecific kleptoparasitisms. Larger fish sizes and soft-shell crabs represent the food types which are stolen

most often. Food parasitisms in the creche became noticeable only after chicks had reached three weeks of age. Both breeding and courting (potential breeders) royal terns were observed stealing food from chicks in the creche. Laughing gulls and herring gulls were also seen stealing food from royal chicks in the creche, often in response to robbing attempts by other chicks.

As chicks grow larger, they show a significant trend towards isolation during feeding. Three types of behavior are thought to represent adaptations against kleptoparasitism in the creche: 1) chicks isolate themselves from others in the creche while being fed, 2) chicks display an excessive begging posture just prior to being fed, and 3) adults make a very rapid food delivery to the begging chick on the ground.

A high degree of similarity exists between fish sizes which are successful in courtship feeding and fish sizes which are fed to chicks. This observation suggests that in royal terns, courtship feeding may act as a predictor of future performance of the male in feeding chicks.

Scrape egression in royal tern chicks occurs at widely varying time intervals and appears to be strongly influenced by human disturbance. Herring gulls are predators of royal tern chicks, especially those chicks which are forced to join the creche at too early an age.

APPENDIX I

PREDATION BY HERRING GULLS

Predation Occurrences

DATE	TIME	REMARKS
7/11/82	1107	HG eats royal chick; this gull stood quietly at creche periphery for 90 min. before rushing into creche and grabbing the chick.
7/11/82	1241	Another chick predation; HG drives back the creche as well as threatening adult terns before rushing in and grabbing the chick.
7/12/82	1058	HG predation on royal tern chick.
7/13/82	0944	HG predation on royal tern chick; this time adult terns dive at predator 5 times.
7/15/82	0830	HG seen flying from colony with a

		chick but drops it.
	0920	HG flies into creche and grabs a chick but loses it while flying out: immediately, another HG flies in, seizes the dropped chick (still alive) and eats it.
7/18/82	0933	HG predation on royal tern chick.
7/19/82	0928	HG rushes into creche, grabs a chick but drops it and chick escapes. (creche alarms)
7/1/83	1548	HG attacks, kills, and eats a downy royal chick in the creche.
	1822	Another HG preys on a royal chick.. This gull landed in the creche, walked straight towards the smallest chick, lunged forward and grabbed it. It flew away with the chick while being dived at by royal terns.
7/2/83	0730	HG grabs a chick, but is harried by royal tern and lets it go.

0850 HG grabs chick again but drops it as tern charges again

0857 Same thing occurs; chick escapes but is getting very weak and limps away.

0900 HG finally kills this chick but does not eat it. Instead it goes back to the creche.

0934 This HG attacks another chick and it escapes.

LITERATURE CITED

Ansingh, F. H., H. J. Koelers, P. A. Van Der Werf, and K. H. Voous. 1960. The breeding of the cayenne or yellow-billed sandwich tern in Curacao in 1958. Ardea 1(2): 51-65.

Blus, L. J., R. M. Prouty & B. S. Neely Jr. 1979. Relation of environmental factors to breeding status of royal and sandwich terns in South Carolina, U.S.A. Biological Conservation 16: 301-320.

Brockmann, H. J., & C. J. Barnard. 1979. Kleptoparasitism in birds. Animal Behaviour 27: 487-499.

Buckley, F. G. & P. A. Buckley. 1972a. The breeding ecology of royal terns Sterna (Thalasseus) maxima maxima. Ibis 114: 344-359.

Buckley, P. A. & F. G. Buckley. 1972b. Individual egg and chick recognition by adult royal terns (Sterna maxima maxima). Animal Behaviour 20: 457-462.

Buckley, F. G., P. A. Buckley and E. K. Dunn. Handbook of the birds of Europe, the Middle East, and North Africa. The birds of the Western Palearctic. Vol. IV Terns (in press).

Burger, J. 1977. Nesting behavior of herring gulls: invasion into Spartina salt marsh areas of New Jersey. Condor 79: 162-169.

_____. 1979. Competition and predation: herring gulls versus laughing gulls. Condor 81: 269-277.

_____, and F. Lesser. 1979. Breeding behavior and success in salt marsh common tern colonies. Bird-Banding 50: 322-337.

Chestney, R. 1970. Notes on the breeding habits of common and sandwich terns on Scolt Head Island. Trans. Norfolk Norwich Nat. Soc., 21: 353-363.

Davies, S. J. J. F., and R. Carrick. 1962. On the ability of crested terns, Sterna bergii, to recognize their own chicks. Australian Journal of Zoology 10: 171-177.

Dragesco. J. 1961. Observations ethologiques sur les oiseaux du banc d'Arguin. Alauda 29: 81-98.

Drury, W. H., Jr. 1965. Gulls vs terns, clash of coastal nesters. Massachusetts Audubon, Summer 1965.

_____, and J. A. Kadlec. 1974. The current status of the herring gull population in the northeastern United States. Bird-Banding 45: 297-306.

Dunn, E. K. 1973a. Robbing behavior of roseate terns. Auk 90: 641-651.

_____. 1973b. Changes in fishing ability of terns associated with windspeed and sea surface conditions. Nature 244: 520-521.

Erwin, R. M. 1975. Comparative foraging and breeding strategies of three seabird species: common tern (Sterna hirundo), royal tern (Sterna maxima), and black skimmer (Rynchops niger). Ph. D. diss. University of Maryland.

_____. 1977. Foraging and breeding adaptations to different food regimes in three seabirds: the common tern, (Sterna hirundo), royal tern, (Sterna maxima), and black skimmer, (Rynchops niger). Ecology 58: 389-397.

_____. 1978. Coloniality in terns: the role of social feeding. Condor 80: 211-215.

_____. 1980. Breeding habitat use by colonially nesting waterbirds in two Mid-Atlantic US regions under different regimes of human disturbance. Biological Conservation 18: 39-51.

Fuchs, E. 1977. Kleptoparasitism of sandwich terns Sterna sandvicensis by black-headed gulls Larus ridibundus. Ibis 119: 183-190.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31: 295-311.

Hartwick, E. B. 1976. Foraging strategy of the black oystercatcher (Haemotopus bachmani Audubon). Canadian Journal of Zoology 54: 142-155.

Hatch, J. J. 1970. Predation and piracy by gulls at a ternery in Maine. Auk 87: 244-254.

_____. 1975. Piracy by laughing gulls (Larus atricilla): an example of the selfish group. Ibis 117: 357-365.

Hawksley, O. 1957. Ecology of a breeding population of arctic terns. Bird-Banding 28: 57-92.

Hays, H. 1970. Common terns pirating fish on Great Gull Island. Wilson Bulletin 82: 99-100.

Hegner, R. E. 1982. Central place foraging in the white-fronted bee-eater. Animal Behaviour 30: 953-963.

Hopkins, C. D., and R. H. Wiley. 1972. Food parasitism and competition in two terns. Auk 89: 583-594.

Hulsman, K. 1976. The robbing behavior of terns and gulls. Emu 76: 143-149.

Kadlec, J. A., and W. H. Drury. 1968. Structure of the New England herring gull population. Ecology 49: 644-676.

Kilham, L. 1980. Pre-nesting behavior of the swallow-tailed kite (Elanoides forficatus), including interference by an unmated male with a breeding pair. Raptor Research 14(1): 29-31.

_____. 1981. Courtship feeding and copulation of royal terns. Wilson Bulletin 93: 390-391.

Kneib, R. T., and A. E. Stiven. 1978. Growth, reproduction, and feeding of Fundulus heteroclitus (L.) on a North Carolina salt marsh. Journal of Experimental Marine Biology and Ecology 31: 121-140.

Kroger, R. L., J. F. Guthrie, and M. H. Judy. 1974. Growth and first annulus formation of tagged and untagged atlantic menhaden. Transactions of the American Fisheries Society 103(2): 292-296.

Kruuk, H. 1964. Predators and anti-predator behavior of the black-headed gull, Larus ridibundus. Behaviour Supplement 11: 1-129.

Nisbet, I. C. T. 1973. Courtship-feeding, egg-size and breeding success in common terns. Nature 241: 141-142.

Orians, G. H. & Pearson, N. E. 1979. On the theory of central place foraging. In: Analysis of ecological systems (Ed. by D. J. Horn, R. D. Mitchell & G. E. Stairs), pp. 154-177. Columbus, Ohio: Ohio State University Press.

Palmer, R. S. 1941. A behavior study of the common tern (Sterna hirundo hirundo L.). Proceedings of the Boston Society of Natural History, 42: 1-119.

Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the great tit (Parus major L.). Journal of Animal Ecology 39: 619-668.

Sall, J. P. SAS User's Guide, 1979 Edition. SAS Institute Inc. pp 221-236.

Smith, A. S. M. 1975. Studies of sandwich terns. British Birds 68: 142-156.

Taylor, I. R. 1974. The feeding behaviour and ecology of sandwich, common, and arctic terns on the Ythan Estuary, Aberdeenshire, Unpublished PhD thesis Aberdeen, Scotland, Univ. Aberdeen.

Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the sandwich tern (Sterna sandvicensis). Behaviour Supplement XX: 1-193.

VITA

William James Ihle

Born in Huntington, New York, April 12, 1956. Graduated from Lee County High School in Fort Myers, Florida, June 1974. Received B. S. degree in Biological Sciences from Florida Institute of Technology in December 1978. Employed temporarily as a laboratory technologist, then as a biologist for the State of Florida from October 1979 to January 1981.

Entered the the College of William and Mary in August 1981 as a graduate student in the Department of Biology.