FACTORS INFLUENCING REPRODUCTIVE SUCCESS AND NESTING STRATEGIES IN BLACK TERNS

by

Betty-Ann Chapman Mosher
B.A. Boston University 1978
M.Sc. State University of New York at Fredonia 1980

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY
August 1986

Approval

Name: **Betty-Ann Chapman Mosher**

Degree: Doctor of Philosophy

Title of Thesis:

Factors influencing reproductive success and nesting strategies in Black Terns

Examining Committee:

Chairman: Dr. R.C. Ydenberg

Dr. Nicolaas A.M. Verbeek, Associate Professor
Senior Supervisor

Dr. Brian Hartwick, Associate Professor

Dr. Mark Winston, Associate Professor

Dr. Alton Harestad, Assistant Professor, Public Examiner

Dr. Kees Vermeer, CWS Biologist, Public Examiner

Dr. Paul Buckley, Director, National Park Service, Rutgers University, External Examiner

Date Approved 26 August 1986

I hereby grant to Simon Fraser University the right to lend my thesis, project or extended essay (the title of which is shown below) to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users. I further agree that permission for multiple copying of this work for scholarly purposes may be granted by me or the Dean of Graduate Studies. It is understood that copying or publication of this work for financial gain shall not be allowed without my written permission.

Title of Thesis/Project/Extended Essay

Factors influencing reproductive success and nesting strategies in Black Terns

Author:

(signature)

Betty-Ann Chapman Mosher

(name)

26 Aug 1986

(date)

ABSTRACT

Factors which might influence reproductive success, coloniality and the timing of breeding in Black Terns (Chlidonias niger) were examined. The most important factors influencing hatching success (overall average 73%) were rising water levels and wind and wave action (average 15.4%). The second largest factors influencing success were temperature and precipitation. Predation was only responsible for 8.6% of the overall losses. The most important factor influencing fledging success (average 61%) was that the last chick to hatch grew significantly more slowly, showed signs of starvation and eventually died, independent of clutch size.

Black Tern young ate 55% odonates, 35% other insects, and 10% fish. Peaks in odonate emergence differed by as much as 15 weeks between years and the overall emergence rate decreased from 1981-1984. Foraging success of adults was 5.09 items/min when catching insects, 0.82 items/min for fish and 2.03 items/min for insects and fish simultaneously.

Black Terns preferred to nest in areas with 33% open water, 42% matted vegetation and 25% standing vegetation in which the stalks occupied 10-50 cm^2/m^2 at the water surface. Water level fluctuations were variable over the years, but greatest early in the season. Changes of 2 cm in water level destroyed some nests. Experimental evidence showed that nests which were surrounded by vegetation or on a platform suffered the least from wind and wave action or fluctuating water levels. Nests in Phalaris habitats survived water level fluctuations better than those in other habitat types.

Predation was low in this study. Observations on potentially predatory species showed that corvids were mobbed equally during the egg and chick phases and Great Blue Herons mainly during the chick phase. The abundance of the potentially predatory species did not vary throughout the breeding season.

Coloniality and the timing of breeding in Black Terns can not be explained by those factors which are usually invoked for other species. The terns nest in loose colonies to benefit from joint mobbing, but are scattered enough to permit some food to be obtained near the nest. More precise synchronization of the breeding season is not favored because the factors which influence timing are unpredictable.

ACKNOWLEDGEMENTS

I would like to thank my senior supervisor, Dr. Nicolaas A. M. Verbeek for always being available and willing to discuss and provide feedback on the project, including design, results and conclusions, as well as editorial comments on the manuscript. My thanks also go to committee members Dr. Brian Hartwick and Dr. Mark Winston for providing useful comments on the project and manuscript.

The staff of the Creston Valley Wildlife Management Area, namely Dwight Moore, Brian Stushnoff, Harold Casemore, Sandra Hopcraft and Carmen Wood were very helpful in terms of access to the study areas and moving large pieces of equipment. I am particularly grateful to Dwight Moore for allowing the use of Management Area equipment and facilities. Many thanks go to Brian Stushnoff for help with the identification of plant species. The following are gratefully acknowledged for assistance in the field: Ingrid Bonsel, Scott Forbes, Penny Ohanjanian, Terry Parsons and Margaret Shamlock. I am also thankful to many people for useful discussions on the project, namely Scott Forbes, Howie Richardson, Craig Orr, Rob Butler and Ron Ydenberg.

This research project was funded by NSERC grant (A0239) to Dr. N.A.M. Verbeek. I am extremely grateful to Santo Wood for financial assistance during the writing stage of this project.

Lastly, I would like to thank my husband, Fred Mosher, for assisting in the work at Elizabeth Lake, providing moral support

during the final stages of the project and for always being so positive, supportive and understanding when I had to return to Vancouver for extensive periods to prepare for the defense.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

TABLE PAGE

I. GENERAL INTRODUCTION

In the past much attention has been given to studies dealing with the breeding biology of birds. In some of these studies, emphasis was placed on explaining the reproductive strategies, namely the degree of coloniality and the timing of the breeding season. Strategies employed by closely related species often proved to be similar (Lack 1968). However, in contrast to other larids, Black Terns (*Chlidonias niger*) are only loosely colonial, nesting in colonies of 20 or fewer pairs (Baggerman *et al.* 1956; Bent 1963), or in solitary pairs. In addition, this species exibits a fairly widespread timing of breeding (Cuthbert 1954; Bochenski 1966). Similar strategies have occasionally been observed within other marsh nesting terns, such as Forster's Tern (*Sterna forsteri*) (McNicholl pers. comm.).

At the time I began this study, much concern was being raised regarding the decline of Black Tern populations across North America (Tilghman 1980). Therefore, the first objective of this study was to obtain a measure of reproductive success in the largest breeding concentration of Black Terns in British Columbia. This would allow a comparison with other published studies dealing with this species. As the breeding and nonbreeding biology of Black Terns differs quite markedly from that of other larids, the second objective of the study was to examine various factors that might influence the nesting strategies of Black Terns.

REPRODUCTIVE SUCCESS

Black Terns, like many other species of terns, have shown signs of a population decline (Tilghman 1980). The decline appears widespread and for this reason the Audubon Society listed the Black Tern as declining in numbers prior to the beginning of this study (Arbib 1978). Marsh drainage was thought to be responsible for the decline of this species in many areas (Tilghman 1980). Faanes (1978) monitored a decline in numbers of Black Terns in Wisconsin which occurred at the same time that water levels dropped. The resultant alterations caused by drainage could have dramatic effects on Black Terns and other species which are dependent on marshes for at least part of their breeding cycle. The decline, coupled with the paucity of information about Black Terns, pointed to a need for a quantitative study of their reproductive biology.

NESTING STRATEGIES

A) COLONIALITY

Larids typically nest in colonies (Robbins *et al.* 1966). McNicholl (1975a) presumed that solitary nesting pairs among larids resulted from the breakup of former colonies, while Lack (1968) and Bergman (1980) stated that solitary nesting pairs were evaluating an area to determine if sufficient food supplies existed at that site. Many birds which feed on aerial insects (e.g. Black Terns) are typically colonial nesters (Lack 1968). This type of breeding is a response to abundant and/or spatially variable food resources (Horn 1968; Hunt and Hunt 1976a). Lack (1968) stated that the chief reason why most nidicolous freshwater birds and nearly all seabirds nested in colonies was that they were nesting on islands that were isolated and limited in size. Colonial nesting thus was dictated by space limitation. Marshes can be considered islands of water surrounded by land, which also tend to be isolated and limited in size.

A number of factors could be responsible for the loose coloniality observed in Black Terns. Factors examined in this study were 1) habitat availability, 2) food supply, 3) foraging effort of adults, and 4) predation.

1. Habitat availability

Lack of suitable habitat could result in the loose coloniality observed in Black Terns. Those areas where the birds nested may not be suitable for colonies. Hogstad (1981) found that distribution patterns of Fieldfare (Turdus pilaris) nests sometimes resulted from a scarcity of suitable nesting areas. Cody (1981) suggested that habitat selection can be dependent on the presence of competitors. Species displacement can be seen in areas where species overlap with competitors which have similar food requirements and foraging techniques (Chapman 1980; Chapman and Parker 1985). Veen (1977) thought that nest distribution was a function of habitat selection, where species nest in areas with few predators. This type of habitat selection is effective in avoiding areas with mammalian predators, but less effective in avoiding areas with avian predators (Kruuk 1964).

2. Food supply

The importance of the food supply as a factor influencing the formation of colonies has received much attention (Perrins 1965, 1966). Some authors have suggested that the size of colonies is influenced by the availability of food (Ashmole 1963; Lack 1968).

Colonial species usually feed on abundant food that is patchy in distribution (Horn 1968). Marsh nesting blackbirds rely extensively on spacially variable prey items (Horn 1968; Orians and Horn 1969). Lack (1968) thought that freshwater bird species were particularly localized because food in freshwater marshes tended to be concentrated near or in the marsh. Ward and Zahavi (1973) proposed that colonies serve an important function as "information centers" for food finding in situations where the distribution of prey is unpredictable. Unpredictable prey distributions can occur in insect as well as fish populations (Hunt and Hunt 1976a). The availability of emergent insects in marshes generally tends to be quite variable in time and space, and shows distinct daily peaks in emergence (Orians 1980).

3. Foraging effort of adults

The distance which a bird must fly between nesting and foraging sites can be important in colony formation. Lack (1968) stated that when birds breed in a colony, each individual must fly further for food than when nesting solitarily. Lack (1968) did not think that the distance flown for food would be an appreciable disadvantage for species feeding on aerial insects. However, it may be limiting for Black Terns, in light of their rather poor reproductive success. The limitation for Black Terns may arise because they return to the nest with a single food item, and thus are single-prey loaders. In contrast, most other insectivores are multiple-prey loaders and only return to their nest after many food items have been captured (Orians 1980). If

Black Terns are forced to fly long distances for food of relatively low caloric reward, it may be energetically costly for them to raise three young, compared to bringing items of high caloric reward from nearby. In general, colonial nesters should watch other birds and thus find food more easily with less search effort, as suggested by Ward and Zahavi's (1973) information center hypothesis. For information centers to be of any use, however, there must be synchrony in the timing of breeding within the colony. The importance of synchronization within the colony has been shown in several studies (Veen 1980; Evans 1982; Findlay and Cooke 1982). Synchrony was considered important in maximizing the potential for social foraging (Emlen and Demong 1975; Erwin 1978). Emlen and Demong (1975) showed that synchrony was very important for young fledglings when they began foraging for themselves.

4. Predation

Predator avoidance may be an important factor determining whether a species nests colonially or not. Some researchers have suggested that this is one of the most important factors influencing tight colony formation (Lack 1968; Ward and Zahavi 1973). Those species experiencing high predation pressure might lessen that pressure by mobbing predators together and therefore benefiting from colonial nesting. Some colonies experience what appear to be high levels of predation, which can be the result of egg specialists (Tinbergen _et al._ 1967). Bent (1963) states that members of the Corvidae, particularly large species, are egg specialists. These specialists are able to capitalize on the proximity of nests within colonies (Gottfried 1978). Although losses due to predation in colonies may seem high, the loss per nest within the colony is often reduced due to the dilution effect.

B) TIMING OF BREEDING

Many researchers have shown that populations of Black Terns lack a well-defined breeding season (Cuthbert 1954; Baggerman _et al._ 1956; Bochenski 1966; Dunn 1979). This species incubates for 3 weeks and feeds young in the nest for another 3 weeks. Since this time span is quite short, one would expect a narrow time period for breeding. The widespread timing of breeding observed in Black Terns may be explained by four factors. These are 1) habitat availability, 2) seasonal abundance of the food supply, 3) foraging effort of adults and growth of young, and 4) water level fluctuations. In addition, predation throughout the season may vary and will be discussed briefly.

1. Habitat availability

Habitat availability in terms of vegetation density could be important to the timing of breeding. The density of vegetation could vary throughout the season making the area unsuitable for nesting. Species may adjust their timing of breeding so that the vegetation is at a critical height or density before nesting begins. During some years, growth of the vegetation may be slow due to yearly weather patterns. This could result in areas being abandoned or breeding being delayed until the vegetation was at the required developmental stage. Dwernychuk and Boag (1972) determined that vegetation cover was very important for marsh nesting ducks.

2. Seasonal abundance of the food supply

Food availability is often used to explain the timing of breeding of birds (Pienkowski 1984). The importance of the food supply and its seasonal abundance to the timing of breeding was demonstrated in a number of species (Lack 1968; Orians 1980). Current theory predicts that birds time their breeding season so that the greatest number of young can be raised (Lack 1968). If food were abundant at the same time every year a well-defined breeding period would be expected. Species generally breed at the time when food is abundant for their young (Lack 1968; Emlen and Demong 1975). Perrins (1965, 1966) suggested that this reasoning needed to be modified because there should be an advantage to breeding early. Perrins (1970) stated that there must be some counteracting disadvantage to early breeding and suggested that the date of laying was related to food supply at the time of laying. The abundance or appearance of some prey species can be dependent on weather. Adverse weather tends to be unpredictable and could alter prey availability, thus producing food shortages for breeding birds (Emlen and Demong 1975). For this reason, species which feed on prey whose abundance depends on weather conditions may experience a more variable breeding schedule.

3. Foraging effort of adults and growth of young

Energy acquisition is important in determining the timing of breeding. Temperature levels are important to the development of gonads in birds and consequently to the date of laying (Welty 1975). Verbeek (1970) collected degree day data in Water Pipits *Anthus spinoletta*, where the first eggs are laid about 4 days after a rise in ambient temperature. The age of the bird may also influence the timing of egg laying. Young birds tend to nest later in the season than older birds. Some late nesting individuals may be young birds or renesters, but in either case their clutches tend to be smaller (Lack 1968; Perrins 1970).

The foraging effort of adults could be a very important factor influencing the timing of the breeding season. If the prey items consumed by adults or brought to chicks varied at different times during the season, the caloric intake could vary over the same time period (Orians and Horn 1969; Dunn 1975, 1976, 1980; Clarke and Prince 1980; Orians 1980). Similarly, obtaining food in a variety of areas at different times during the breeding season could result in various long distances being travelled, hence altering energetic demands on breeding at various times throughout the season.

4. Water level fluctuations

Fluctuating water levels may also affect the timing of breeding by altering available nesting sites, and causing nests to be washed out. The fluctuations in water level can be caused by a number of factors which have a wide array of results (Bourn 1939; Johnsgard 1956; Kadlec 1962; Anderson 1967; Cowan 1975; Hudec 1979). In some areas, water level fluctuations may occur at predictable times throughout the breeding season (e.g. spring runoff). If this were true, one would expect a well-defined timing of breeding. Weather has very dramatic affects on aquatic nesting birds. Single storms can sometimes do much immediate damage (McNicholl 1979). Species in which weather effects are important, may show no selection pressure to schedule their breeding during a narrow time period.

5. Predation

Predators may have some effect on the timing of breeding. If the intensity of predation varied throughout the breeding season, shifts in the timing or a permanent spread in the timing of breeding might be expected. This was observed in other tern species nesting in two different areas, one with predators at certain times, the other without (Lemmetyinen 1971). If the number of predators present did not change throughout the summer, it is unlikely that predators would influence the timing of the breeding season.

II. STUDY AREA AND SEASONAL CHRONOLOGY

CRESTON VALLEY WILDLIFE MANAGEMENT AREA

The study took place at the Creston Valley Wildlife Management Area (C.V.W.M.A.), Creston, B.C. during the summers of 1981-1984 (Fig. 1). The Management Area consists of approximately 6,800 ha of marshland managed for wildlife. The marsh receives water from the Kootenay River and runoff from the Selkirk Mountains to the west and the Purcell Mountains to the east. Species breeding in the area which might compete with Black Terns for food or nesting resources included Forster's Tern, American Coot (*Fulica americana*), Pied-billed Grebe (*Podilymbus podiceps*), Red-necked Grebe (*Podiceps grisegena*), Marsh Wren (*Cistothorus palustris*), Red-winged Blackbird (*Agelaius phoeniceus*), and Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). Muskrat (*Ondatra zibethica*) and American Coot may cause reproductive losses to Black Terns by accidental destruction of nests and eggs when they climb on the nest platforms. Other species present in the area could affect reproductive success through direct predation. These species included Great Blue Heron (*Ardea herodias*), American Crow (*Corvus brachyrhynchos*), Common Raven (*C. corax*), Great Horned Owl (*Bubo virginianus*), Northern Harrier (*Circus cyaneus*), Mink

(Mustela vison), Long-tailed Weasel (M. frenata), and River Otter (Lutra canadensis).

The Management Area consists of 5 major areas, Duck Lake, Duck Lake Nesting Area, Six Mile Slough, Leach Lake and Corn Creek (Fig. 1). These areas are then divided into smaller marsh units separated by dykes. Water levels within each unit can be independently regulated by a system of pumps and culverts. Marsh units were drained periodically to maintain the vegetation at a density suitable for breeding waterfowl. Various marsh units contained different types of vegetation. Plant species were identified using Hitchcock and Cronquist (1976). Three habitat types were used by the Black Terns for nesting. The habitat of the Corn Creek Unit consisted predominantly of water horsetail (Equisetum fluviatile) and beaked sedge (Carex rostrata) as well as sparse common cattail (Typha latifolia). A second habitat type was found in the study area in Leach Lake which consisted largely of reed-canary grass (Phalaris arundinacea) with patches of hardstem bulrush (Scirpus acutus) and common cattail. Duck Lake Nesting Area had two differing habitat types in various areas. One habitat type consisted of rings of common cattail and hardstem bulrush, the other habitat type was similar to that found in Leach Lake with predominently reed-canary grass and patches of hardstem bulrush and common cattail.

During the breeding season, pairs of Black Terns were scattered over the Management Area, with concentrations in Corn Creek Pond 2, Leach Lake Ponds 1 and 6, Six Mile Slough, and

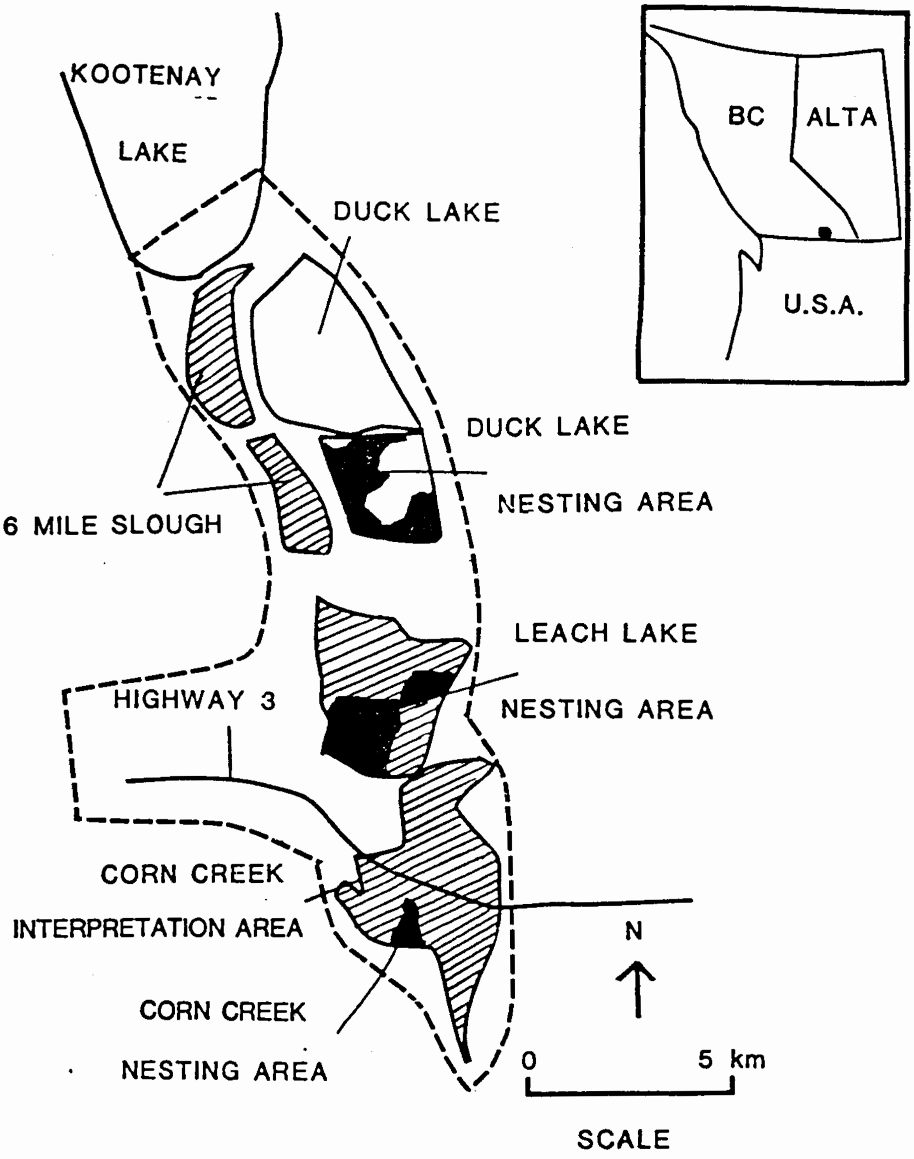

Figure 1. Creston Valley Wildlife Management Area, Creston, British Columbia. Dashed areas represent marsh units not studied, and shaded areas indicate where the Black Terns nested. The dashed line represents the border of the Management Area.

Duck Lake Nesting Area. Birds in Six Mile Slough were counted during aerial surveys and were not disturbed in any other way. In 1983, the emergent and submergent vegetation in Corn Creek Pond 2 was very dense, resulting in the loss of open water areas. Consequently, the Management Authority drained that unit in 1984 to control the vegetation and no terns nested there that year. Another site abandoned by the terns in 1984 was Leach Lake Pond 1. At this site, reed-canary grass beds did not regenerate during the spring and summer of 1984. Leach Lake Pond 6 also had little use during 1984 because water levels were too low and access was impossible because of an unsafe bridge, preventing the raising of the water level.

The seasonal chronology of the breeding cycle of Black Terns in British Columbia is similar to the chronology found elsewhere (Baggerman et al. 1956; Bergman et al. 1970; Bailey 1977). Black Terns were present in the Creston Valley from early May to mid-August. The terns usually arrived in pairs which spent about 1 week gathering together and foraging over large open water segments of the Management Area, namely Duck Lake. Following this period, the pairs moved into the different units of the Management Area. Courtship feeding then began and pairs chose nesting sites. When the young fledged, family groups tended to move back to areas of open water. In these areas the young began to forage for themselves, but for 2 weeks following fledging they were still frequently fed by their parents. By the beginning of August, the Black Terns prepared to migrate southward.

ELIZABETH LAKE

A second study area, Elizabeth Lake, was examined for comparative purposes during 1984. This lake is located at the city limits of Cranbrook, B.C. The Elizabeth Lake Waterfowl Project was initiated by the B.C. Fish and Wildlife Branch to increase waterfowl breeding in this abandoned mill pond. Waterfowl production is still quite low in the area, although the Black Tern population seems to be increasing. This area differed in a number of respects from the C.V.W.M.A. Elizabeth Lake contained large amounts of open water, and the predominant vegetation was hardstem bulrush. This area also differed from the wetlands at Creston because it is a small, isolated, 100 ha marsh. A few small lakes were located within a radius of 4-15 km, but the terns seemed to stay at Elizabeth Lake most of the time and did not travel to other areas. Avian species diversity, as well as overall numbers, were low at Elizabeth Lake. This resulted in few competing species and potential predators. Other species observed at Elizabeth Lake included American Coot, Red-winged Blackbird, Pied-billed Grebe and muskrat. Raven and Common Crow were rarely seen at this site. Due to these differences, a comparison of reproductive success and habitat availability between Elizabeth Lake and the marshes at Creston was conducted.

III. REPRODUCTIVE SUCCESS

INTRODUCTION

Of all tern species, Black Terns are one of the least studied, perhaps because they nest in inaccessible marsh habitats. Most work conducted on this species has dealt with the reproductive ecology (Baggerman *et al.* 1956). Goodwin (1960) conducted an extensive study on the ethology of Black Terns. Knowledge of behavior and descriptive aspects of reproduction are essential for a basic understanding of a species' biology.

Black Terns typically occupy nest sites that are low and wet (Bergman *et al.* 1970; Haverschmidt 1978), and they have a clutch size of 2 to 3 eggs, with 3 the usual number of a mid-season nest and 2 eggs in a late nest. Black Terns typically have very low hatching success. Bergman *et al.* (1970) determined a hatching success of 29%, Dunn (1979) found a hatching success of 27%, and Bailey (1977) determined a 34% hatching success. All studies attributed losses to wind and wave action, predation or muskrat activity.

The objectives of this study were to compare the laying schedules and reproductive success in a British Columbia marsh to that of other North American studies. Other studies mentioned the possible causes of reduced nesting success, but did not quantify the magnitude of the losses to different factors. The Creston marshes are managed for wildlife, and therefore allow the manipulation of certain environmental variables. One manipulation involved maintenance of water level. By controlling water level to some degree, hatching success might be enhanced. Careful recording of other variables could lend some insight into factors responsible for reduced reproductive success. The objective of comparing the population of terns in the Creston marshes to the population at Elizabeth Lake during 1984 was to compare a managed to an unmanaged area. As well, a comparison of nesting success was obtained between a large and a small marsh system.

METHODS

Once pairs began to breed, nest searches were conducted. Nests were located by following the compass bearing of adults which settled among the vegetation. Nests were reached by canoeing across deep channels and chest wading in shallow water. In some locations with sparse vegetation it was possible to approach the nests by canoe, but more often the vegetation was too dense to force a canoe through it without risk of damaging the floating nests. Nests were plotted on a map and marked by placing masking tape around the nearest stalk of vegetation and writing the nest number on the small flap. Marking nests in this way resulted in the least amount of visibility to a visually oriented avian predator.

The mean date of clutch initiation was calculated at the end of each season. Each calendar year was standardized so that 21 May was considered Day 1, since that was the earliest date a freshly laid tern egg was found in all years of the study. The mean was then determined using the appropriate number by date. Some nest records (n=10) were eliminated because the exact date of clutch initiation was unknown.

Reproductive success was determined by visiting nests 3 times per week. These visits were kept to a minimum to reduce disturbance to nesting birds. The nest searches and visits were run similarly over all 4 years of the study. Three different measures of nesting success were calculated. Hatching success per nest was the proportion of nests that successfully hatched at least one egg. Total hatching success was the proportion of all eggs laid that successfully hatched. Fledging success was the proportion of nestlings that survived until fledging. Some nests were enclosed to obtain fledging success. Enclosures were constructed similarly to those used by Dunn (1979). They were made of hardware cloth, 4 squares per inch, with a height of 0.35 m and a diameter of 0.5 m. The bottom third of the enclosure was covered by fiberglass screening to prevent chicks from pushing their bills through the mesh. The chicks were fitted with aluminum and color bands just prior to fledging.

The actual height of different plant species in each area was measured throughout the breeding season by placing permanent graduated sticks in each of the 3 study areas in Creston. Plant height above the water was then measured at approximately weekly intervals. Vegetation surrounding the nests was quantified in a method similar to Verbeek (1981).

RESULTS

Number of nesting birds

The size of the Black Tern population in Creston averaged 450 breeding birds throughout the 4 years of the study. During 1981 the population was estimated at 600 individuals, in 1982 there were 490 individuals and 410 individuals during 1983. In 1984, several previously occupied nesting areas were altered due to changes in plant growth, and only 300 birds were present. At least 95% of all Black Terns present each year were paired. A total of 292 complete nest records were gathered throughout the study in Creston, while 34 nest records were obtained from Elizabeth Lake in 1984. During 1984, only 28 nests were studied in Creston.

The greatest proportion of the 292 nests in Creston were found in the Leach Lake segment (61%). Corn Creek contained 6% of the nests and Duck Lake Nesting Area 33%. The available nesting habitat in Corn Creek was slightly less than that in the other areas. In addition, Corn Creek was only used for nesting in 2 out of 4 years. The vegetation densities in Corn Creek in 1983 were extremely high (see Chapter 4), leaving very few open areas for the terns to place their nests in. Corn Creek was drained in 1984 to try to manage the vegetation and therefore no nesting occurred there. Leach Lake and Duck Lake Nesting Area were used in 3 out of 4 years.

Laying dates

The spread in laying date was similar throughout the study (Fig. 2). Three of the 28 late clutches (11%) were in nests where birds laid a replacement clutch after the original nests had washed out. During 1981, 2 small peaks in laying occurred with a definite spread over the season possibly due to the weather patterns which occurred. The latest mean date for breeding occurred in 1981 and 1984. Data for 1984 was pooled from both Creston and Elizabeth Lake as there were no statistical differences in the mean date of laying between the two areas (median test=0.52, p >0.05). Egg laying was spread similarly during 1982 and 1983, but the mean date of laying between these two years differed. The mean date of clutch initiation for all years fluctuated around 7 June, with the earliest mean occurring on 3 June 1982.

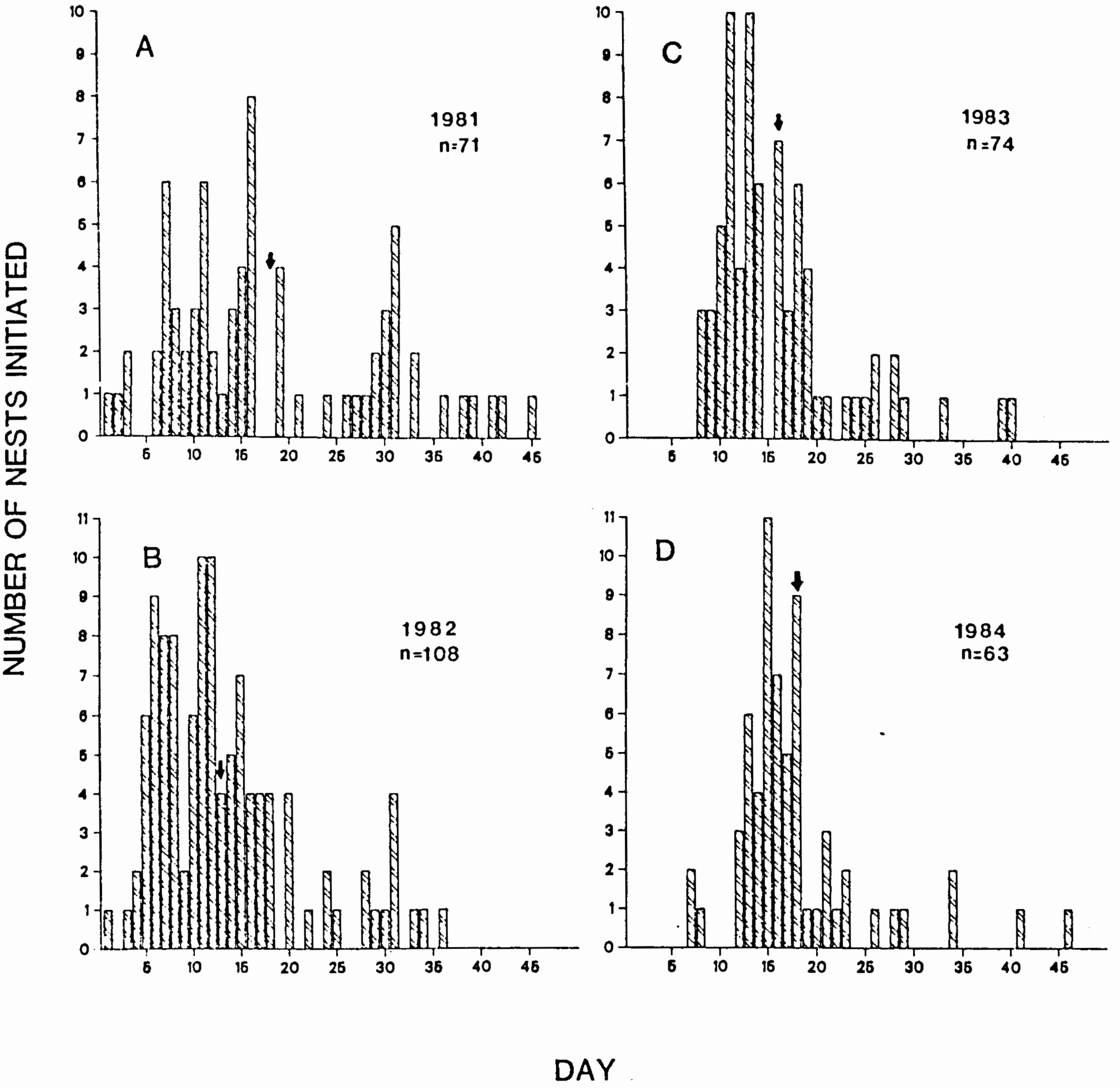

Figure 2. Clutch initiation dates for 316 Black Tern nests. Day 1 represents 21 May, Day 46 represents 5 July. Arrows point to the mean date of clutch initiation. A, B, and C represent Creston nests only and D are Creston and Elizabeth Lake nests combined.

Reproductive success

The average hatching success over the study was 73%. Both measures of hatching success increased significantly over the 4 years of the study (K=11.9, 24.7, $p < 0.01$, $p < 0.001$ Kruskal-Wallis) (Table 1). One reason for the differences in success could be due to weather conditions because the 4 years of the study were all quite different. The amount of precipitation decreased throughout the years of the study and the amount of sunshine in May and June increased throughout the years (Environment Canada weather records 1981 1982 1983). Another reason for the steady improvement in hatching success over the years was the more consistent control of water levels, thus reducing the wash-out of nests. In 1981, the water level fluctuated widely due to heavy precipitation during the first 8 weeks of the study. In 1982, excessive runoff caused water levels to rise until the second week of July, at which time most eggs had hatched. As the water level rose, pumps removed water from the nesting areas, but not fast enough. In 1983 and 1984 water levels either remained the same or declined slightly. The percentage of washed out nests decreased throughout the study from 27.1% in 1981, 21% in 1982, 13.5% in 1983 to no apparent losses to wind and wave action in 1984. On average, 15.4% of the nests were lost to wind or wave action. The average fledging success throughout the study was 61%. Fledging success did not

Table 1. Reproductive success of Black Terns in Creston from 1981-1984 and at Elizabeth Lake in 1984. Hatching success/nest represents the proportion of nests in which at least one egg hatched, total hatching success was the proportion of all eggs laid that successfully hatched and fledging success was the proportion of those hatched eggs that survived to fledging.

	1981		1982		1983		1984		1984 EL	
	N	%	N	%	N	%	N	%	N	%
# of nests	70		105		89		28		34	
# of eggs	170		281		258		76		92	
Mean # of eggs /nest	2.4		2.7		2.9		2.7		2.7	
Hatching success/ nest ** a		67		70		79		96		100
Total hatching success ***		56		68		76		90		99
Fledging success		62		55		58		67		53
# Fledged/nest	1.6		1.5		1.6		1.7		---	

a) ***=significance < 0.001, **=significance < 0 .01,

Table 2. Reproductive success of Black Terns nesting in different marsh units.

	Corn Creek		Leach Lake		Duck Lake Nesting Area		
	N	%	N	%	N	%	
# of nests	49		178		65		
# of eggs	121		479		168		
Mean # eggs/nest	2.5		2.7		2.6		
Hatching success/nest		68		80		63	
Total hatching success		60		78		54	*** a
Fledging success		78		52		50	**

a) ***=significance < 0.001, **=significance < 0.01

differ significantly among years ($K=1.9$, $p > 0.05$). Total hatching success differed significantly among areas ($K=14.89$, $p < 0.001$, Kruskal-Wallis) (Table 2). Total hatching success was higher in Leach Lake than in both Corn Creek and Duck Lake Nesting Area ($K=6.00$, $p < .05$; $K=12.08$, $p < 0.001$). The fledging success also differed significantly among areas ($K=10.89$, $p < .01$). Fledging success in Corn Creek was significantly higher ($K= 7.44, 5.09$, $p < 0.05$) in both years the birds nested there than in Leach Lake and Duck Lake Nesting Area. Predation affected nesting success and will be dealt with more specifically in Chapter 8.

The Black Tern population at Elizabeth Lake increased over the 4 years. Prior to 1984 the population there was estimated at 10-15 pairs, while 34 nests were found in 1984. The hatching success that year was very high (99%), probably because 1/3 of the nests were placed on floating boards, remnants of an old mill. These boards varied in size, from 12 by 20 cm to 3 by 6 m. Fledging success at Elizabeth Lake was 53%, which was similar to the success found in Creston.

Factors influencing reproductive success

The relationship between different environmental factors and reproductive success was determined. Only fledging success was correlated significantly with the height of the plants in different habitats, where success was greatest in the areas with the shortest plants (Table 3). The *Equisetum* was the shortest vegetation and was also the densest (see Chapter 4). Fledging success differed significantly among habitat types. High fledging success was again correlated with nesting in *Equisetum*. Only hatching success was significantly influenced by wind and wave action. Black Terns lost as many as 27% of their eggs due to water level fluctuations and wind or wave action.

Table 3. Relationship between Black Tern reproductive success and different environmental factors pooled for all years and all study sites. The data were tested by using spearman rank correlation coefficients. n.s. represents nonsignificant comparisons. Sample sizes are in parentheses.

Factor	Hatching success	Fledging success
Plant height (117)	0.125 n.s.	-0.324 $p<0.05$
Habitat type (326)	-0.171 n.s.	0.305 * $p<0.01$
Wind/Wave (326)	-0.217 $p<0.05$	-0.129 n.s.

*high fledging success associated with Equisetum

In 1984, nesting success was very high and no eggs were lost to wind and wave action. One reason for this could be that most of the 60 nests in 1984 (73%) were completely surrounded by vegetation. This vegetation was mostly dense, where more than 75% of the area contained vegetation, and in a few instances the vegetation was sparse, where 50-75% of the area contained vegetation. Of the remaining nests in 1984, 21% were protected mainly from the north to northwest, which also happens to be the direction of the prevailing winds in Creston. Since eggs did wash out of nests in other years, nest protection probably was important for higher success measures. The topic of water level fluctuations will be dealt with in more detail in Chapter 7.

DISCUSSION

Black Terns have nested in the marshes of the Creston Valley Wildlife Management Area since the 1950's (Munro 1950). Since that time, the population has steadily increased to a high in 1981. The population of Black Terns nesting in the Creston Valley Wildlife Management Area showed signs of a decline over the 4 years of the study, which is consistent with other populations across North America (Tilghman 1980). A major factor influencing the decline was the loss of nesting habitat. The population at Elizabeth Lake, however, showed a slight increase in recent years. One possible explanation for the apparent continent-wide decline may be the lack of suitable censuses (Tilghman 1980). The Federation of British Columbia Naturalists published a distribution map of Black Terns in the province in their newsletter (Fed. B. C. Nat. 1977). Both the Elizabeth Lake and the Creston Valley Wildlife Management Area populations were missing from the distribution map. The Elizabeth Lake population is one of the three largest in the province. The Creston Valley population, although absent from the map, is actually the largest population in all of British Columbia. Prior to this study, the population in Creston had been increasing steadily since Munro's 1950 study, when only a few birds were in the area. The discrepency between the status map for B.C. and the populations studied in the Kootenays show that Black Terns seem to be doing well in British Columbia.

The spread in the timing of breeding in Black Terns noted by other researchers, was also observed in this study (Fig. 2). Spread in extreme dates was comparable to other published studies (Bent 1963; Bergman et al. 1970; Dunn 1979). Peaks in laying occurred during the last week of May and the first week of June. The timing of these peaks was similar to those found by Bailey (1977). Some variation in laying date was attributable to yearly differences in weather patterns.

The reproductive success found throughout this study was much higher than has been reported in past studies (Bergman et al. 1970; Bailey 1977; Dunn 1979). Water level fluctuations are an important concern to marsh nesting species. Seasonal runoff and precipitation can cause water levels in areas located in mountain valleys to rise. Heavy rain can do much immediate damage to marsh nesting birds (McNicholl 1979). Bailey (1977) found a 37% loss of Black Tern nests due to bad weather. The Creston population had a higher nesting success, perhaps because they bred in a managed area. Since the area was managed, there were fewer problems with rising water levels through a season and fewer washouts. Similarly, since the management area attempts to maintain wet marsh areas and stop the successional process, the vegetation was managed to some degree and therefore may have provided more suitable habitats.

Black Tern reproductive success in Creston varied from year to year (Table 1). Environment Canada weather records documented the differences in mean temperature and precipitation over the years. The birds had lower success in years of high precipitation due to eggs washing out of nests. As well, fledging success was affected when water levels continued to rise during the chick phase. Rising water resulted in a loss of dry areas for chicks to sleep on (Chapman Mosher personal observation). Black Terns were also less successful during colder years. Lowered success in cold years may be partially due to foraging restrictions, and will be discussed in more detail in Chapters 5 & 6.

Reproductive success differed among the various marsh units in Creston. Areas varied in terms of habitat type and vegetation density. Reproductive measures were correlated with various habitat measurements (Table 3). Plant height generally depended on the species. Only fledging success was correlated with plant height, and negatively; probably because the shorter vegetation was *Equisetum*, which happened to be the most dense habitat type so that chicks could hide from predators. Within the Creston marshes, terns had the highest hatching success at Leach Lake

(Table 2). Leach Lake supported the greatest number of nests in the Management Area from 1981 through 1983. The abundance of nests in this area may be due to the habitat type, *Phalaris*. Fledging success, however, was significantly higher in Corn Creek. The density of vegetation in a habitat may also be an important factor influencing reproductive success. Vegetation density in Corn Creek was very high and it probably provided suitable cover for chicks to hide in. Lack of vegetation could also lead to lack of cover from weather conditions. This cover may also be important in camouflage as shown in waterfowl (Dwernychuk and Boag 1972).

Hatching success was shown to be correlated with wind and wave action (Table 3). When nests were lost, it was frequently because waves washed over them and removed the contents. McNicholl (1979) found that wind storms caused waves which could seriously affect marsh breeders. Bergman *et al.* (1970) stated that the vegetation around nests could be important in reducing wind and wave action. Most nests in 1984 were surrounded by vegetation on all sides. For this reason, vegetation surrounding nests could play a very important role in protecting eggs from washing out of nests. Elizabeth Lake had extremely high hatching success compared to the Creston marshes, probably because many of the nests were on boards which allowed them to float up, down and laterally with the waves. In addition, Elizabeth Lake had fewer predators, so potentially fewer eggs and young would be lost due to predation.

Black Tern reproductive success was influenced by a number of factors, of which wind and wave action were the most important. The best way to improve reproductive success would be to concentrate on proper management of the vegetation density, which would provide protection from wind and wave action. Vegetation density and water level fluctuation, will be examined in more detail in Chapters 4 and 7.

IV. HABITAT AVAILABILITY AND NEST DISPERSION

INTRODUCTION

Marshes are typically regarded as an unstable habitat because they change constantly through time. For this reason, birds which nest in this habitat are faced with changing vegetation densities and fluctuating water levels (Morse 1980). Species which rely completely on marshes to breed in must be able to deal with a fairly wide range of vegetation densities. Most likely there are nesting requirements that dictate the tolerable ranges of habitat that are occupied.

Habitat management of marshes is a poorly understood topic. Some management techniques have been developed over the years to deal with marsh vegetation. Both prescribed burning and plowing are used by different managers. These methods are normally used during the nonbreeding seasons and are shown to affect some marsh breeders (Bray 1984).

Many studies of birds have dealt with various aspects of nest site characteristics or habitat quality. The majority of these studies among the larids have dealt with species which occupied more stable land habitats (Burger 1982; Severinghaus 1982; Spendelow 1982; Thompson and Slack 1982). In addition, these habitats contained little vegetation in comparison to a marsh environment. As well, these studies and others have dealt with habitats in a more qualitative than quantitative manner (Burger and Lesser 1979; Winnett-Murray 1979). Since Black Terns can be affected greatly by habitat characteristics (Hoffman 1926; Cuthbert 1954; Bochenski 1966; Bergman *et al.* 1970; Dunn 1979) quantitative evaluation of the surrounding vegetation could be extremely important.

Black Terns in the Creston marshes nested in a variety of habitat types. In past studies the terns were noted to nest mainly in stands of *Typha* or *Scirpus* (Cuthbert 1954; Bergman *et al.* 1970; Dunn 1979), *Equisetum* (Haverschmidt 1978) and *Phragmites australis* (Bent 1963). In the Creston marshes Black Terns nested in *Typha latifolia*, *Scirpus acutus*, a complex of *Equisetum fluviatile* and *Carex rostrata*, and most frequently *Phalaris arundinacea*. Richardson (1967) was the only other researcher to note them nesting in *Phalaris*.

The objectives of this study were to provide quantitative data on the different habitat types used by Black Terns. These data could provide information on how the different habitat types might influence nest dispersion. Quantitative assessments of the vegetation might also lend insight into the effects habitat may have on the timing of breeding.

METHODS

Intensive vegetation measurements were made during May and August in 1983 and 1984. The May sampling was done just prior to nest building. The August sampling was done just after the chicks had fledged. Line transects were laid out to measure the proportion of fishable water, standing vegetation and matted vegetation in the areas where the terns nested. The proportion was estimated in a belt 4 cm on either side of the line. These three measures summed to 100. Fishable water was any open water which was sufficiently devoid of vegetation so that a Black Tern could dive in it. Although the Black Terns were primarily insectivorous they did consume some fish. Proximity to fishable water was deemed important to minimize having to travel long distances to obtain fish. The standing vegetation category was the proportion consisting of actual stalks of vegetation, as opposed to a proportion of cover, which would estimate the plant growth near the top of the plant. Standing vegetation was considered very important in blocking wave action. The proportion of matted vegetation was any portion which contained floating vegetation and/or floating algal mats. Matted vegetation was the floating base on which Black Terns built their nests. These mats were also important, because as water levels dropped, the nest and mat dropped with the water. However, the mats were usually intertwined with the vegetation so that when water levels rose, they did not always rise with the water, resulting in nest washout.

Transects were run in all 3 study areas in Creston: Duck Lake Nesting Area, Leach Lake, and Corn Creek. Line transects were started at one corner of the habitat occupied by nesting terns. In addition, areas which were used by the terns for nesting in past years were sampled and were referred to as unoccupied areas. Fifty-meter line transects were laid along compass bearings and the various proportions recorded in each meter. Random numbers were then used to move between 1-100 steps at a 90 degree angle to the original bearing. Once at that point, the line was laid out along the same bearing. This process continued until the far edge of the habitat occupied by nesting terns was reached. At that point the bearing was reversed 180 degrees. This process was repeated until the starting edge was reached.

Two measures of vegetation, density and the area occupied by each stalk of vegetation, were considered important because they allowed a quantification of the ability of different habitat types to block waves. The data were obtained by using a 1 by 1 m quadrat made from copper tubing. Quadrats were laid out through the middle of the breeding area. Each quadrat was located by moving a random distance between 1-10 paces from the previous quadrat along a predetermined bearing. Within each habitat type, the total number of stalks per m^2 was counted. In addition, the diameter of each of the four cornermost stalks of each vegetation type in the quadrat were measured at the water surface. The measurements were then used to calculate the area occupied by each stalk of vegetation. Different shapes were used to approximate the areas of the vegetation stalks. The formula for a circle was used to calculate the area of *Scirpus*, *Equisetum* and *Phalaris*. *Carex* was approximated by an equilateral triangle and *Typha* by a modified ellipse. Once the average area occupied per quadrat was determined, it was multiplied by the total number of each type of stem per quadrat. In each habitat the average area occupied by stalks per m^2 was then determined.

Internest distances were measured for all nests located. These distances were determined by using a 0-30 and 15-150 m rangefinder. Once internest distances and triangulations to other nests were obtained, an accurate map of the nesting area was constructed. An edge of a nesting habitat was determined by large open water channels which isolated the area. The outside edges of the nesting habitat were then measured and the measurements were added to the nesting maps so that nesting dispersion could be calculated, according to Hammond and McCullagh (1978), for each area. Nesting dispersion was then compared to the vegetation assessment to determine if habitat types and/or vegetation densities were having any effect on the observed dispersion patterns.

A comparison of hatching and fledging success in nests located different distances from their nearest neighbors was done. Each nest was placed into 1 of 5 nearest neighbor categories: less than 10 m, 11-20 m, 21-30 m, 31-40 m, and greater than 40 m.

RESULTS

In May 1983, the proportion of standing vegetation differed slightly between occupied and unoccupied areas (K=6.09, $p < 0.05$, Kruskal-Wallis) (Table 4). In August the proportion of standing vegetation in the unoccupied area was significantly different than in the occupied area (K=17.5, $p < 0.001$). The mixed Equisetum and Carex vegetation in the unoccupied area became very dense (92% standing vegetation). When the sampling was done in May, the vegetation had not yet broken through the surface of the water. Within a week after sampling it had, thus explaining the significant difference in the proportion of standing vegetation between the May and August data (K=57.4, $p < 0.001$). The proportion of standing vegetation for unoccupied areas in 1984 was significantly lower than the proportion in occupied areas (K=11.75, $p < 0.001$). Vegetation in these areas failed to regenerate in the spring of 1984 and they were not used by the terns to nest in. The dieback occurred in stands of Phalaris, an introduced species, which grows best when it is not flooded 12 months a year (Stushnoff pers. comm.). Black Terns tended to nest in areas averaging about 25% standing vegetation, 42% matted vegetation, and 33% fishable water.

Areas containing Phalaris tended to have the greatest density of stalks/m^2 (Table 5). The areas with the smallest

Table 4. Proportion of matted and standing vegetation, and open water in Creston in 1983, and all study areas in Creston and Elizabeth Lake in 1984. Occupied areas were those locations where birds nested that year. Unoccupied areas were those locations where birds nested in the past but which were not used in the given year.

	May		August	
	1983	1984	1983	1984
Occupied				
% matted	40.6	29.7	53.8	42.3
% standing	18.9	22.7	28.3	30.4
% open water	40.5	47.6	17.9	27.3
Unoccupied				
% matted	58.6	32.8	7.9	---
% standing	14.3	8.5	92.1	---
% open water	27.1	58.7	0.0	---

number of stalks were the pure stands of Scirpus. When looking at density in terms of stalk count, it must be remembered that stalk diameter increases greatly from Phalaris, to Carex, Equisetum, Scirpus, and Typha. For this reason, it was difficult to make comparisons among habitat types in terms of density only. The area occupied per m^2 at the water surface (Table 6) differed statistically among habitat types in both May and August in 1983 ($K=27.6$, $df=3$, $p< 0.001$; $K=46.2$, $df=3$, $p < 0.001$, Kruskal-Wallis). The last two categories are areas which were not used by the terns in 1983. Data on the area occupied by stalks of vegetation per m^2 also differed statistically in both sampling periods during 1984 ($K=12.7$, $df=1$, $p< 0.001$; $K=18.5$, $df=2$, $p< 0.001$). Low values in pure stands of Phalaris represented an area where the vegetation failed to regenerate. The terns moved to a second stand of Phalaris which was not as dense as the birds normally occupied. The last two habitat categories represent typical values for nesting habitat.

Black Tern nests were initiated at different times throughout the season. For this reason, the nests were plotted on a map as they were found and the internest distances were calculated at the end of the season. Habitat type and density also varied among units. The average internest distance varied significantly in different habitat types on the Management Area ($K=240.3$, $df=2$, $p< 0.001$) (Table 7). Birds tended to nest more solitarily in areas which contained bulrush and cattail

Table 5. Vegetation densities (stalks/m^2) obtained from quadrat measurements in different habitat types. Within the study areas, the terns nested in a number of areas containing Phalaris, so more than one stand is included. An asterisk represents densities in areas where terns nested in previous years, but not in the years sampled.

	May		August	
1983	Mean	SD	Mean	SD
Phalaris	205	124	267	177
Phalaris	159	97	676	335
&Typha	3	3	3	1
Equisetum	263	215	679	176
& Carex*	2	11	33	21
1984				
Phalaris*	170	83	---	
Phalaris*	230	98	---	
Phalaris	---		574	247
Phalaris	457	165	371	177
& Typha	1	1	3	4
Scirpus	---		88	31

Table 6. Area (cm^2/m^2) occupied at the water surface by stems of vegetation per meter square in different vegetation types during 1983 and 1984. Asterisks are as in Table 5.

	Area occupied by stems at water surface	
1983	May	August
Phalaris	7.7	9.3
Phalaris & _Typha_	17.5	26.7
Scirpus & _Typha_*	12.2	91.3 a
Equisetum & _Carex_*	50.0	154.9 b
1984		
_Phalaris_*	6.4	6.4
Phalaris	---	15.7
Phalaris & _Typha_	17.4	52.7
Scirpus	---	47.3

a=significance < 0.001 between the two samples

b=significance < 0.01 between the two samples

Table 7. Average internest distance (m) in different vegetation types over the years of the study. One Phalaris stand was at Duck Lake Nesting Area the other at Leach Lake.

	1981		1982		1983		1984	
	Dist	n	Dist	n	Dist	n	Dist	n
Phalaris	----		10.70	38	22.31	18	39.80	12
Phalaris	----		11.45	87	18.72	67	15.00	17
Equisetum	13.77	24	19.81	22	----		----	
Scirpus &/or Typha	51.18	20	----		----		20.16	34

stands among much open water (Mean distance=35.67 m, SD=21.9). Phalaris habitats tended to be quite variable in internest distance (Mean distance=19.66 m, SD=10.8). The birds were the densest in Equisetum stands, where small colonies of up to 7 pairs were observed (Mean distance=16.79 m, SD=4.3). The most common dispersion patterns of tern nests was clumped or random tending toward clumped (Table 8). Birds in Equisetum and Carex areas had a clumped distribution ($z=2.87$, $p < 0.01$, Dispersion Test), or a random distribution with a tendency toward clumping ($z=1.59$, $p > 0.05$). This distribution pattern also occurred in

Table 8.Dispersion pattern of nests in different vegetation types over all years of the study, determined by a Dispersion Test. R= random, C= clumped R(-)= random tending toward uniform, and R(+)= random tending toward clumping.

	1981	1982	1983	1984
Phalaris	--	C ***	C ***	C ***
Phalaris	--	R(+)	R(+)	C *
Equisetum & *Carex*	C **	R(+)	--	--
Scirpus &/or *Typha*	R(-)	--	--	R

***=significance <0.001, **=significance <0.01, *=significance <0.05

stands of *Phalaris*. The only random or random toward uniform distribution patterns occurred in habitats of *Scirpus* and/or *Typha* with much open water. Figure 3 shows an example of each type of distribution pattern in the nesting areas.

Nests located at different distances from their nearest neighbors were compared for the different reproductive success measures (Table 9). Birds which nested in the different categories all had similar hatching success/nest, total hatching success and fledging success (K=2.4, 1.8 and 0.2, p >.05,

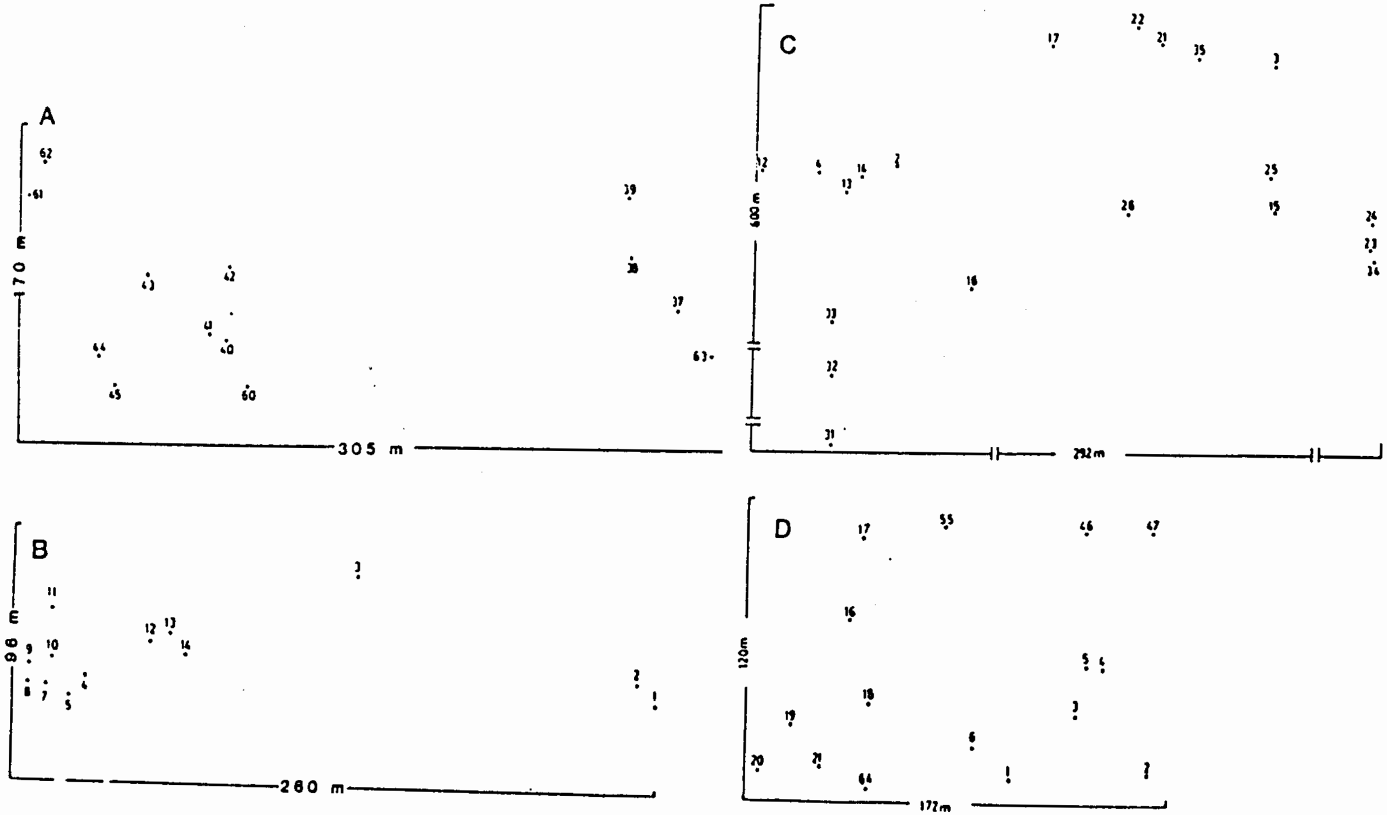

Figure 3. Distribution patterns of Black Tern nests in Creston. A) random distribution B) clumped distribution C) random tending toward a uniform distribution and D) random tending toward a clumped distribution. Each number represents an individual nest.

Table 9. Average reproductive success of birds nesting different distances from their nearest neighbors over all years of the study.

	Hatching sucess per nest	Total hatching success	Fledging success
Distance to neighbor			
0-10 m	87.7	75.5	60.5
11-20 m	85.6	80.3	63.3
21-30 m	85.6	74.4	66.5
31-40 m	75.0	75.0	64.3
>40 m	70.3	64.3	70.0

Kruskal Wallis). Hatching success tended to be slightly lower in nests with nearest neighbors greater than 40 m away. Fledging success was not influenced by distance.

DISCUSSION

Various areas within the marsh differed in terms of habitat type and vegetation density. Plant height generally depended on the species. The proportion of vegetation in a habitat could be important to nesting species. Within the Creston marshes, Leach Lake supported the greatest number of nests in the Management Area from 1981 through 1983. Reasons for the abundance of nests in this area could be due to the large areas containing _Phalaris_.

Black Terns tended to nest in areas containing 25% standing vegetation, 42% matted vegetation and 33% fishable water (Table 4). When the proportion of standing vegetation was greater than 70%, the birds did not nest there. In these areas, there were probably few openings in the vegetation so that terns could not feed as easily or get to the floating vegetation at the water level to place their nests on. As well, when the proportion of standing vegetation was less than 10%, the birds did not nest there. In these areas, the vegetation was probably too sparse to aid any protection to a floating nest or provide cover from predators. The proportion of the surface area occupied by stalks of vegetation was another measure of vegetation density (Table 6). The area occupied at the water surface by the stalks of different species of plants did differ, and the terns usually nested in those places where the area occupied on the water surface at the end of the season varied from 10-50 cm^2/m^2 (Table 6).

Habitat type had some effect on the amount of coloniality observed, as was seen in the comparison of internest distances (Table 7). In stands of _Typha_ and _Scirpus_ or _Scirpus_ by itself, the nests were distributed randomly (Table 8). Where the habitat type was *Phalaris*, nests tended to be slightly clumped, but they were still considered to be distributed randomly although variation was high. The greatest nesting density of Black Terns was observed in *Equisetum* and *Carex* habitat where there was little variability in distance. The most common patterns of distribution were random tending toward clumping and clumped. Only in *Typha* and/or *Scirpus* habitats were the distribution patterns random or random tending toward uniform. Vegetation density may in some ways affect the distribution patterns of nests. When the proportion of standing vegetation ranged between 19-35% the birds nested randomly with a strong tendency toward clumping. As the proportion of standing vegetation reached the upper part of this range nests became more clumped. When the proportion of vegetation exceeded 70%, as in Corn Creek in 1983, the terns did not nest in a previous nesting area.

For colonial nesting to occur, there must be suitable areas available where colonies could exist. If such areas are lacking, the birds may be forced to nest solitarily. In different habitat types on the Management Area the degree of coloniality varied from a random dispersion of nests to a slightly clumped distribution. Minimal spacing of nests would not seem a logical explanation for the loose coloniality observed because in 1983, there were 2 nests in Leach Lake which were only 1 m apart. In each of the areas studied the vegetation density was similar throughout the entire area and there was an adequate amount of matted vegetation present to place nests on. Since these two characteristics are important to Black Terns for nesting, it does not seem that these characteristics could be causing the loose coloniality observed. The loose coloniality observed could be due to low tern densities, but this does not appear to be the case, or to a scattered arrival of the birds. Reproductive success measures (Table 9) showed that pairs which tended to nest closer to others had similar hatching and fledging success as those birds which nested solitarily. Since reproductive success was similar regardless of the distance to the next nest, there appears to be no selection pressure at the moment to favor any given dispersion pattern of nests in Black Terns.

Plant growth within a season could affect the timing of breeding. If the vegetation were slow to grow during a given year, due to weather conditions, the timing of breeding could be delayed. Species like Black Terns, who rely greatly on vegetation in their nesting areas, may be forced to look for other nesting areas if sufficient vegetation is not available at a previously used site. There were few differences in the proportion of standing vegetation between measurements in May and August (Table 4). The only habitat type which showed drastic changes in density was the *Equisetum* and *Carex* complex. *Equisetum* was quite variable in growth over the 4 years of the study. In some years (1981 & 1983), *Equisetum* was below the water surface in early May and in other years (1982 & 1984) it was well above the surface by that time. This could influence the timing of the breeding season if this were the only breeding habitat available. The <u>Phalaris</u> habitat also varied some in density between May and August. This change was less important as new stalks grew around already exposed stalks, causing little overall change in structure of the habitat. Also, <u>Phalaris</u> grew quickly within the measurement period in May. In 1984, <u>Phalaris</u> experienced a dieback and it did not regenerate at all (Chapman Mosher personal observation).

In summary, Black Terns tend to nest in habitats containing 25% standing vegetation, 42% matted vegetation and 33% fishable water. The quantity of vegetation within each area did not differ significantly throughout the season, so should have little influence on the timing of the breeding season. A plot of the dispersion pattern of nests showed that sometimes they were clumped in distribution, but more often they were randomly distributed, with a tendency toward clumping. Within each nesting site the habitat seemed suitable for more clumping of nests and larger colonies. Since suitable habitat was unoccupied, habitat availability is probably not responsible for the loose coloniality observed in this species.

V. SEASONAL ABUNDANCE AND UTILIZATION OF PREY

INTRODUCTION

The availability of food, as well as the seasonal abundance of food has been shown to influence both the degree of coloniality and the timing of breeding in birds (Lack 1968). Coloniality has been shown to be influenced by prey dispersion (Lack 1968). Birds which nest in tight colonies tend to feed on prey which is unpredictable in distribution (Lack 1968; Hunt and Hunt 1976a; Orians 1980).

Food has been shown to be very important in the timing of breeding not only for the breeding adults, but also for those young which are fledged (Emlen 1966; Emlen and Demong 1975). The dispersion of prey may be such that coloniality is disadvantageous (Lack 1968). Colonial breeders typically feed on food sources which are locally abundant but patchy in distribution (Horn 1968). Ward and Zahavi's (1973) information center hypothesis suggests that colonial breeders derive information from other individual's success about where to find food. Avian species which feed on evenly distributed prey would have less need to obtain information on good feeding areas and would therefore not need to nest colonially. The apparent lack of a well-defined timing of breeding in Black Terns at Creston was noticable with new nests found anytime between 15 May to 10 July. Birds are thought to time their breeding with peaks in food supply. Where the food supply lacks a predictable peak in abundance, no peak in the timing of breeding may occur. As well, if peaks in prey abundance occur, but their timing is unpredictable, one might expect a less rigid timing of nesting. The seasonal abundance of insects may vary due to weather patterns (King 1974). Orians (1980) found that emergence rates were influenced by weather conditions (i.e. temperature, precipitation and sunshine). In studies of the abundance of damselflies and dragonflies, some peaks did occur in mid season (Orians 1980). Avian species which are highly dependent on emergent insects may therefore be subject to different pressures in timing their breeding season.

Most of the work done on the foraging ecology of Black Terns has involved identification of the food items consumed. Some researchers (Cuthbert 1954; Dunn 1979) have quantified the frequency of different food items fed to young. Known food items of these terns include damselflies, dragonflies, other small insects and occasionally fish (Cuthbert 1954; Godfrey 1966; Dunn 1979). Most foraging during the breeding season at Creston took place in the marsh areas where the birds nested. In other regions of the world Black Terns occasionally have been observed to forage over land for insects (Angles 1957; Bundy 1971) and to follow plows, a method frequently used by other larids (Brewer 1969; Goethe 1970). Black Terns and Gull-billed Terns (Sterna nilotica) are primarily insectivorous, unlike other members of the subfamily Sterninae. However, Black Terns do consume a small proportion of fish. Prior to this study, it was unclear what proportion of the diet consisted of fish and insects.

The primary objectives of this study were to determine the seasonal distribution of prey abundance and the importance of insectivory versus piscivory in Black Terns. The study examined the fluctuations in emergence and the abundance of prey items in the nesting areas and other nearby locations. This information would show whether peaks of emergence were similar in all areas, or whether they differed, resulting in an unpredictable and patchy prey distribution which might influence coloniality. By frequent sampling in the same areas from year to year one could determine if peaks in prey items were predictable. This knowledge could shed light on the observed spread in the timing of breeding.

METHODS

Parents returning to 17 nests over 3 years of the study were observed to determine the types of prey which they carried. The enclosures described in Chapter 3, allowed individual young of known age to be observed while being fed by their parents. Thirty-six young within enclosures were watched through a spotting scope from a blind placed 10-20 m from each nest, to determine the proportion of each type of food item brought to the young.

The seasonal abundance of various prey items was examined throughout the study. Different insect sampling techniques are known to select for different types of insects (Johnson 1950). For this reason, insect emergence and abundance was monitored in three ways.

Since adult odonates were known to form a large proportion of the diet, the most extensive data collection involved emergence traps. The 30 by 90 cm traps were modelled after Cook and Horn (1968) and each trap sampled the emergence rate in 30 cm of shoreline. Emergence traps were placed in roughly the same locations on the shore or floating over the vegetation stalks within the different areas from 1981 to 1984. This information provided data to evaluate how prey items that were fed to the young differed in emergence rates among areas, as well as years. Average emergence per trap per day was calculated throughout the season. The 4 years of the study were standardized for emergence into weekly periods, with the first week of May as week 1 and the second week of August as week 16.

A second method involved sticky boards placed in the same locations as the emergence traps during 1982 and 1983. Each sticky board consisted of a cardboard base mounted horizontally which sampled an area of 2256 cm^2. Each base was covered completely with waxpaper taped in place. The boards remained the tan color of cardboard. This is important, as various colors, particularly yellow, are known to select for different insect species (British Museum 1974). Subsequently, the wax paper was painted with Stikem Special, from Napco Products. This product was heated in a pan to a liquid consistency and applied by brush. Each sticky trap was placed at the same compass bearing, so as to avoid any wind biases between the 4 sites (Peterson 1964). Boards were removed once weekly and replaced with clean sticky wax paper. Once insects on the boards were counted, the wax paper was removed and the process repeated.

The third method of sampling involved two nets that were mounted on an airboat, one just above water level and the other at 76 cm, which was about half the average height of the vegetation. Each net had a diameter of 24 cm. The monthly sampling was completed between 0700-1000 hrs. Sampling with the airboat was made by travelling a set path at the same relative speed so that the results were directly comparable from year to year. This method was used in 2 ponds of Corn Creek during the first 3 years of the study, but was discontinued in 1984 when the drawdown occurred in that marsh unit. Sampling in 1981 was only done in August to evaluate the technique of sweep net sampling by airboat and data for that year do not appear.

Fish populations were seined in 1982-1983 in the various ponds where terns foraged using a seine net which measured 20 x 2.5 m with a 6 mm mesh. Seining was done in the areas twice during the breeding period, to determine when the various species were spawning. The most important segment of the fish community for Black Terns was year-class-1 individuals. The drop trap technique of fish sampling and modifications of it were used briefly (Higer and Kolipinski 1967; Kahl 1963; Kushlan 1974). These techniques proved to be useless, however, as sampling never resulted in any fish capture.

RESULTS

There was a significant difference ($X^2=11.51$, $p< 0.001$) in the number of items in each category fed to nestlings (Table 10). Parents returned to nests 90% of the time with insects of various types. Damselflies and dragonflies made up a large proportion of the items consumed in all study areas. Small insects included mainly dipterans. Also included in the small insect category were moths and grasshoppers which were brought to chicks in very low proportions (< 2%). Fish made up about 10% of the diet fed to chicks. The fish species most often brought to chicks were yellow perch (*Perca flavescens*) and pumpkinseed (*Lepomis gibbosus*). Black bullheads (*Ictalurus melas*) were consumed less often (< 5%).

Average emergence of adult damselflies decreased over the 4 years of the study ($K=20.6$, $p< 0.001$, Kruskal-Wallis) (Fig. 4A). Peaks in emergence differed by 3 weeks between years ($X^2=39.99$, $p< 0.001$, Friedman). The same decreasing trend in the capture of damselfly nymphs occurred in emergence traps (Fig. 4B). Dragonfly emergence (Fig. 5) remained similar during most years except for the significant decrease in emergence in 1983

Table 10. The percentage of different food items fed to nestlings. Sample size for each year is given in parentheses.

Food items	1982 (499)	1983 (1017)	1984 (65)	Mean (1581)
Fish	15	10	5	10
Damselflies	39	17	57	38
Dragonflies	25	14	11	17
Small Insects	21	59	27	35

($K=10.68$, $p<0.05$, Kruskal-Wallis). Peaks in dragonfly emergence differed by 1-15 weeks between years, but not significantly ($X^2=10.45$, d.f.=13, $p>0.05$, Friedman).

Black Terns obtained some food from 100 m surrounding the nest (8.8%), but most of the time they went further away to feed. Since most food was obtained from areas other than where the birds nested, the abundance of food items may differ between the nesting sites and areas travelled to for foraging. This was not the case for emergent insects. The peaks of damselfly emergence in Corn Creek where the terns nested were actually higher than in Corn Creek Interpretation area, located 1 km from the nesting area, to which they flew to feed (Fig. 6). In 1982, the damselfly peak in Corn Creek was 2.6 damselflies per trap

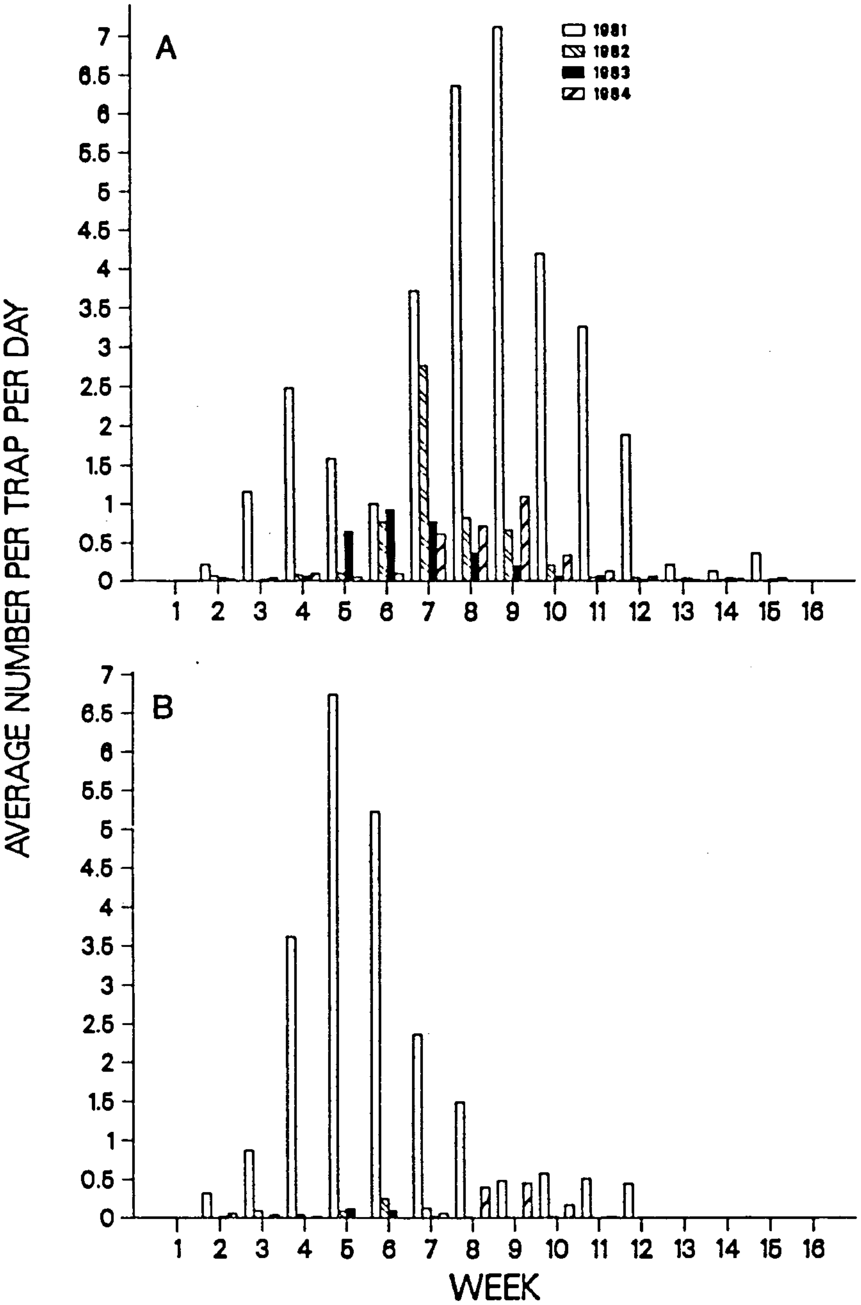

Figure 4. A) Average emergence rate of adult damselflies per trap per day in all areas of the Management Area combined. B) Average number of damselfly nymphs found per trap per day in all areas of the Management Area combined. Week 1 represents the first week of May and week 16 the second week of August.

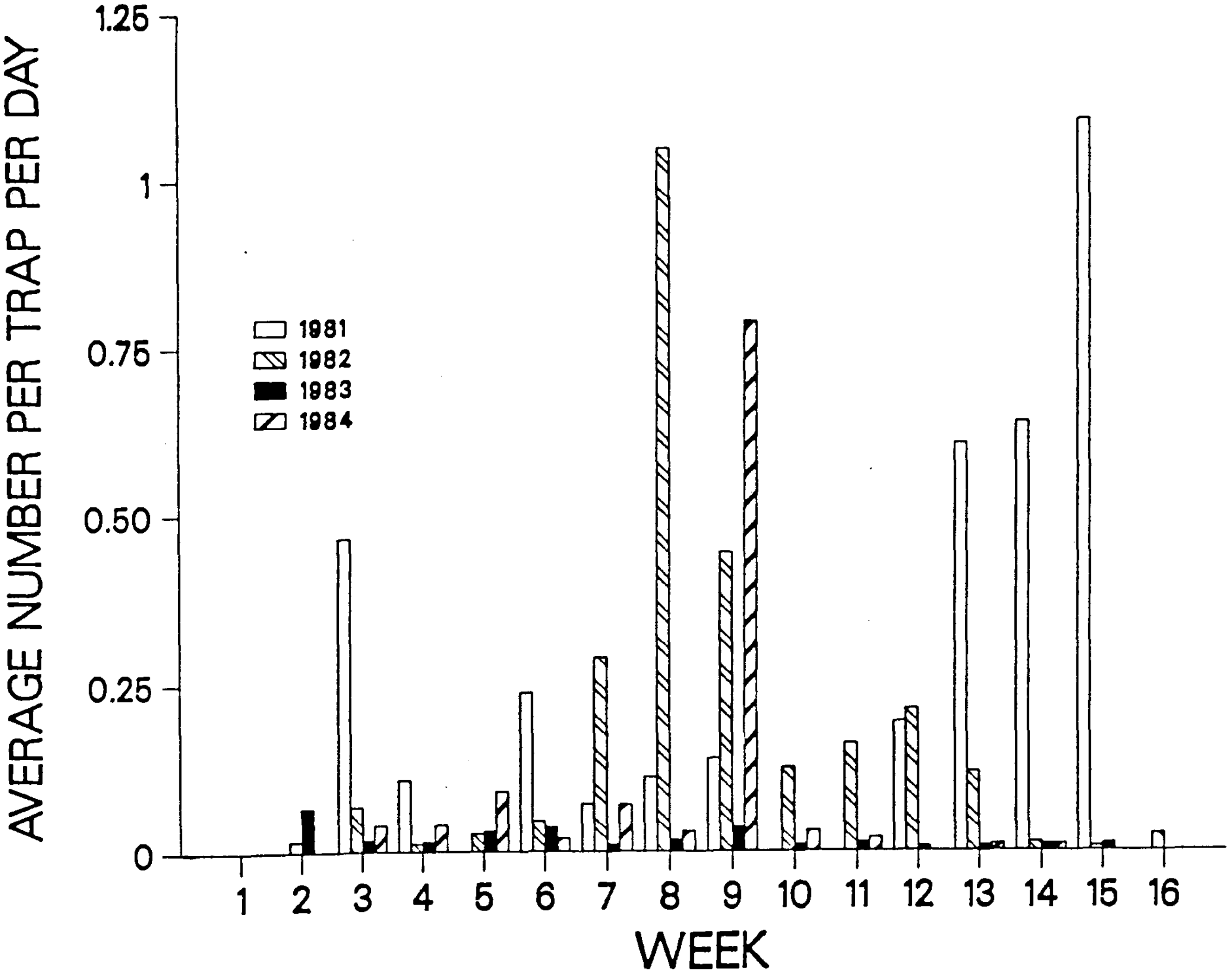

Figure 5. Average emergence rate of dragonflies per trap per day in all areas of the Management Area combined.

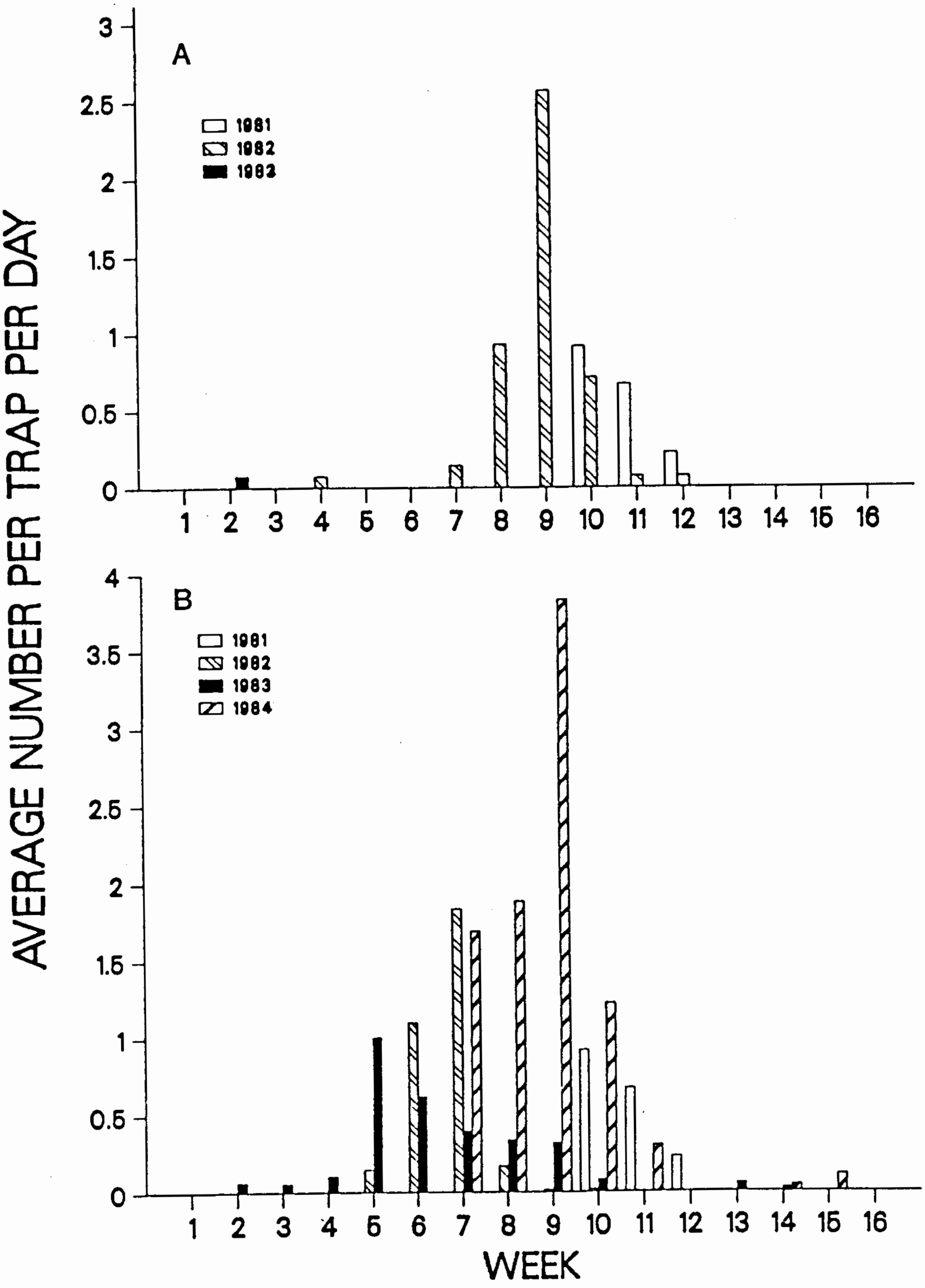

Figure 6. Average emergence rate of damselflies per trap per day in A) Corn Creek Nesting Area and B) Corn Creek Interpretation Area where to birds flew to forage.

per day, while in the area to which the birds flew to feed, Corn Creek Interpretation Area, the peak was only 1.8 damselflies per trap per day. Another important difference is that the peaks of emergence in the two areas differed by 2 weeks. The peaks of damselfly emergence in Leach Lake Nesting Area, and 2 other areas where the Leach Lake birds foraged occurred at different times (Fig. 7). Emergence in the nesting area in Leach Lake in 1982 was 1.4 damselflies per trap per day. In that year, one area travelled to, Corn Creek Interpretation Area, had a higher emergence rate 1.8 damselflies per trap per day, while the emergence in another pond travelled to, Leach Lake Pond 2, had an emergence rate of 0.15 damselflies per trap per day. During 1983, peaks in the Leach Lake Nesting Area were 2.3 damselflies per trap per day, while at Corn Creek Interpretation Area the peak was 0.99 damselflies per trap per day and in Leach Lake Pond 2 the peak rate was 1.4 damselflies per trap per day. Another difference between areas was that peaks in emergence differed slightly. In 1982, the peak was in week 7 for two areas with no noticable peak in the other area. During 1983, the peak occurred in week 6 in the two areas of Leach Lake, but occurred in week 5 at Corn Creek Interpretation Area (Fig. 7).

Sticky trap sampling does not adequately sample odonate populations compared to observations and emergence trap data (Tables 11 and 12). It proved most effective in sampling dipterans. In general, dipterans were most abundant early in the season. Other orders sampled in small numbers on the boards were

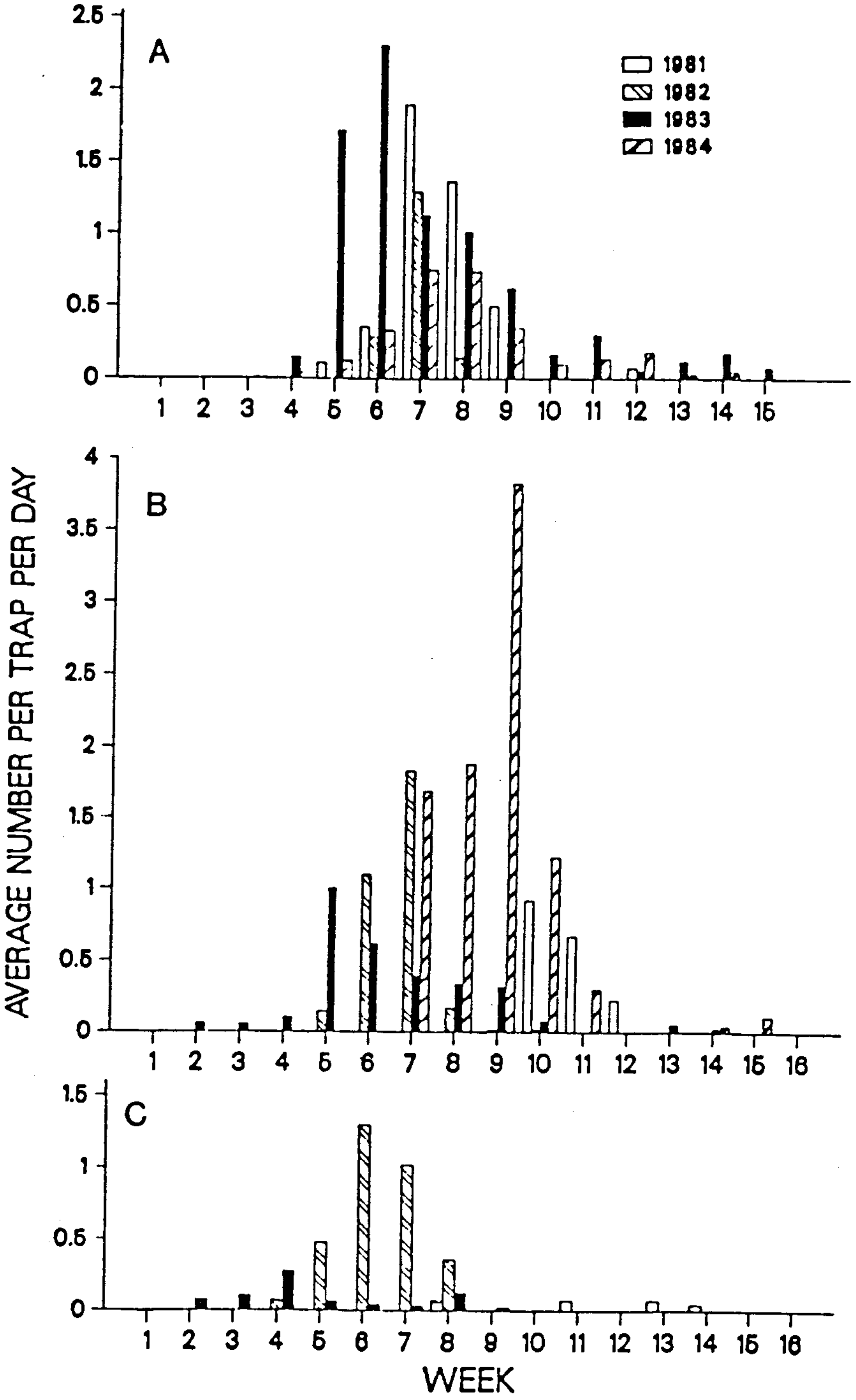

Figure 7. Average emergence rate of dragonflies per trap per day in Leach Lake nesting area and two areas to which the birds travelled to forage. A) Leach Lake Nesting Area (Pond 1) B) Corn Creek Interpretation Area C) Leach Lake (Pond 2).

Table 11. Mean numbers of insects monitored on sticky boards per week during 1982. Area codes CCNA- Corn Creek Nesting Area, CCIC- Corn Creek Interpretation Centre, LL- Leach Lake, DLNA- Duck Lake Nesting Area.

		Diptera		Coleoptera		Odonata	
Area	Date	small	large	small	large	damselflies	dragonflies
	May	3051	30	97.0	104.0	0.0	0.0
CCNA	June	791	19	20.0	1.0	1.0	0.0
	July	1750	17	110.0	1.0	0.2	0.6
	May	2122	26	18.0	1.0	2.0	0.0
CCIC	June	354	2	1.0	2.0	0.5	0.0
	July	1371	4	0.6	0.0	0.6	0.0
	May	5837	4	0.0	0.5	0.5	0.0
LL	June	4243	12	0.5	0.0	0.0	0.0
	July	1677	22	0.0	0.2	0.4	0.0
	May	3099	76	5.0	1.0	1.0	0.3
DLNA	June	403	10	2.0	0.7	2.0	0.0
	July	157	72	0.8	0.0	0.2	0.0

Table 12. Mean insect abundance monitored on sticky boards per week during 1983. For area codes see Table 10.

		Diptera		Coleoptera		Odonata	
		small	large	small	large	damsel-flies	dragon-flies
Area	Date						
	May	1197	17	6.0	1.0	0.3	0.0
CCNA	June	353	27	2.0	2.0	0.3	0.0
	July	376	12	19.0	0.0	0.0	1.3
	May	126	4	5.0	2.0	0.5	0.5
CCIC	June	350	4	0.5	0.8	1.5	0.0
	July	638	2	0.3	0.0	0.0	0.0
	May	2116	8	0.8	0.0	0.3	0.0
LL	June	1239	7	0.5	0.0	2.0	0.0
	July	3093	8	1.5	0.0	0.3	0.0
	May	452	10	3.0	0.0	2.3	0.0
DLNA	June	213	9	8.0	0.0	2.5	0.0
	July	226	33	1.5	0.0	0.5	0.3

Trichoptera, Hemiptera and Lepidoptera. Black Terns consumed Lepidoptera, but only 2% of all the items eaten were in that category. The birds did consume some Diptera and other small unidentified insects, which were probably dipterans. Since these traps sampled mainly dipterans, these data provided information on their abundance.

Although sticky traps provided a measure of insect abundance, they did not sample odonates adequately. On the other hand, emergence traps provided good data on the rate of emergence of odonates but they did not represent a measure of their abundance. Since odonates were important to Black Terns, nets were used in one study area (Corn Creek) to measure the abundance of these insects and compare the results with those obtained with emergence traps. Black Terns fed by flying low over open water areas and over the top of the vegetation, dipping down to obtain food items. For this reason insect abundance was measured by a net placed 4 cm from the water surface and one placed higher in the vegetation. These samplings permitted a comparison of open water areas and areas which contained vegetation, such as nesting sites. The most abundant items in the samples were odonates (Table 13). Some Lepidoptera, Coleoptera and Diptera were caught as well, but their totals were of minor importance in the samples. The data show that the peak of abundance in 1982 occurred in July, while in 1983 it fell in August. The net which sampled in the vegetation contained larger numbers of insects than the net near the water

Table 13. Abundance of odonates sampled seasonally in Corn Creek Pond 2 and 3 by net sampling from the airboat.

		Pond 2				Pond 3			
		Damselflies		Dragonflies		Damselflies		Dragonflies	
Date		high	low	high	low	high	low	high	low
1982	June	11	43	21	4	12	11	1	1
	July	143	52	1	1	150	55	21	7
	Aug	49	75	0	0	1	18	4	1
1983	June	1	121	46	0	14	8	7	0
	July	24	50	0	0	60	158	0	0
	Aug	411	168	24	3	150	143	136	19

surface. Further, the abundance of damselflies was greater in the open water areas (Pond 2), while dragonfly abundance was greater in areas containing heavy vegetation (Pond 3). Figure 6 shows that emergence rates of damselflies were actually greater in open water areas, such as Corn Creek Interpretation Area, than they were in areas containing denser vegetation, Corn Creek

Nesting Area. The emergence rates of dragonflies in the open water were much lower than in areas containing dense vegetation (Fig. 8). Dragonfly emergence was also much greater in the areas of Corn Creek containing dense vegetation, than in the open water areas. Both findings on odonate abundance are therefore consistent with the trends observed in odonate emergence.

Very little data, that was directly useful for the tern study, was collected on fish populations. Fish sampling was done together with Mr. Scott Forbes and the results have been reported elsewhere (Forbes 1985). Areas in which the terns foraged were sampled using seine nets, but very few year-class-1 fish were actually caught. Smaller fry and year-class-1 fish were the only sizes which Black Terns were seen to consume.

DISCUSSION

The data on prey items fed to nestlings (Table 10) showed that insects represented a very large proportion of the diet. Observations on actively foraging adults suggested that adults consumed similar proportions of insects and fish. Their diet actually may have been more heavily weighted toward insects, particularly smaller dipterans, which they consumed while searching for a large item to return to the nest with. This topic will be dealt with further in Chapter 6.

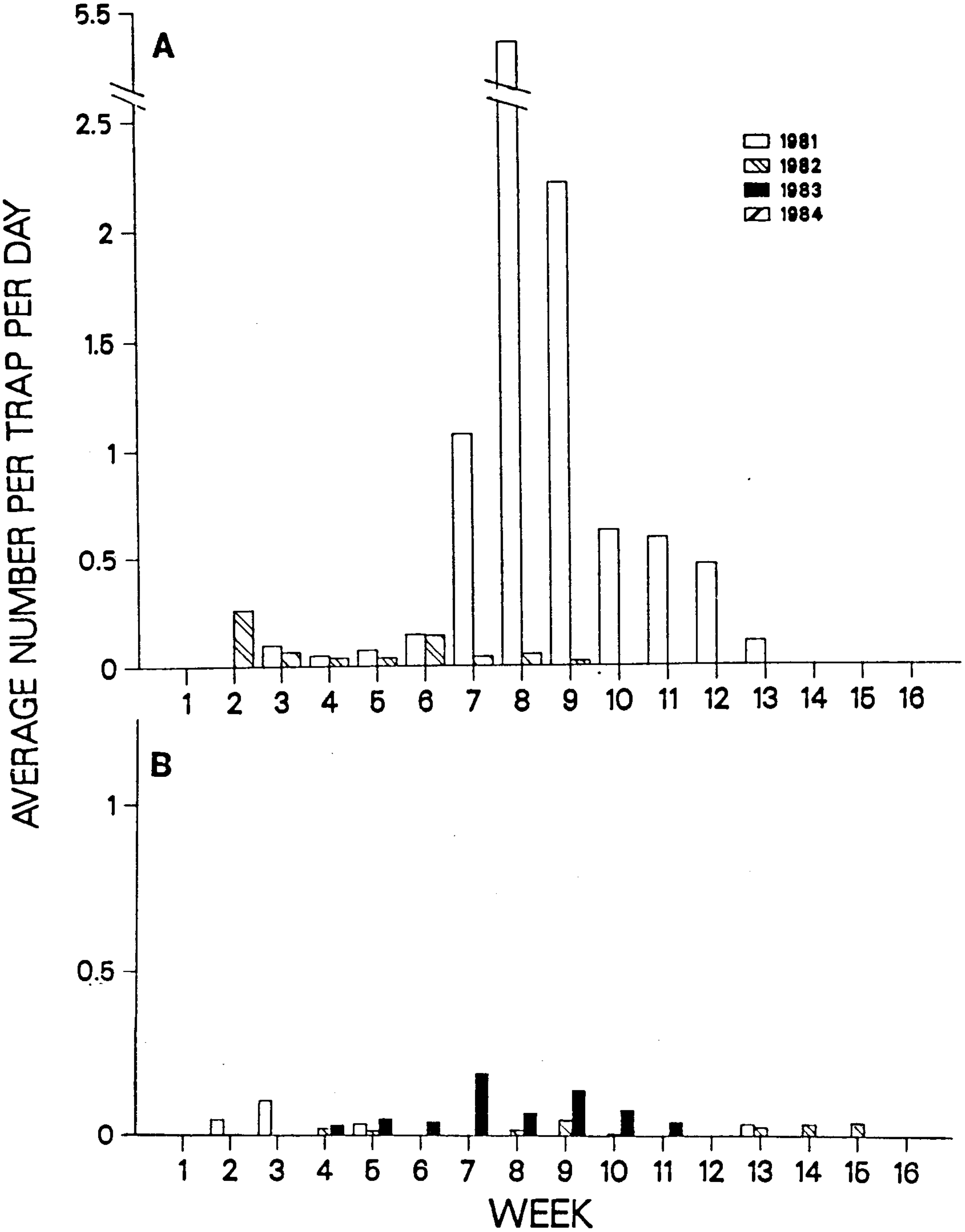

Figure 8. Average emergence rate of dragonflies per trap per day in two areas of Corn Creek. A) Area with dense vegetation B) Area with open water.

Odonates played an important role in the diet. If the peak in abundance of prey occurred predictably at the same time each year, one would expect to see a well-defined breeding time. For Black Terns, shifts of 1-15 weeks in peaks of emergence of odonates from year to year, could have an important effect on the timing of breeding. This fact should tend to promote a spreading of the breeding time for Black Terns. Changes in yearly weather patterns were partially responsible for some of these shifts. Orians (1980) showed that odonate emergence was reduced during periods of colder weather. In 1981, the weather was very cold and wet well into the middle of the breeding season. That year, birds which nested in mid-season in Corn Creek had the highest fledging success of all enclosed nests. These chicks were in the nest when food was most abundant. During 1981, late nesting birds in Corn Creek had significantly higher hatching success than earlier nesting birds in all of the areas, because young hatched when odonates were abundant. These chicks hatched in early to mid-July when the abundance of prey insects was beginning to decline. Although the hatching success was high for these late nesting birds, the fledging success was lower than for earlier nests.

Odonate availability was quantified through emergence data. Trends in odonate abundance were consistent with the trends found in odonate emergence. Damselflies were more abundant in open water areas, while dragonflies were more abundant in areas containing more vegetation.

Dragonflies and damselflies tend to have higher emergence rates in the morning (Corbet 1962; Orians 1980). By afternoon, the odonates which emerged that morning move away from the ponds and lakes (Corbet 1962), where they remain for the next few weeks to mature (Corbet 1980; Orians 1980). After maturing, they return near water to mate. There may be a tendency for mature damselflies and dragonflies to congregate near areas of open water. Most nesting sites were not near large bodies of open water. Although insect emergence peaks were higher in the nesting areas, insect numbers may become depleted in these areas, forcing the birds to travel long distances for insects. In addition, seasonal peaks in emergence within a year varied slightly among different areas (Figures 6 and 7). This could be an additional reason that the terns travel to areas more than 100 m from the nest site.

Fish populations in general tend to be patchy and unpredictable in abundance (Hunt and Hunt 1976a). Year-class-1 fish tend to remain in areas with submerged vegetation to avoid predation (Mittlebach 1981; Werner et al. 1983). Black Terns caught primarily fry and year-class-1 fish. The most extensive fish sampling was done in Duck Lake. Forbes (1985) showed that pumpkinseed were the most abundant fish in seine hauls while yellow perch and pumpkinseed were the most abundant in gill net samples. Forbes (1985) also documented that the 1981 year class failed before the 1982 season. Normally this category forms a very important prey for Black Terns. In 1983, year-class-1 fish were well represented in the overall biomass of fish. Forbes and Chapman Mosher (personal observation) found that these fish were hard to sample, although terns did catch them. If fish were more difficult to capture, the terns might have relied more heavily on other food types.

Birds breeding in colonies usually feed on prey that are abundant but patchy in distribution. The distribution of fish has been documented as unpredictable (Hunt and Hunt 1976a). In general, the unpredictability should be less important for marsh birds which feed on fish, because there are few areas available for fishing. Since open water areas for fishing are small in comparison to large lakes or expanses of ocean, the terns should be able to see others foraging successfully, without having to follow them from the nest. Since there are few large areas of open water within marsh systems, all Black Terns may be familiar with their location. If this were so, information centers may not be needed. Orians (1980) has shown that insect emergence is quite variable in space and time. Odonate emergence rates and abundances varied a great deal throughout the breeding season (Fig. 6 and 7, Table 13). Abundance measures showed that open water areas had more damselflies than areas with moderately dense vegetation (Table 13). If these open water areas can be easily located, as previously mentioned, then coloniality would be less important.

In summary, odonates appeared to be highly prefered by Black Terns. Peaks in odonate emergence varied by 1-15 weeks between years. Since this large spread exists, there is probably no selection pressure to narrowly time their breeding season. All prey items which Black Terns feed on are patchy or unpredictable in distribution. Areas of open water were important for fishing as well as the fact that adult odonates tended to congregate there. By nesting near areas of open water, the birds were able to forage for fish and odonates, allowing them to be more piscivorous.

VI. FORAGING EFFORT OF ADULTS AND GROWTH OF YOUNG

INTRODUCTION

Since Black Terns are only loosely colonial, it is possible that the lack of tight coloniality is influenced by energy requirements. Coloniality affects the energetics of a species by forcing adults to travel further to feed because nearby food supplies become exausted (Lack 1968). The increased travel cost may be too great for species in which food limitation is important, therefore influencing the species to nest more solitarily, so that fewer long distance foraging trips are needed. For these reasons, travel costs for Black Terns could be higher for colonial than for solitary nesters.

The timing of breeding may also be influenced by the food items fed on at different times throughout the season, as well as where those items come from. If the proportion of different prey items differs throughout the season, then birds should time their breeding when the items of greater food value are consumed most often. When birds have to travel different distances to forage throughout the breeding season, they should schedule their breeding at the time when fewer long distance trips are necessary.

Foraging effort and its cost have been noted in some species through time budget analyses, and a number of time budget studies have been conducted on a variety of species (Verbeek 1964, 1972; Emlen 1966; Schartz and Zimmerman 1971; Utter and LeFebvre 1973; Schememski 1975; Tiainen 1978). Generally, the food demand placed on adults by young can be detrimental to the condition of the adults (Ricklefs 1974; Dunn 1975, 1976; Ashkenazie and Safriel 1979; Holmes *et. al.* 1979; Ricklefs and White 1981). Also, having too many young can slow down the growth rates of chicks and/or cause starvation (Emlen and Demong 1975; Tiainen 1978; Veen 1980). Little work has been conducted on the energetics of terns. Nisbet (1973, 1978) studied the relationships of courtship feeding to egg size and parental performance in Common (*Sterna hirundo*) and Roseate Terns (*S. dougallii*). Buckley and Buckley (1974) studied the foraging efficiency of Royal Terns (*Sterna maxima*). Other work has been more physiological in nature and has involved the calculation of the growth energy requirement of young from the lipid and protein contents of chicks (Ricklefs 1974, 1979; Ricklefs and White 1981). Bailey (1977) and Dunn (1979) have determined growth rates of a few Black Tern chicks and compared them to those of other tern species.

The first objective of this study was to analyze the distances adults travelled to obtain food for their young at different times throughout the season, to determine the relationship to coloniality and timing of the breeding season. A second objective was to examine the growth rates of young Black Terns to determine if adults were energetically stressed resulting in some young growing slower than others.

METHODS

The foraging effort of adults was measured in a number of ways. Observations made from blinds described previously, allowed the quantification of the direction from which the adult returned with food to the nest, which chick received the food item, and how often parents returned with food. The distance and direction in which adults travelled to obtain food were further quantified by one of two methods. Adults leaving the colony on a foraging trip were observed and followed from a vantage point where possible. The second method consisted of observing actively foraging birds and then following them as they returned to their respective nests. When possible, adults were followed by a single observer. If birds were lost from sight (i.e. due to rows of Northern Black Cottonwood trees, Populus trichocarpa) simultaneous observations were made from both sides of the trees to verify that the birds were indeed going from observed foraging sites back to known nest sites.

During 1983 an experiment was conducted to attempt to reduce the travel distances of adult birds. An artificial fish pond was constructed and placed in one of the study areas. The pond, 4 by 4 m and 1 m deep, consisted of seine material with a

6 mm mesh. The pond was placed in a channel in the marsh. Fish were caught elsewhere in the marsh by seining and then released in the pond or stored away from the nesting area in storage pens. As the density of fish in the pond decreased, more fish were added from the storage pens. For this reason, the density of fish in the pond was greater than in the waters where the terns nested. The birds that used the pond were watched from a dyke, approximately 200 m from the pond, through a spotting scope.

Throughout the study, some data were collected on the foraging rates of adult birds while they were actively feeding. Observations began by opportunistically selecting a foraging bird and following it until it was lost out of sight or until it left the area. During these observation periods the number and type of items caught were noted as well as any unsuccessful dives. An observation on a particular bird generally ended when it caught a food item and headed back toward the nest site.

Fledging success was measured as mentioned in Chapter 3. The success was compared in nests which were located at different distances from open water areas. All nests were placed into 1 of 3 categories: 0.0-0.25 km, 0.26-0.75 km, and >0.76 km.

Chicks within enclosures were monitored three times weekly to determine survivorship at the end of each period. During these visits the following measurements were made on a total of 246 chicks. Weights were taken using a 30 or 100 g Pesola scale depending on the age of the young, during all years of the study. Length measurements were made to the nearest 0.01 mm with Vernier calipers of the culmen, skull, tarsus and ulna, during the first 3 years of the study. The culmen was measured from the tip of the bill to the mid-feather line on the upper mandible and skull from the tip of the bill to the furthest point on the back of the skull. Both the tarsus and ulna measurements were made from the tips of the respective bones, with the adjacent bones at right angles.

RESULTS

Foraging effort of adults

Since Black Terns are single-prey loaders, one would expect them to obtain food as close to the nest as possible. As seen in Chapter 5, only 8.8% of the items brought back to the nests came from within 100 m around the nest. In all areas, most birds (60%) travelled distances greater than 0.5 km to obtain food for their nestlings, and they travelled to the same areas during all months of the study. When they did travel long distances, it was to areas with more open water than at their nesting sites. The average one-way distance travelled to these areas was 2.4 km (SD=1.2 km). While at those distant areas, adults usually foraged for themselves first, and then obtained an item to take to the nest. All areas were used for foraging at all times during the summer.

Birds nesting in Corn Creek nesting area travelled the shortest distance to feed (average 0.9 km one way). When foraging at this distant site they returned an average of 16.3% of the time with fish. It was rare that a fish was obtained immediately surrounding the nest. Birds nesting in Leach Lake foraged in 3 locations: the pond in which they nested, another pond in Leach Lake to which the average one way distance was 1.5 km, and at Corn Creek Interpretation Area, which averaged 3.9 km from the nesting site. When Leach Lake birds foraged in the pond where they nested the birds returned on average with 45% fish. If the birds foraged in the other pond in Leach Lake the proportion of fish was 50% and 85% when feeding at the most distant site, Corn Creek Interpretation Area. Birds nesting in Duck Lake Nesting Area rarely foraged there, with the majority of food coming from Duck Lake. Although Duck Lake was located within 0.5 km from the nesting area, it was not uncommon for the birds to fly to the opposite shore to feed, an average distance of 2.9 km one way. Birds returned from Duck Lake 79% of the time with fish.

An experiment was conducted to test if adult Black Terns were flying long distances just to find fish during 1983 by placing an artificial fish pond in one area in Leach Lake. The experiment was designed to give the birds a ready source of fish, without having to travel long distances to obtain it. Some adults in the area consistently used the pond while others were never observed to use the pond. Nestlings of adults that used the experimental fish pond were compared with young in the same study colony whose parents did not use the pond. An increase in weight gain of chicks fed from the pond was not seen until after Day 7. For some ages, above 7 days old, chicks whose parents used the pond grew slightly faster, but not significantly (see Growth measurements, page 82). Nestlings in the area with the experimental fish pond did not have higher fledging success (56.8%) than nestlings raised in the area without the pond (59.6%). Birds which nested in the area with the pond returned with a fish 3% of the time, while those in the area without the pond returned with a fish 31% of the time (Table 14). The proportion of different food items fed to young in the experimental area with the pond and the area without the pond differed significantly ($X^2=41.0$, df=3, $p < 0.001$).

Adults concentrated their foraging efforts around areas of open water. When adults were observed foraging for themselves they often consumed a mixture of food items so that it was difficult to calculate foraging rates for insects and fish separately. A total of 50 birds were observed to have an overall foraging rate of 3.28 items/min (SD=3.74). Some of the foraging birds only took fish or insects, so the data were divided into two categories to quantify insect versus fish foraging (Table 15). The highest foraging rate was observed when birds took exclusively insects. However, the terns rarely took exclusively fish, as can be seen from the small sample size for that

Table 14. Proportion of different food items fed to young in the experimental area with the fish pond and the area without the pond in 1983. Sample sizes are given in parentheses.

	% of food items fed	
Food type	Pond (790)	No Pond (227)
Fish	3	31
Damselflies	20	8
Dragonflies	18	2
Small Insects	59	59

category. Most often they captured both types of prey in the same foraging bout. They seemed to be searching for fish, but when insects became available they would capture them. When at open water foraging areas, the adults consumed mainly insects. During foraging bouts for fish, the terns often made a number of unsuccessful dives before actually capturing a fish. The rate of unsuccessful dives per successful capture was determined for 34 birds. On average it took 3.8 unsuccessful dives before a tern successfully captured a fish. The first fish capture often resulted in the immediate return to the nesting site (73%). In

Table 15. Mean foraging rates of adult Black Terns feeding on different types of prey items.

Food Type	N	Mean rate/min	SD
Insects	22	5.09	4.47
Fish	3	0.82	0.08
Insects and fish	26	2.03	2.44

19% of the foraging birds observed the adult ate the first fish caught and returned to the nest after the second capture of a fish. In only 8% of the foraging birds, did the adult consume more than 2 fish before returning to the nest. The adults flew singly to the same main foraging areas during the entire breeding season. There was an increase in foraging at all sites, near and distant, once young began hatching.

Fledging success was compared between birds which nested at different distances from open water, namely, near open water, 0.26-0.75 km from open water, and greater than 0.76 km from open water (Table 16). Data were pooled from all years because the same trend was seen over all years of the study. A significant difference in fledging success was found among the categories (K=17.8, p< 0.001, Kruskal-Wallis). Birds which nested greater than 0.75 km from open water had higher fledging success than

Table 16. Mean fledging success of Black Terns pooled over all years which nested at different distances from open water.

Distance to open water	No. of nests	Mean
0.0-0.25 km	24	51%
0.26-0.75 km	50	48%
>0.75 km	40	78%

those which nested less than 0.75 km from open water. If travel costs to open water areas were important those birds nesting near open water should have greater fledging success.

Growth measurements

The most significant differences in growth measurements, as determined by an F-test, occurred among years so growth curves had to be plotted separately for each year. The least useful measure of growth was tarsus length, as it changed only slightly throughout the nestling period due to the chicks' precocial nature. Since swimming is an important activity for young Black Terns the tarsus reaches its full length within 10 days. For this reason, data on tarsus growth is not presented. Culmen length was a measure sometimes difficult to obtain because of matting on the feather line on the culmen. Skull length was also sometimes variable because the back of the skull tends to be soft. The ulna measurement was determined to be the most easily and accurately measured length because the ends of hard bones are measured. For this reason, only ulna length will be included in the discussion of growth.

Weight

Young attained weights similar to adults (63 g) by the time they were approximately 2 weeks old (Fig. 9). The peak in weight of young was reached earlier in 1982 and 1984, and mean weight of young after Day 13 was higher in 1983, than in the other years.

Late nestlings were defined as birds which hatched after the 9th of July. There were more late nesting birds in the first 2 years of the study than in the last 2 years. Many significant differences occurred in weight measures between early and late season nestlings at different ages in 1981. Late nestlings grew slower in Corn Creek (Age 12=44.0 g) than earlier nestlings (50 g) (K=4.07, $p < 0.05$, Kruskal-Wallis). In 1983, a comparison was impossible because all late nesting birds suffered early loss of their broods. During 1982 and 1984, there were very few differences in weight gain observed.

There were fewer differences in growth between areas.

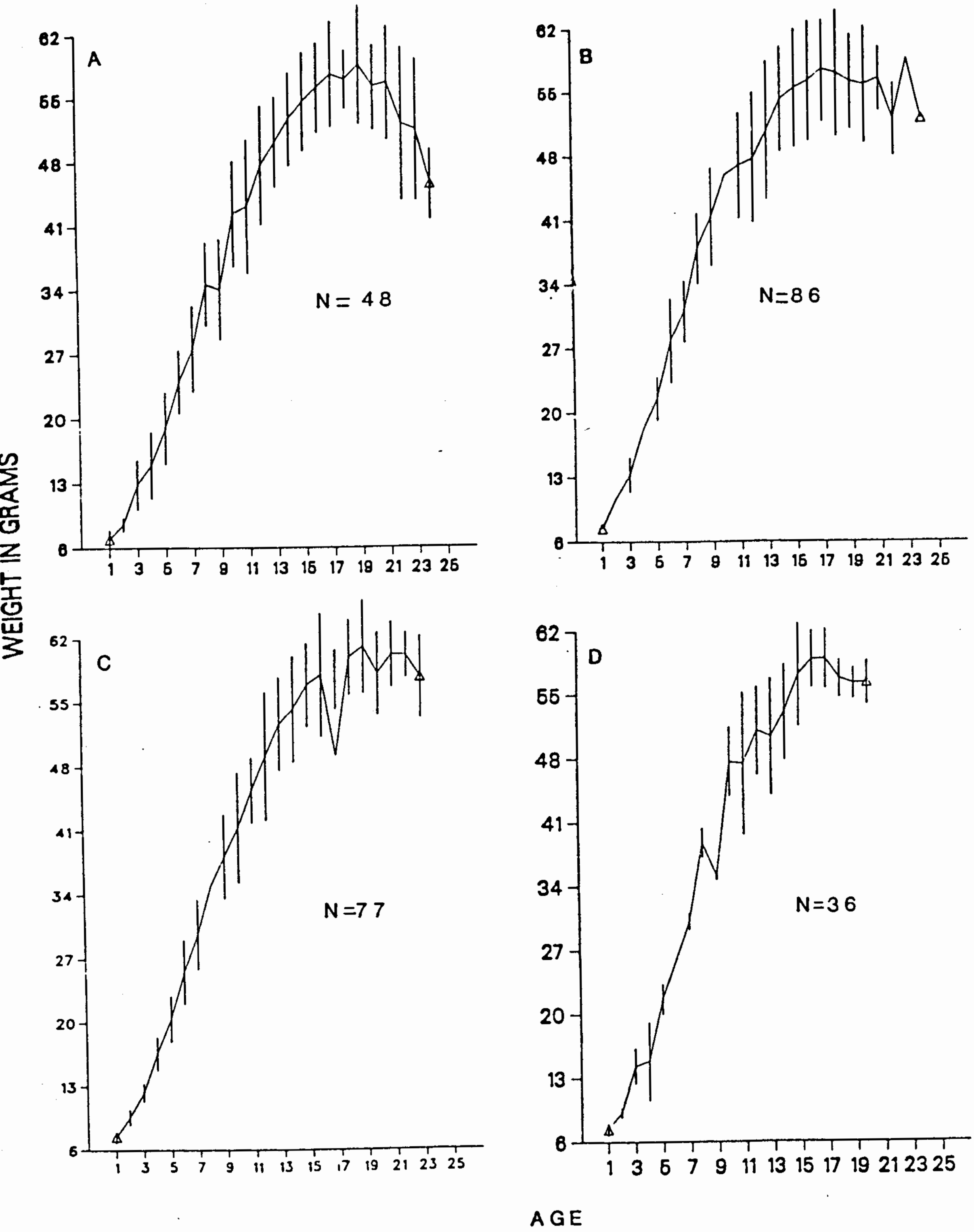

Figure 9. Weight measurements of young Black Terns. The data were generated from a number of young each year. Vertical bars represent the standard deviation. A) 1981 B) 1982 C) 1983 D) 1984.

During 1982, Corn Creek nestlings (Age 13=49.3 g) tended to gain weight slightly slower than Leach Lake nestlings (53.4 g), although no significant differences were found. In 1983, Duck Lake nestlings (Age 3=13.0 g) were slightly heavier than Leach Lake young (11.9 g) ($K=4.62$, $p< 0.05$).

A comparison of weight gain by position of chick within the brood showed a number of differences. At Leach Lake the first chicks to hatch within a brood were significantly heavier (Age 3=12.6 g) than second chicks of the same age (11.7 g) ($K=6.97$, $p< 0.01$). Third chicks almost always appeared notably smaller than their siblings by Day 5. A feeding hierarchy usually developed within a brood, so that the greatest differences in weight would be seen between first and third chicks.

Third chicks, as noted above, were usually significantly smaller than their siblings. In addition, of all chicks in the brood, third chicks were always the ones which died before fledging, unless predation occurred and all chicks were killed. When third chicks died, examination of the body indicated that they had starved to death (low weight compared to siblings and protruding keel on death). The proportion of chicks which appeared to starve to death averaged 20% from 1981 to 1983. A lower proportion (10%) was seen in 1981 and a higher proportion (32%) in 1983. A comparison of weight gain was made between all chicks which appeared to starve to death and those that appeared healthy. Significant differences were seen most frequently in 1982 in Corn Creek ($K=4.0$, $p< 0.05$,) with normal 4-day chicks weighing 17.5 g, while those which appeared to be starving weighed only 13.6 g. In 1983, significant differences were found in Leach Lake (K=4.8, $p < 0.05$) where 8-day chicks which appeared to be starving weighed 25.8 g compared with normal size chicks of 34.4 g. This data corresponds with the general increase in temperature and decrease in precipitation from the weather records over the years of the study (Chapter 3, Environment Canada weather records). During 1981, weather in the nestling period was warm and sunny, so weather-dependent prey were more abundant during that period. Corn Creek had the largest number of late nesting birds that year. By the end of July, when these chicks hatched, the food supply was starting to decrease. The weather in early July 1982 and 1983 was poor (cooler temperatures and increased precipitation). This is the main period when chicks are in the nest and when parents must find large quantities of food. If weather is poor at that time, one would expect to see more apparent starvations, hence the greatest number of significant differences n weight among normal chicks and those which appeared to starve were seen in 1982 and 1983.

Nestlings from nests where the adults used the experimental fish pond were compared to nestlings from the same area whose parents did not use the pond. Although nestlings whose parents used the pond were slightly heavier (Age 11= 46.7 g, Age 14= 47.3 g) than those whose parents did not use the pond (Age 11= 43.4 g, Age 14= 50.5 g), the differences were not significant.

Ulna growth

Weight is a measure that can be influenced by the timing and amount of the last feeding (Ricklefs 1979). Measurements of other body dimensions, such as bone lengths, often provide a more accurate picture of changes in growth. Hard bone measurements tend to be more accurate than those which involve soft tissue bones (Tiainen 1978; Ricklefs 1979; Ricklefs and White 1981). For these reasons only ulna growth data will be presented. Since the plot of ulna length shows very little difference between years, the plot for 1983 is shown as representative (Fig. 10). The trends which were noted for weight measures among different comparisons were also seen in the ulna measures. In some instances the differences were more numerous and more significant.

The increase in length of the ulna was slightly slower in 1981 than in the other 2 years. In Corn Creek during 1981, late season nestlings had a significantly smaller ulna length (Age 12= 38.1 mm) than early season nestlings (42.7 mm) (K=10.25, $p < 0.001$, Kruskal-Wallis). Duck Lake nestlings had a significantly longer ulna measurement (Age 13= 46.8 mm) in 1981 than Corn Creek nestlings (42.5 mm) (K=4.88, $p < 0.05$). During 1983, Duck Lake nestlings (Age 3= 15.4 mm) had a significantly longer ulna than young from Leach Lake of the same age (13.9 mm) (K=5.19,

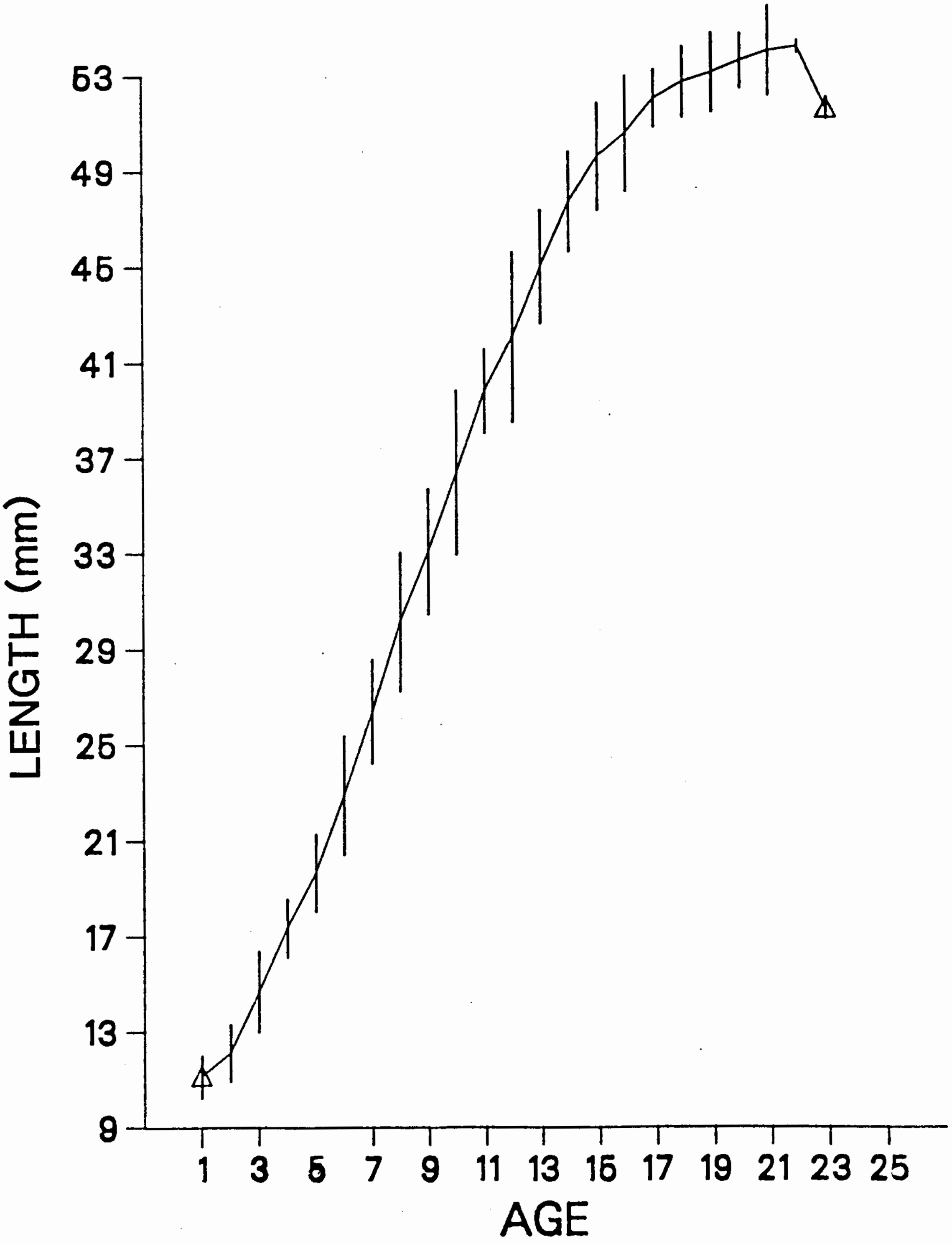

Figure 10. Growth measurements of ulna in young Black Terns during 1983.

$p < 0.05$). Over all years the length of the ulna tended to be greater in first chicks of the brood than in second and third chicks ($K=4.50$, $p < 0.05$, $K=4.86$, $p < 0.05$). Lastly, chicks which appeared to starve to death (Age 8= 25.8 mm), had significantly shorter ulnas than healthy young (34.4 mm) ($K=4.03$, $p < 0.05$).

DISCUSSION

Black Terns feed by flying low over the vegetation in the marsh or low over open water areas. Over open water areas they feed by making periodic dips on or below the water surface, as was noted in the White-winged Tern (*Chlidonias leucopterus*) and Whiskered Tern (*C. hybridus*) (Crawford 1977). All fish were captured by a dip of the bill below the surface of the water, or by plunge diving. The foraging rate of Black Terns capturing insects was much greater than the rate when capturing fish (Table 15). Part of the difference in rate may be due to the availability of the two food types and the ability of the terns to capture them. When the terns made an attempt to catch an insect, they were successful 95% of the time. The terns on average captured a fish after 3.8 unsuccessful attempts. Since the terns were more successful at obtaining insects, combined with a faster capture rate of insects they may benefit by specializing on that type of food.

During 1983, when birds flew one-way distances of 2 km, they returned to the colony with more fish than when they obtained an item near the nest. When the adults travelled these long distances, they returned with both fish and insects. Adults flew similar distances at all times throughout the season; however, the frequency of these trips increased once young were in the nest and being fed. Table 16 shows that there was a significant difference in overall fledging success when birds traveled different distances to open water, and the trend was consistent over all years. Those which travelled greater than 0.75 km experienced higher fledging success than those which had large bodies of open water nearby, so travel cost alone is probably not a strong factor influencing success. The fledging success result may be influenced by some other confounding factor such as habitat.

Experiments with the fish pond showed that birds used the pond, but also travelled longer distances to feed. Reproductive success and weight gain in nests of birds which used the pond, were not increased when compared to the nests in the area without the pond. The birds which used the pond made long distance flights travelling an average of 1.5 km or 3.5 km depending on which foraging site they travelled to. Since fish were readily available near the nest sites, the distance flights were probably not only for fish. However, when the birds flew longer distances, they should return with a higher proportion of fish because of caloric considerations. Although caloric analysis was not conducted on the different prey items, wet weight measures should provide some information on the possible caloric differences between the different food items. The average length of a fish consumed by Black Terns was 2.5 cm. On a wet weight comparison, it would take 16 dragonflies and 80 damselflies, to equal the weight of one fish typically fed to the young. The birds may be forced to return with insects from these areas because it may occasionally require too much time to catch a fish. If an insect became available first, a tern may decide to take that item first, consume it or return to the nest with it, and then resume the search for fish. The data collected on adult foraging success showed that the terns successfully caught insects 95% of the time while only successfully catching fish approximately 20% of the time. The higher success rate at capturing insects may point to one reason why the terns tend to be more insectivorous. However, flying 1 km one-way with a damselfly could prove quite costly when trying to raise three chicks. As well, in cool, wet weather, odonate emergence decreased (Chapter 5). When the weather was poor for more than 2 days, the youngest chick in the brood gained weight much slower than its siblings. After 4 days of this type of weather the smallest chick usually died. If the weather continued to be poor, it was not uncommon for the second chick to die as well. In order for all nestlings to survive, it is important to return with an item of high caloric value.

Weight gain and growth measurements (Fig. 9 and 10) of different age chicks in this study were comparable to those of other studies (Bailey 1977; Dunn 1979). One measurement, namely the ulna, differs somewhat between studies due to measuring technique. The ulna was found to be a good indicator of linear growth for this study. Weight gain differed the most between years, and late season nestlings gained weight significantly slower than early season nestlings. Long dependence of young on adults would increase the possible food stress problem in young from late nests and further emphasize the importance of smaller clutches. Molting of the adults often began while the young were still on the nest, particularly in late nesting birds. This may inflict an energetic deficit on the parents which nested late in the season when combined with a reduction in prey abundance late in the season. There did seem to be some area-related differences in weight gain. The differences between areas could be related to the distance travelled to forage, because in each significant case, the area where growth was better was close to open water. Comparisons of chicks within a brood showed the most significant differences in weight gain between chick 1 and chick 3. Nestlings which appeared to starve gained weight slightly slower than those which seemed healthy.

Fledging success (Chapter 3) showed that 39% of the chicks which hatched never fledged. The most important factor influencing low success was the fact that the third chick within a brood rarely fledged. As time in the nest progressed, the third chick grew slower than the others and the size difference between chicks widened until the smallest chick died. This fact could be related to the kind of food items the birds were feeding on, as well as where those items were obtained. The adult terns seemed to be unable to meet the total food demand of all chicks.

One way for Black Terns to reduce their food demand for chicks would be to nest near open water areas, so that travel costs are reduced and the opportunities to catch fish are greater. The Duck Lake Nesting Area birds did that in 1983 when they moved close to the open water area of Duck Lake. Birds in this new location only needed to fly 200 m to use the open water, but in many instances they travelled distances of 2 km or more to forage. Being located that close to open water provided the adults with a more ready source of fish for their young. Young in Duck Lake Nesting Area received a very large proportion of fish (35-50%) in their diet compared to the average consumed by young from all areas (Table 4, Mean=10%). Because of the close proximity to open water fishing sites, coloniality was probably less important at that site. The average internest distance (Table 7) in the _Phalaris_ habitat at Duck Lake Nesting Area was 24.3 m compared with the _Phalaris_ habitat at Leach Lake (15.1m). Since the open water was only 200 m away individuals could readily see where the others were foraging without having to follow them from the nest site. Most other species of gulls and terns nest on islands and forage over great expanses of open water. For them, tight coloniality may be more important so that birds can follow others to good foraging sites. In marsh breeders which only feed within the marsh, this may be less important. Marshes typically have few areas of open water, and those that are present are quite small. If birds tend to congregate in large open water areas of the marsh when they first arrive in the area, then they may be familiar with their location.

In summary, growth measurements of young Black Terns showed that some of them grew more slowly than others and eventually starved to death. This is reflected in a fledging success averaging 61% of those chicks that hatched. The main reason for this appears to be that adult Black Terns are unable to feed all their young. A size differential among the young in each nest provides the mechanism to eliminate one chick, when the food supply is insufficient. Adult Black Terns were much more successful at capturing insects (95%) than at capturing fish (20%). Due to these success differences, the terns are probably better off to remain primarily insectivorous unless colonies can be located near areas of open water, thus reducing travel time and allowing more opportunity to capture fish. If colonies serve as information centers, fledging success should be greater in colonial than solitary areas. Success in colonial and solitary areas (Table 9) in Black Terns in Creston was not shown to differ. These birds which nest in small marsh systems may be able to obtain information about foraging without being social, so there is probably no selection pressure which might increase the degree of coloniality. Also, since distances flown for food did not differ throughout the season there was no apparent need to narrowly time the breeding season.

VII. WATER LEVEL FLUCTUATIONS

INTRODUCTION

Variable water levels can have very dramatic effects on breeding waterbird populations. Fluctuating water levels can affect the timing of breeding by altering available sites and causing nests to be washed out. Water levels which fluctuate a great deal throughout the season, could result in widespread timing of breeding, if selection pressure does not favor breeding at a set time. In some areas, fluctuations may be common at certain times and selection pressure might be expected to favor a set timing of breeding.

Water level fluctuations can be caused by a number of factors which have a wide array of consequences. Weather can have very dramatic effects causing water levels to rise and fall. In addition, storms produce waves which in turn can wash eggs from nests (McNicholl 1979). Seasonal runoff from mountains can cause marshes in mountainous regions to have increased water levels.

Few studies have dealt with the effects of water level fluctuations on nesting birds. Of the few studies, most have dealt with the artificial manipulation of water levels (Bourn 1939; Kadlec 1962; Anderson 1967; Cowan 1975; Hudec 1979). Other studies have dealt with natural water level fluctuations and vegetation changes (Johnsgard 1956). No work to date has looked at the influence which vegetation surrounding the nest might have on wind and wave action.

Since Black Terns place their nests on floating vegetation, water level fluctuations can be important to their reproductive success. Black Tern nests are usually placed on floating mats of vegetation and in some cases on boards or logs (Richardson 1967; Bergman _et al._ 1970; Bailey 1977; Haverschmidt 1978; Dunn 1979). Although dry land provides a more stable base, Black Terns have rarely been observed to nest there (Turner 1920). Nests of Black Terns can vary from well-made, elaborate structures to slight depressions in closely matted vegetation (Bent 1963). Nests on floating mats of vegetation are usually intertwined with the surrounding vegetation (Richardson 1967) and are therefore vulnerable when water levels fluctuate. If these fluctuations were more prevalent at certain times than at others, one would expect to see a well-defined timing of the breeding season in Black Terns.

One objective of this study was to document the seasonal fluctuations in water level in the marsh units where the terns nested. This was done each season to determine if these fluctuations were predictable. A second objective was to determine experimentally to what extent the different species of vegetation around the nest protected the nests from wave action.

METHODS

Following the 1981 field season, the importance of water level fluctuations to the reproductive success and timing of Black Tern nesting became apparent. Calibrated stakes were placed in each of the study areas from 1982 through 1984, and bi-weekly depth readings were taken. The readings allowed the calculation of depth profiles in relation to starting week 1, the first week of May. Profiles allowed the analysis of within and between year water level fluctuations and the comparison of reproductive losses due to associated water level changes.

In 1981, two nests were found on boards floating in the marsh. For this reason, floating platforms were made and placed in the marsh. They varied in size over the years from 1 x 2 m to 1 x 1 m. Each platform had a wooden base with styrofoam packed under the board so that it would float higher above the water. Small 2 cm barriers were placed along the edges of each board to prevent eggs from being lost in the water if they were washed out of the nest.

Water level changes were shown to be important to Black Tern nesting success, but more pressing was the influence that wind and wave action might have on hatching success. Wave height was measured by using a device designed for the project. The wave gauge consisted of a float which rested on the water. Attached to the float was a small dowel which was held upright by eye screws in the device support. A pencil was attached to the top of the dowel and index cards were inserted to make the measurements. Ten trials were run at each location. Locations were chosen so measurements were made in different associations with the surrounding vegetation.

During 1983 and 1984 the previously mentioned vegetation measurements were made (Chapter 4). The area occupied by vegetation per m^2 was thought to be an important habitat measurement. As well, the area occupied by vegetation might provide a measure to compare the effectiveness of the different plant species in their ability to block waves in the nesting areas.

During 1984 an experiment to investigate egg loss due to wave action and water level fluctuation was conducted. At each marsh unit where the terns nested, man-made nests were constructed. These nests were designed to represent a typical Black Tern nest. Vegetation was piled to mimic the nests and a tennis ball was used to create a nest cup depression. Nests in each area were placed in association with vegetation growing in different densities so as to provide varying degrees of protection from the four major compass directions. Fifteen nests were constructed in each of the three nesting areas in Creston, and nine nests at Elizabeth Lake. Each nest was supplied with fake eggs made from domestic Japanese Quail (<u>Coturnix japonica</u>) eggs obtained from the genetic stock center at the University of British Columbia. Jumbo-size quail eggs were very suitable mimics in size, shape and coloration. Eggs were blown through small holes and rinsed a number of times to assure they were empty and clean. Two types of eggs were made from the empty quail shells: those representing developed eggs and those representing freshly laid eggs. A developed egg was filled with an alcohol and water mixture to the proper weight and floating characteristics to represent a developed egg. Freshly laid eggs were made by filling the eggshell with sand to the appropriate weight, or by using the eggshell as a mold to form an egg made of fiberglass resin. These freshly laid mimics would sink immediately when washed from nests, an important characteristic. The eggshell was peeled from the resin eggs on hardening, and this left the eggs the color of the resin, a tan or brown color. All sand eggs were painted a similar color so that the fresh versus developed eggs could be easily distinquished. The outside of the sand-filled and developed eggs was then painted with fiberglass resin to add a hard outer shell to the eggs. When resin was being applied to all the eggs, a string was inserted through the blow hole so that the final end product was a completely sealed egg with a string attached.

Each nest received one fresh and one developed egg. The strings were then tied to the nearest stalks of vegetation and this allowed the quantification of eggs washing out of nests. Eggs were placed in the nests at the approximate time when actual egg laying was initiated. The fake nests remained in place until late July when all eggs within the areas had hatched. This allowed a comparison of washouts at different times throughout the breeding season. All nests were checked at approximately weekly intervals.

A trial was run during the third week of the experiment when an unaltered quail egg (unblown) was placed in a nest in each of three categories in each area. These categories were 1) nests that always washed out 2) nests in which the eggs were present but underwater and 3) nests in which the eggs and nest were undisturbed. This allowed quantification of any effect the strings had on the washout potential of nests.

RESULTS

Water levels in Corn Creek did not fluctuate much in 1982, when the terns nested there (Fig. 11). The water level in 1983 was increased after week 6 by opening culverts into the area because the terns did not nest there. Fluctuations were not recorded in 1984 because the area was drained. Duck Lake Nesting Area was partly drained for management purposes in 1982, and fluctuations were minimal during 1983 and 1984 (Fig. 12). In the Leach Lake nesting area (Fig. 13) the fluctuations were moderate in 1982 and 1983, although early in the season, when most of the eggs were in nests, the fluctuations were minimal. During 1984, few terns nested in Leach Lake, and the Management Authority lowered the water level to reduce the flooding effect in the decreasing *Phalaris* beds.

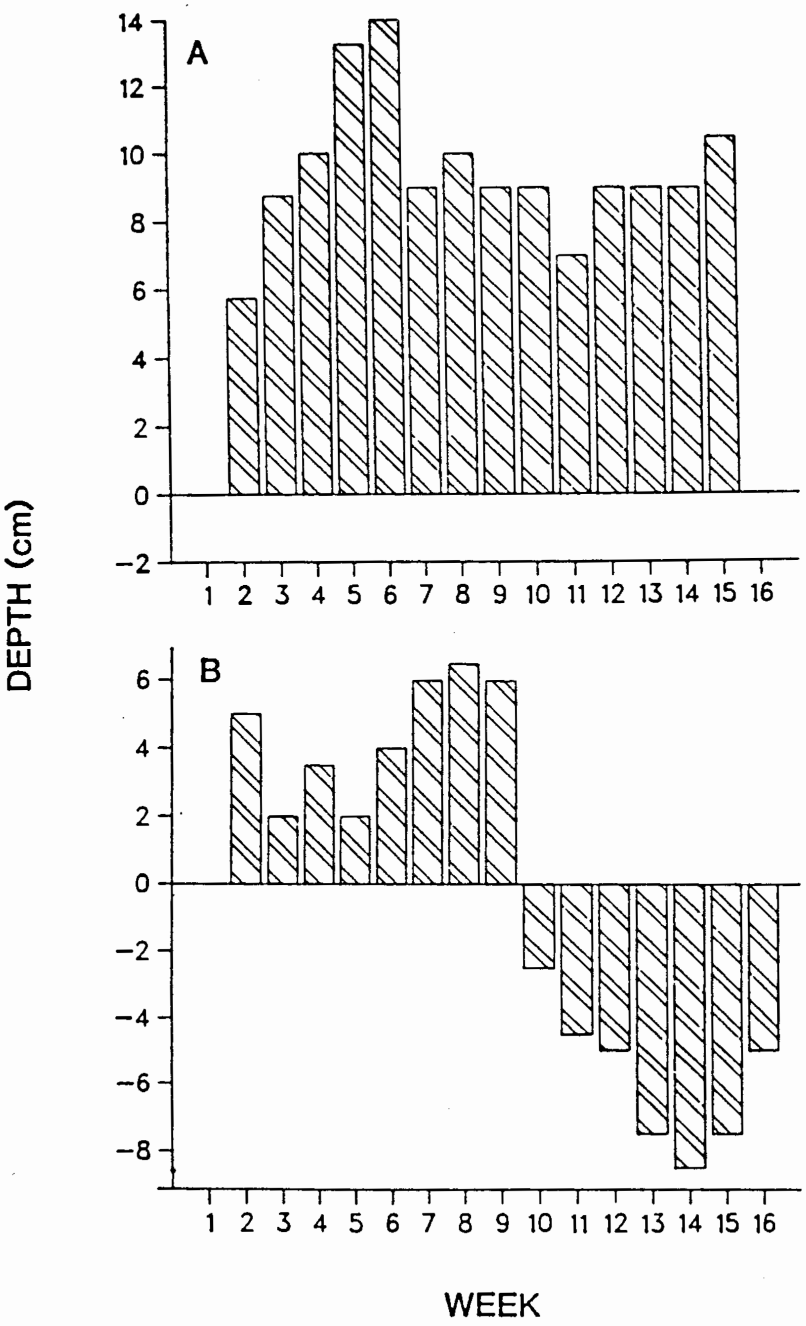

Figure 11. Water level fluctuations throughout the season in Corn Creek nesting area. Water level was standardized to 0, the height in an area during the first week of each study season. A) 1982 a year when the terns nested there, B) 1983 a year when the terns did not nest there.

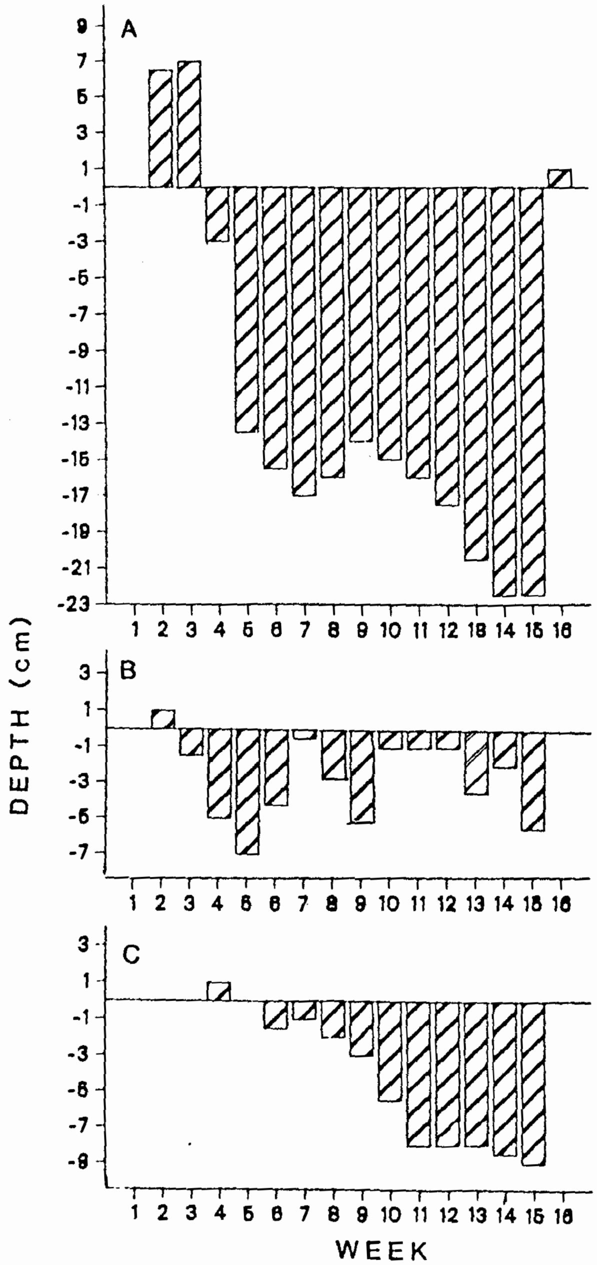

Figure 12. Water level fluctuations throughout the season in Duck Lake Nesting Area. A) 1982, B) 1983 , C) 1984.

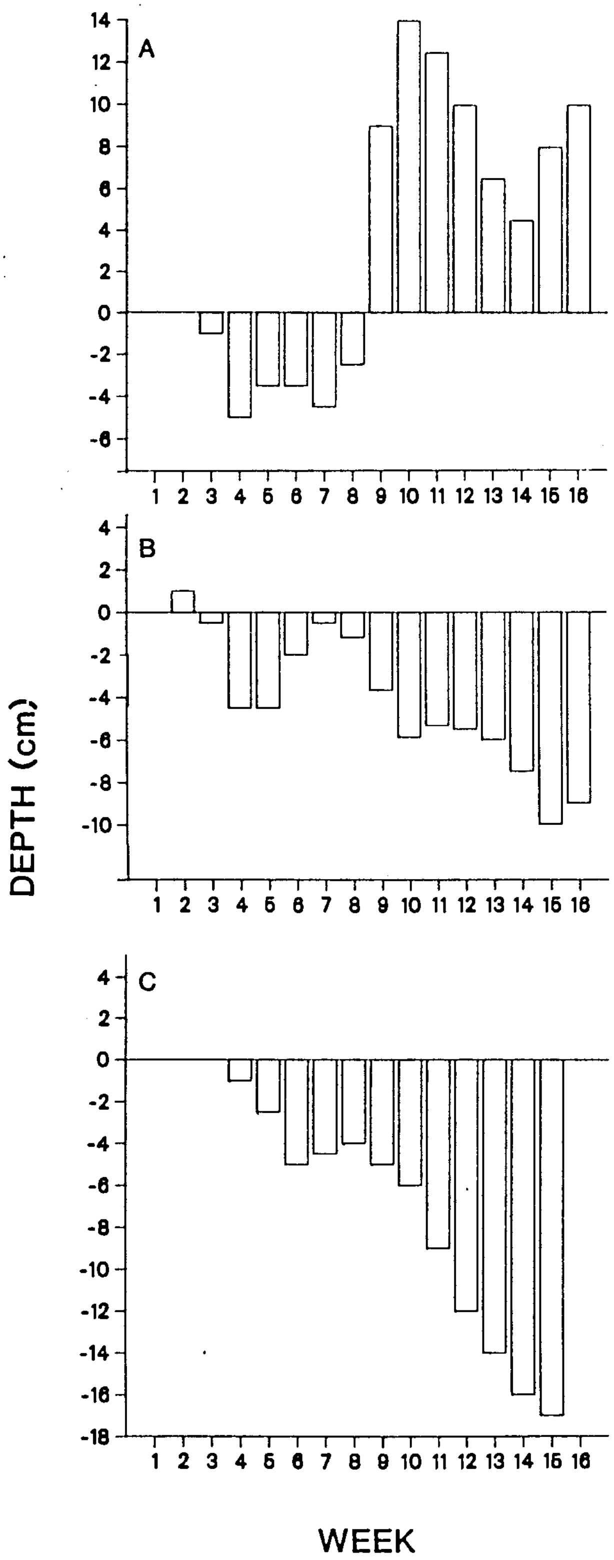

Figure 13. Water level fluctuations throughout the season in Leach Lake nesting area. A) 1982, B) 1983, C) 1984.

Water levels within different units of the marsh varied by as much as 0.3 to 0.7 m (Fig. 11-13), depending on runoff and active pumping by the Management Authority. Local environmental conditions responsible for the fluctuations were noted throughout the years of the study. In 1981 fluctuations were quite variable due to heavy precipitation for the first 6 weeks of the breeding season. During 1982, water levels rose until the second week of July, the time when most eggs had hatched. This rise in water level was due to excessive runoff. In 1983 and 1984 water levels either remained the same or declined slightly due to active pumping of water out of the units, or passive movement of water into units through culverts. The pumping was an attempt to minimize fluctuations in those years.

Wind and wave action was highly correlated to hatching success (Chapter 3). Many eggs washed out of nests following storms and when water levels rose. Black Terns lost up to 27.1% of their eggs from nests due to water level fluctuations and wind or wave action. A 2 cm rise in water level was seen to destroy some nests. Wave measurements were made with the wave gauge during different wind velocities. When wind speeds were 20-30 km per hour it was common to have waves averaging 2.0 cm in open areas, 1.4 cm in areas covered sparsely with vegetation and 0.7 cm in more protected areas.

The proportion of standing vegetation was very similar in the different habitats (Table 4). It was thought that the various types of vegetation might have a different blocking effect on waves. Quadrat measures of vegetation density and area occupied by stalks led to the measurement of the area occupied by vegetation per m^2 (Table 6). There was a statistically significant difference between the different habitats in terms of the area occupied by vegetation (Chapter 4). Sites used previously for nesting were abandoned when the vegetation was too dense and also when it was too sparse, probably because in the latter case the remaining vegetation did not adequately block the waves. The terns seemed to prefer habitats where the vegetation stalks occupied between 10-50 cm^2/m^2, although they nested in habitats where the area occupied by stalks was as low as 8 cm^2/m^2 (Chapter 4).

Sixty-nine percent of the 326 nests with complete nesting success records were in Phalaris habitats. Although the amount of Equisetum to nest in was limited, the amount of Typha and Phalaris was roughly the same. If one compared a Typha to a Phalaris habitat, one average sized Typha stem occupied the same area at the water surface as 64 average sized Phalaris stems. When a wave hits one Typha stem, the area on the lee side of the stem receives some protection but the wave washes around the stalk. If a wave hits 64 spaced Phalaris stems, the wave tends to be damped out. The overall effect of these different vegetation types is clearly much different. If the area occupied in a Typha and Phalaris habitat were equal, small Phalaris stems should be able to block waves more effectively.

Since eggs did wash out of nests, nest protection could be important. To further test the relationship between vegetation and reproductive success, the egg/wave action experiment was conducted. Unaltered quail eggs washed out of nests with the same frequency as stringed, artificial eggs. In addition, developed, artificial eggs washed out of nests more frequently than freshly laid, artificial eggs due to their natural floating characteristics. Open nests, with very little protection around the nest, were not successful (Table 17). If there was some vegetation on the side of the nests other than the prodominant wind direction (i.e. E, S, W), success improved slightly. When protection from only the northerly directions was provided there was further improvement in success. The most successful nests were those that were completely surrounded by vegetation or on platforms. *Equisetum* and *Phalaris* seemed to have better success rates than *Scirpus*. The high values in *Equisetum* were confounded by the fact that water levels in that area were dropping rapidly due to marsh management and by the first week of August there was no water left. For this reason, *Phalaris* should probably be a better habitat choice. Therefore, the birds did seem to be doing the right thing by nesting in *Phalaris*. When these same data were analyzed throughout the breeding season, there were more washed out nests earlier in the season (91%) than latter (9%). Nests made on platforms were the most successful because the platforms would rise and fall with all water level changes and waves. One platform which was made for the study, had a

Table 17. Results of the artificial egg and wave action experiment. The number of nests sampled are in brackets.

Nest protection	% of successful nests		
	Equisetum (75)	Phalaris (150)	Scirpus (40)
Open	0	0	0
Protected E,S OR W	20	20	0
Protected NW,N OR NE	50	50	33
Surrounded 360 degrees	100	80	66
Platform	100	100	--

successful tern nest on it during 1984. In addition, the birds at Elizabeth Lake, which were nesting on various sizes of ordinary boards, had 100% hatching success.

DISCUSSION

Since water levels in marshes can vary greatly during storms (McNicholl 1979), it is important that nests be maintained throughout the breeding season. Some species, such as Franklin's Gulls (Larus pipixcan), are very adapt in maintaining the nest to keep it from sinking (Burger 1974). In Black Terns, the maintenance of nests seemed to be more related to their original quality. No quantitative data on nest quality was collected. However, the qualitative impression was that those birds which made well-built, elaborate nests tended to maintain them, while those nesting in depressions did not.

Weather tends to be a very unpredictable factor influencing organisms in many ways. One of the more important aspects of weather for Black Terns is precipitation and the degree of runoff from the mountains. There was more control of the water level as the study progressed. The water depth measurements included both precipitation and runoff. In years when water levels were not being maintained, the water level in the marshes tended to rise most early in the season. This would be the most detrimental time for Black Terns, since most eggs were in the nests then. As well, the weather tended to be more variable early in the season, so that storms caused more wind damage early. Poor weather conditions often caused waves to wash over nests, removing eggs when the parents were not in attendance, a frequent condition before clutches were completed. An average Black Tern nest varies between 3.0 cm high (Bochenski 1966) and 3.3 cm high (Bergman et al. 1970). Although the average nest may be 3.0 cm above water level, a number of them are less high and fall into the category which are vulnerable when rising water levels or high winds occur. Rainstorms combined with runoff can also cause water levels to rise 2 cm in as little as 24 hr. In addition, the weather frequently caused problems in midseason when both eggs and young were affected. Rises in water level of 2 cm were observed to destroy nests which were not well constructed. Since Black Terns are so vulnerable to weather conditions there is probably no selection pressure to time the breeding season to one set time. Although fluctuations in water level tend to be more prevalent early in the season (Fig. 11-13), short periods of cool and wet weather in mid to late season are also common.

Black Tern hatching success in this study was shown to be greatly affected by wind and wave action. Vegetation density was shown to have an important influence on the likelihood that eggs were washed out of nests. Nests in habitats containing *Phalaris* seemed to have greater success in tests with the experimental eggs than nests in *Scirpus*. Birds nesting on platforms of all types and sizes at Elizabeth Lake (Chapter 3), also had high hatching success.

In summary, Black Terns can improve their reproductive success by nesting in habitats where certain types of vegetation are available. Given the opportunity, the birds seemed to favor the more stable habitat structure of *Phalaris*. An effective aid to Black Tern hatching success can be the use of floating boards in the marsh areas where they nest. These boards need not be of any specific size or shape, as long as they are at least 12cm by 20cm, so that a tern nest can fit on the platform. This is one way to overcome the effects of waves and water level fluctuations. As well, as Black Tern nesting success can be greatly influenced by unpredictable water fluctuations there is probably no selection pressure to narrowly time their breeding season.

VIII. PREDATION

INTRODUCTION

One of the main explanations for the evolution of coloniality is that, collectively, colonially nesting birds are better able to detect predators than individually breeding pairs (Lack 1968; Ward and Zahavi 1973). Colonial breeding is thought to be a response to relatively heavy losses caused by nest predators (Lemmetyinen 1971). Wilkinson and English-Loeb (1982) suggested that large colonies diluted the effect of local predators, by causing a swamping effect, resulting in lower losses per nest. For the dilution effect to work there must be a high degree of synchrony in the colony so that the swamping occurs (Nisbet 1975). On the counter side, there is more activity in large colonies than in small ones, which could draw the attention of predators (Skutch 1949).

Some researchers have found a positive relationship between nest density and predation intensity (Tinbergen *et al.*1967; Goransson *et al.* 1975). Tinbergen *et al.* (1967) showed that a crowded colony was actually exploited faster than a widely spaced colony. Some species, like Aleutian Terns (*Sterna aleutica*), exibit antipredator responses such as widely spaced nests (Buckley and Buckley 1979). Other researchers have proposed that birds nesting in colonies benefit by joining in a group defense effort such as mobbing (Siglin and Weller 1963; Goransson et al. 1975; Morse 1980; McNicholl 1981).

Adult birds have three methods of protecting their eggs, young and themselves from a predator (Veen 1977). If predators are a threat mainly to a clutch or brood, the response of the adult is to remain sitting on the nest, thus preventing the predator from getting at the contents. When predators pose a threat to young and adults, the species can respond by mobbing the predator from the air and driving it from the area (Kruuk 1964; Morse 1980). Lastly, if predators are a threat only to adults, those vulnerable can avoid any confrontation by flying away.

Various kinds of organisms have different types of predators to deal with. In marsh environments, the main predators causing the most losses are visually oriented birds and mammals (Hammond and Foreward 1956; Dwernychuk and Boag 1972). Visually oriented predators continue to search for more nests once they locate one. Thus, such predators are able to deplete nests in colonies faster, while expending very little energy themselves (Tinbergen et al. 1967; Picozzi 1975). This illustrates the importance of cryptic nests, eggs and young in species that nest in large, tight colonies (Buckley and Buckley 1979). As the degree of crypsis decreases, nests generally tend to be more widely spaced (Tinbergen et al. 1967).

The importance of the degree of coloniality shown in Black Terns may be related to predation pressures on individual populations. In general, marsh nesters are thought to be less susceptible to predation since there are fewer possible predators. Members of the Corvidae, which occur in the same areas as the Black Terns, are known to be egg specialists during the breeding season (Godfrey 1966). Bailey (1977) found that 7.9% of Black Tern eggs and 61.5% of their chicks were lost to predators. Although other workers (Bergman et al. 1970; Dunn 1979) found low nesting success, no calculations were made of losses caused by different factors.

Predation has been suggested as a possible cause for altering the timing of breeding observed in some species (Lemmetyinen 1971). Black Tern predators in Creston were present throughout the breeding season. It is possible, however, that certain species which frequent an area may deter Black Terns from nesting there (Chapman and Forbes 1984). The deterrent may result in birds breeding later in the season than those which began nesting in the first site they chose.

The first objective of this study was to determine how important predation was on Black Terns. A second objective was to determine if the presence of predators differed in loose colony versus solitary nesters. The third objective was to determine how the presence of predators and the reaction to them varied over the breeding season.

METHODS

Prior to 1983, only incidental observations of predation were made. It was obvious that certain cases of reproductive loss were attributable to predation. During 1983, observations on interspecific interactions were made while other data were being collected. Throughout those observations, only vocal reactions were noted. Since some reactions might result in little or no vocalization, some data might have been missed.

In 1983, Black Terns appeared to abandon nesting in one specific location, probably because Great Blue Herons were present in the area (Chapman and Forbes 1984). The herons began standing in the same area where the terns had begun nest building. Within a few days of the arrival of the herons, the terns abandoned the location. Throughout the study, herons were frequently mobbed when they flew over the tern nesting areas. Because of this observation, Leach Lake Nesting Area, and to a lesser extent, Duck Lake Nesting Area, were censused before Black Terns returned during 1984. The object was to see whether species which have a potential negative effect on terns were present in these areas prior to the arrival of the Black Terns. Unfortunately, the terns hardly used Leach Lake Nesting Areas in 1984, because the vegetation failed to grow and water levels were too low.

During 1984, 74.5 h of intensive observations were made over the entire breeding period at Leach Lake, Duck Lake Nesting

Area and Elizabeth Lake. This allowed the quantification of any difference in reaction of adults to interacting species during the egg and chick stages. Species of concern were American Crow, Common Raven, Great Blue Heron, American Coot, Muskrat and any raptors. The marsh was scanned at 2 min intervals for a period of at least 3 hours, and all possible interacting species were recorded. As well, the distance of the species from the nesting aggregation and reactions or lack of reaction by the terns to them was recorded. In addition, all vocal reactions between scans were noted along with distance.

Various models of potentially predatory species were tested in the nesting areas to determine what cues the birds were using to identify various species as well as how far away from the nest the nonmobile models could be placed and still elicit a response. Live mounted models were made of the American Crow and American Coot. Styrofoam models, painted and hardened with fiberglass resin, were used for the Muskrat and Common Raven. Models were placed in colonies at different times throughout the breeding season and were covered before entering the blind. The models were then tested after other observations were made from the blind. While all adults were absent from the area the cover was removed by a string extended to the blind. Tests were run for at least 5 min after the model was uncovered, to allow adults time to return to the area and see the model.

RESULTS

Adult Black Terns were occasionally killed by predators. Species of greatest threat to adult terns were Great Horned Owls and Northern Harriers. The more important predation risk was to young. Losses to predation varied between 6.5 to 11.2% and they were equally divided among the egg and the chick phase (Table 18). The losses in the two phases were similar over the years with the proportion varying insignificantly ($Z=0.37$, $p > 0.05$, Wilcoxon Rank Test). Four of the 18 instances (22%) of losses to predation during the egg stage were incidental. They occurred when muskrats returned to use their feeding platforms, on which the terns had placed nests. In each of these cases, freshly cut vegetation across the nest and/or feces on the platform provided clear evidence that muskrats caused the loss.

Throughout the study nearest neighbor distances were calculated, as discussed in Chapter 4. Although Black Terns nest in loose colonies, more than 3 nests were rarely found in a group. If two nests had nearest neighbors of 20 m or less, the next nearest neighbor was often 100 m away. The nearest neighbor data over the years of the study showed that there was a difference in the proportion of nests in each of the nearest neighbor categories. Nests with neighbors less than 20 m away accounted for 62.4% of all nests, with equal proportions in the categories of 0-10 m and 10-20 m. The total proportion in the category 20-30 m was 18.6%, 30-40 m was 9.1% and greater

Table 18. The proportion of Black Tern eggs and chicks lost to predators.

		% Predation				
	N	1981	1982	1983	1984	Mean
Eggs	18	2.8	8.7	7.8	0.0	4.8
Chicks	11	4.3	1.0	3.4	6.5	3.8
Total		7.1	9.7	11.2	6.5	8.6

than 40 m was 9.9%.

Comparisons were made between the proportion of losses due to predators and nearest neighbor distances. No correlation was found between distance to the nearest nest and predation frequency (RHO=-0.019, $p > 0.05$, Spearman Rank Correlation). Since losses due to predators in some years were almost half the value in other years, the data were analyzed on a yearly basis. No differences were found between nearest neighbor distances and the frequency of predation in any of the study years (Kruskal-Wallis, $p > 0.5$).

If coloniality were important to a breeding population, one would expect that "more colonial breeders" would do better in terms of success than "less colonial" individuals. Each nest was compared in terms of success with the various nearest neighbor categories during each year of the study. In general, as mentioned in Chapter 4, there was no statistically significant difference between reproductive success and nearest neighbor category.

As the breeding season progressed, mobbing reactions of Black Terns appeared to increase. Attacks on human intruders became more intense as eggs neared hatching. Reactions to human and non-human intruders differed in terms of the type of response and duration of the response. Responses to humans involved many birds circling over their nests as long as the person was moving among active nests. Reactions to non-human intruders involved vocalizing and diving, but usually the terns did not circle over the nest sites. The mean rates of response to intruders did not differ between egg and chick phases (Table 19). A total of 197 interactions were observed between Black Terns and other species. The greatest number of interactions with intruders (54%) were directed towards coots and muskrats, while corvids represented 21% of the responses, and herons 8%. The remaining 17% of the interactions were with Ospreys Pandion haliaetus, American Bitterns Botaurus lentiginosus, Ring-billed Gulls Larus delawarensis, and Red-winged and Yellow-headed Blackbirds. When terns laid their first eggs they would often fly up when interacting species were present and sometimes leave the area. After clutches were complete the terns would often fly up at intruders and call above them. As eggs neared hatching

Table 19. Mean response rate to interacting species during the egg and chick phases in 1984. The no response category was the proportion of scans when no interacting species were present and all birds were quiet.

	Mean # of Responses/min	SD	No response	SD	# of scans
Egg phase	.043	.022	93%	6%	771
Chick phase	.045	.018	94%	4%	1215

after week 2 of incubation, terns would fly up, call and dive at intruders. During the total hours of observation most scans resulted in no observed responses. Mobbing reactions became more frequent starting on approximately 8 June, at which time a number of clutches were completed. Most corvids were present in the morning between 0500-1300 hr. After 1730 hr, responses to intruders and their presence in the areas declined. The minimal distance that corvids were allowed to approach nests during the egg phase was about 100 m. Once hatching occurred, the response rate to corvids decreased. At this time, the terns would only mob corvids if they were within 20 m of their nest. As soon as chicks were present in the nest the reactions to Great Blue Herons increased.

Experiments with the models of various predatory species showed that Black Terns reacted similarly during the egg and chick phases. All models, except those of American Coot, elicited mobbing by the terns. The lack of response to the coot may have been because the model was stationary and normally coots bob up and down while swimming. The distances at which the models were presented varied from 5-30 m. There was no difference the in response to different models. Birds reacted by calling over the model and diving at it. In one instance, the cover was partially blown off the raven model before presentation. Although only the tail of the raven was visible the terns reacted to it.

DISCUSSION

Predation rates during the egg stage in this study were lower than in other published studies (Bailey 1977; Dunn 1979). Egg losses in this study and Bailey's (1977) study were comparable. Dunn (1979) found most predation during the egg stage. Past researchers have often used large poles or stakes to mark nests (Bergman et al. 1970; Dunn 1979). This form of marking, however, may attract visually oriented predators (Picozzi 1975). The lower predation rates in this study thus could be the result of the more conservative marking scheme of nests. Additionally, nest searches and visitations were made during hours when visually oriented predators, especially corvids, were least abundant. Egg losses due to predation in this study were rarely determined to be caused by corvids. During 1986, one Black Tern nest was attacked by a Common Raven (Chapman Mosher personal observation). Muskrats were responsible for 22% of all predation losses, because they pushed eggs from nests when they climbed on the platform. This disturbance was also noted by Siglin and Weller (1963). Another explanation for lower predation rates could be that fewer potential predators were present in this study area compared to other published studies, but no data were available from other studies.

Predation rates during the chick stage were much lower in this study (3.8%) than in Bailey's (1977) study (61.5%). Bailey attributed high predation rates to the presence of a large number of predators and the restraining pens used to keep young at nests. Dunn (1979) also reported that some chicks in enclosures were killed by mink. Some chicks within enclosures in this study were attacked, but the enclosures did not seem to increase the probability of a nest being predated, as only 4 nests out of 130 which were enclosed lost their young due to predation. Dead chicks from unenclosed nests were sometimes found with obvious signs of predation. As well, unenclosed chicks were observed being taken by Great Blue Herons (Chapman and Forbes 1984). Observations conducted prior to nesting in Leach Lake showed that a number of Great Blue Herons were present in the area early in the season. This fact, plus the lack of abundant vegetation may have caused the abandonment of the area. One reason for the low predation rates of chicks in this study may arise from the habitat used. Researchers have noted the importance of shelters or predator exclosures for the survival of chicks (Jenks-Jay 1982; Nol and Brooks 1982). The vegetation in most areas where this study was conducted was too dense to push a canoe through without damaging nests. In contrast, most work in other studies was done from a canoe (Bergman et al. 1970; Bailey 1977; Dunn 1979). The greater density of the vegetation may have provided the chicks with better camouflage from aerial predators.

Lemmetyinen (1971) showed that solitary breeders were just as capable of defending their broods as colonial nesting birds. Black Terns showed similar success rates whether they nested in loose colonies of 4 to 5 pairs or in more solitary situations. Since predation pressure on Black Terns was relatively low, one would expect nesting success to be similar whether nesting solitarily or colonially. Coloniality is therefore probably not as important for this species, as it can be for others.

Mobbing behaviour can be very effective at deterring predation (Siglin and Weller 1963; Morse 1980). Terns are known for the effectiveness of their social mobbing behavior because of the velocity of their dives which are accompanied by piercing cries (Siglin and Weller 1963). Mobbing behavior increased as more birds were sitting on eggs and again as chicks approached fledging. Nesting in mixed species colonies can be beneficial when less aggressive species nest among more aggressive species

(Goransson *et al.* 1975; Buckley and Buckley 1979). As well, some colonial ground nesters are able to benefit from nesting in association with colonial shrub nesters, because of the increased awareness at different levels to approaching predators (McNicholl 1981). These associations can lead to greater mobbing potential, because of the increased number of individuals present in the area. Mobbing groups sometimes consisted of only Black Terns and at other times they were joined by Forster's Terns, Red-winged and Yellow-headed Blackbirds, a phenomenon noted by others (McNicholl 1981). The reaction to human and non-human intruders or ground predators tends to differ among species (Pienkowski 1984). Species generally react to human intruders at greater distances and with slightly different reactions than to natural predators. Human disturbance can sometimes result in increased predation losses (Hammond and Forward 1956). Quinn (1984) covered some of the nests in Caspian Tern colonies during human disturbance and found that fewer eggs were lost to predators. Black Terns react to human intruders by circling their nests, a trait not usually seen when other natural intruders were present. Since the birds are inadvertently pointing out their nests, it is important that human disturbance be minimized so that natural predators do not learn the exact location of nest sites. McNicholl (1973) noted that Forster's Terns habituate to predators which nested near or in the colonies. Habituation to natural predators or people near a nest was not noticed in this population of Black Terns.

The interaction observations showed that the intensity of responses remained similar throughout the season (Table 19). The presence of interacting species did not differ over time as well, hence these species did not provide a strong influence on Black Terns to time their breeding season more narrowly. Watanuki (1983) found that Black-tailed Gulls (Larus crassirostris) respond differently to predators during the egg and chick phase. The type of response and its frequency did not differ between the two phases in Black Terns (Table 19), but the response to different species did. Fifty-two percent of the reactions of Black Terns to corvids were during the egg phase, while 48% were during the chick phase. Great Blue Herons were reacted to the most during the chick phase (93%). Since predators were seen only in 6% of all scans (Table 19), predation was probably not an important factor. It may be possible that the number and type of predators in Creston could vary between different units of the marsh. However, there appeared to be no such differences. When the Creston marsh was compared with Elizabeth Lake there were differences. Elizabeth Lake had few potentially predatory species. Corvids were rarely seen there. In 17 hrs of observation at Elizabeth Lake, 510 scans were made and only 12 scans resulted in a corvid present in the area. The terns only reacted during 3 of these 12 scans with corvids present. At Elizabeth Lake only 10-15 American Coots were present. Absent from this area were Great Blue Herons and Western Painted Turtles. The only interacting species commonly seen at Elizabeth Lake was the muskrat. Elizabeth Lake had very high hatching success (Chapter 3), which probably partially reflects a negligable amount of predation.

Tests with the models of potentially predatory species showed that only the American Coot model elicited no response. Although no losses from nests were ever directly linked to American Coot activity, the potential existed for these birds to cause losses. Black Terns showed a strong mobbing reaction to American Coots when they were as far as 40 m from a tern nest. Attacks usually involved at least two terns with 5-6 birds often observed, which is in contrast to results reported by McNicholl (1975b). Coots often climb onto platforms to get out of the water. Although tern nests tend to be low and wet, they still act as a platform out of the water. Problems may arise when the platform a coot climbs onto contains a tern nest. This is probably the reason for the strong mobbing behavior shown against coots. Siglin and Weller (1963) noted that turtles could cause similar problems. Although turtles were present in the Creston marshes, the terns were never observed to react to them.

In summary, predation rates on young and eggs of Black Terns were relatively low compared to other studies on this species. This may partially reflect the care given to causing as little disturbance to colonies and their habitat as possible. For this reason, visually oriented predators were less able to detect any sign. Since reproductive success was similar between birds nesting in loose colonies and those nesting more solitarily, and predation rates were low, there is no inherent reason why the birds should be more colonial. The presence of potentially predatory species did not differ throughout the season, so there was no evidence that the terns needed to time their breeding season over a shorter time span to avoid peak predator occurrences or to swamp predators.

IX. GENERAL DISCUSSION AND A FEW MANAGEMENT CONSIDERATIONS

REPRODUCTIVE SUCCESS

Black Tern reproductive success in Creston, B. C. was much higher than that found in other studies (Bergman *et al.* 1970; Bailey 1977; Dunn 1979). One factor influencing Black Tern reproductive success was weather (Figure 14). Rainfall and temperature patterns varied from year to year. Water level fluctuation data (Chapter 7) showed that the magnitude of water level changes decreased throughout the years of the study. Black Terns had lowered nesting success (Table 1) in years of high precipitation due to eggs washing out of nests. As well, fledging success was affected by rising water levels because it resulted in a loss of dry areas for chicks to sleep. Black Terns also were less successful during colder years. This could be due to lower food availability caused by a reduction in emergence rates of odonates during colder periods (Orians 1980), and chilling of the chicks.

Birds nesting in various areas of the marsh differed somewhat in terms of reproductive success (Table 2). The various marsh areas contained diverse habitat types as well as different vegetation densities within those habitats. These may be the likely factors which influenced the differences in

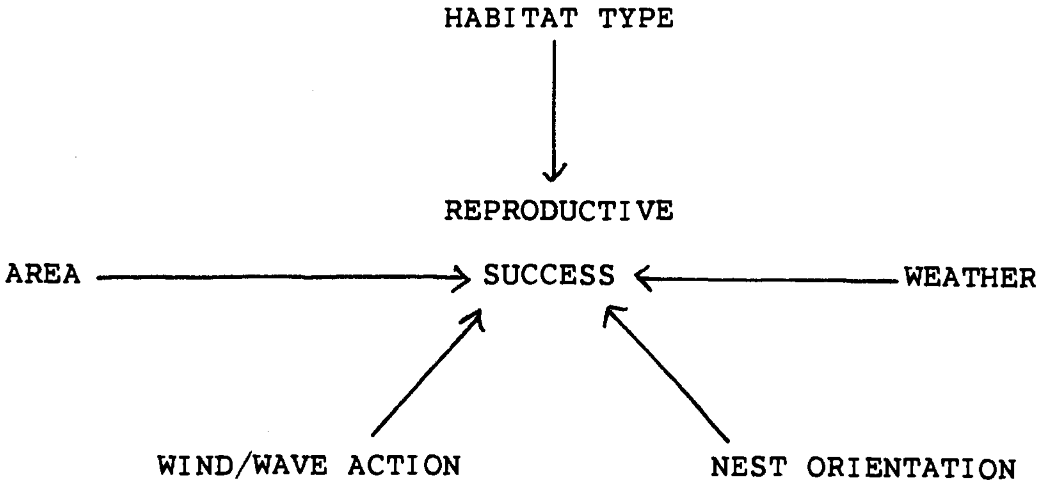

Figure 14. The influence of various factors on the reproductive success of Black Terns in Creston, B.C.

reproductive success between geographical location in the marsh. The highest hatching success was observed in Leach Lake, an isolated area dominated by <u>Phalaris</u>. Fledging success was significantly greater in Corn Creek. This area contained very dense vegetation which provided cover for chicks to hide in. There was a slight difference in success in Corn Creek during the 2 years that it was used by the terns. During 1981, there were two subareas within Corn Creek which were approximately 400 m apart. These two areas varied by 3-4 weeks in nesting chronology, although within each subarea, nests exibited close synchrony. During 1982, both subareas were occupied, but there was no synchrony within each area. That year showed lowered reproductive success when compared to 1981.

The most important factor influencing Black Tern hatching success was wind and wave action (Table 3). This factor was responsible for egg losses as high as 27%. The detrimental effect of wind storms on Black Terns was similar to that found for other marsh-nesting species, regardless of the nesting substrate (McNicholl 1979). Bergman _et al._ (1970) suggested that vegetation surrounding nests of Black Terns could reduce the effect of wind and wave action. The wind and wave action experiment (Chapter 7), showed that wind and wave action had less influence on nests that were protected by vegetation on the windward side. This experiment further illustrated that nests in _Phalaris_ habitats had the least number of wash outs resulting from wind and wave action. Work conducted at Elizabeth Lake showed that when birds nested in some vegetation types (i.e. _Scirpus_), they readily nested on floating boards of any size and shape which were present in the marsh. Birds nesting on these platforms had 100% hatching success.

Fledging success of Black Terns was quite low and differed little among areas and years. Of the 70% of eggs that survived to hatch, only approximately 60% resulted in fledged chicks. The proportion of chicks lost to predation averaged 3.8% over the years of the study (Table 17). Other researchers found predation to cause higher losses (Bailey 1977; Dunn 1979). Predation alone could not be responsible for the large observed reduction in fledging success. The third chick within a brood rarely fledged.

This fact alone reduced fledging success by 33%. Data on growth measurements (Chapter 6) showed that the largest chicks (the first ones to hatch) usually grew faster than second and third chicks of the same age. The last chick that hatched was the first chick to suffer when food abundance decreased. When food abundance decreased, the adults seemed unable to feed all the young and the smallest one was selectively starved. If food abundance decreased further, it was not uncommon for the second chick to die a few days later.

COLONIALITY

Habitat availability (Chapter 4) did not seem to exibit any selection pressure to favor Black Terns to nest more colonially (Figure 15). Lack (1968) suggested that some birds nest in colonies because of space limitation in suitable areas. If the habitat where the terns nested was quite variable, large enough areas may not be available to allow the birds to nest close together. Variability in habitat measurements (Chapter 4) in the areas where the birds nested was quite low, indicating that these areas were probably capable of supporting denser colonies than was observed.

Species which breed in freshwater marshes often feed on food items which only occur within the marsh (Lack 1968). For Black Terns this was definitely the case. The terns were completely dependent on the marsh for nesting and feeding sites.

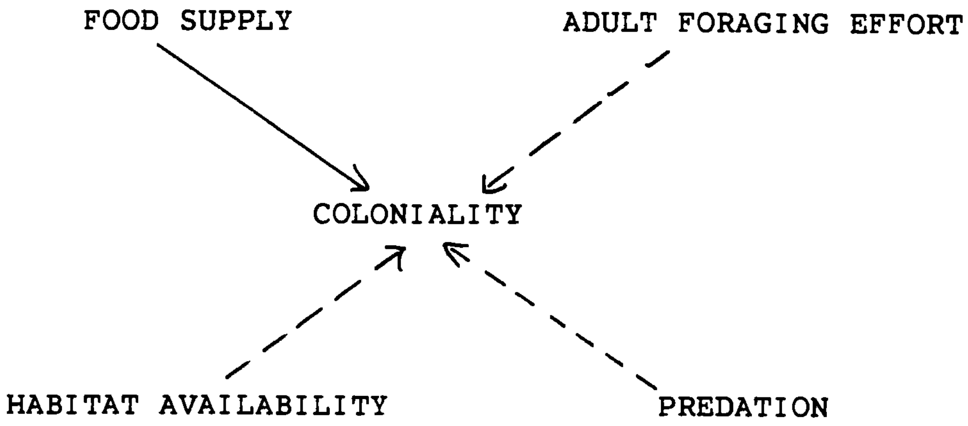

Figure 15. The influence of various factors on coloniality in Black Terns in Creston, B.C. Broken lines indicate that no selection pressure was found in the factor to favor coloniality.

The availability of emergent insects was shown to be variable in space and time. Fish populations are well documented as being patchy and unpredictable in distribution (Hunt and Hunt 1976a). Colonial breeding can be a response to abundant and unpredictable food resources (Hunt and Hunt 1976a). The information center hypothesis states that breeding in colonies serves an important function for food finding in species which rely on unpredictable food items (Ward and Zahavi 1973). Since the prey items which Black Terns rely on are so unpredictable one would expect them to nest more colonially than they in fact did. Although the marsh area in Creston consisted of 6800 ha, the areas of open water were relatively limited and they were easy to find. The Black Terns congregated in these open areas when they first arrived on the breeding ground. Since the locations of these open water areas were probably known and their size was relatively small, the need to nest in tight colonies to obtain this information was probably not needed.

One result of nesting colonially is that birds must fly further to obtain food (Lack 1968). For Black Terns this may pose a problem since they are single prey-loaders. By examining adult foraging effort, it was determined that birds which nested greater than 0.75 km away from open water did not have a lower fledging success than birds which nested closer to open water. For this reason, travel costs alone are probably not a limiting factor. Growth measurements of young Black Terns did show that some young, usually the youngest in the nest, were the first to die within the brood. When these smaller young died, there was usually strong evidence to suggest that they had starved. Since young Black Terns seemed to be food-limited, were fed mainly odonates, and the adults feeding them were single prey-loaders, the food items should be obtained as close to the nest as possible. For this reason, the terns are probably better off to nest more solitarily so that more locally available food can be used, instead of having to make more long distance trips. In some species of birds, one adult often stays with the young and broods them while the other is off feeding. For Black Terns, this was rarely the case. Both adults usually spent most of the daylight hours flying back and forth between nest site and foraging areas. This further emphasizes why Black Terns should nest more solitarily to cut down on travel time.

Predation was found to be responsible for some losses in reproductive success (Table 18), although the proportion was relatively low (8.6%). By nesting in colonies, more birds were available to mob potential predators and drive them from the area. Black Terns were shown to be quite effective at mobbing potentially predatory species, even when nesting solitarily. They also benefitted from joint mobbing with other species. If coloniality were important in deterring predators, colonial nesting birds should have fewer losses to predation than more solitary nesting birds. This study showed that Black Terns nesting in loose colonies and those nesting more solitarily experienced the same frequency of predation. Since predation rate was similar, there is probably no selection pressure to favor dense coloniality due to the intensity of predation.

TIMING OF BREEDING

The availability of suitable habitat could be important to the timing of breeding of Black Terns in terms of vegetation density in the nesting areas (Figure 16). Generally the nesting areas were suitable by the time the terns returned to the breeding area. Some differences in the density of vegetation were noted between the May and August samplings (Table 4). One thing which must be remembered is that the May sampling was done

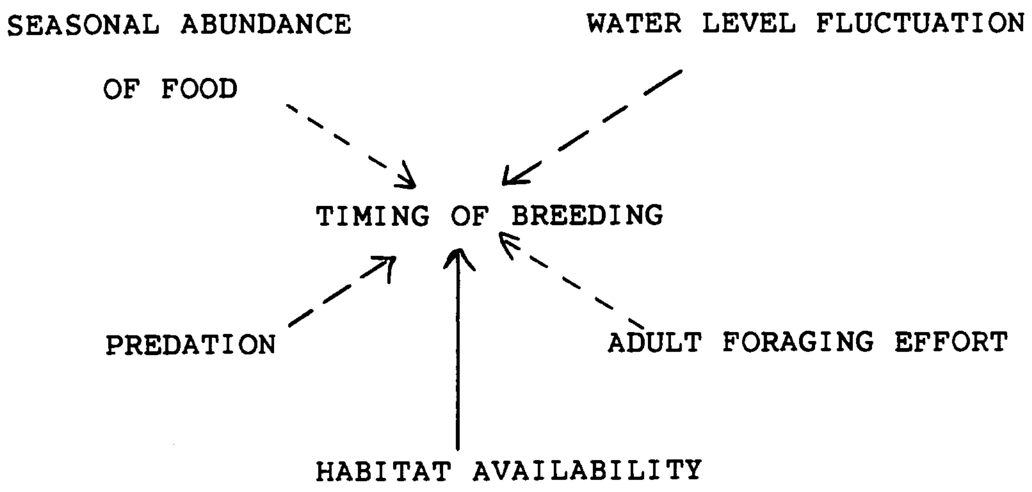

Figure 16. The influence of various factors on the timing of breeding in Black Terns, in Creston, B.C. Broken lines indicate that no selection pressure was found in the factor to favor a narrow timing of breeding.

just prior to the return of the birds to their breeding sites. The growth of emergent vegetation was greatest during the first two weeks of May. After the third week of May, when most terns returned to their nesting areas, the density of vegetation remained relatively stable for the rest of the season. The only factors which changed were plant height and the area which the plant occupied at the water surface. Area occupied by stalks at the water surface (Table 6) would be important in blocking waves and thereby improving reproductive success. The terns may have to delay their breeding if the density or area occupied by vegetation is not sufficient, resulting in a delay of breeding, therefore narrowing the timing of breeding. Dwernychuk and Boag (1972) found that vegetation cover was important for breeding waterfowl. Plant height tended to be more important to the chicks of Black Terns. The plant height and/or vegetation density could provide important cover for the chicks.

All aspects of the examination of seasonal abundance of the food supply showed no reason why there should be a selection pressure to favor breeding during a narrow time period. Many researchers have suggested that birds time their breeding with a peak in food supply (Lack 1968; Emlen and Demong 1975; Pienkowski 1984). Orians (1980) showed that the emergence of odonates varied in time and space within a season. This study showed that not only did they vary in abundance within a season, but the peak in abundance varied from year to year. One major reason for this variation was the fact that odonate emergence varies with weather conditions (Orians 1980). Since odonates were the major food items fed to the young, and since they were highly variable from year to year, there is probably no selection pressure for the birds to time their breeding within a short time span.

The only aspects of adult foraging effort which might influence the timing of breeding were the food items fed on at different times throughout the breeding season, and where those items came from. This study showed that the food items brought to young did not differ throughout the breeding season. The only slight difference was that fish were usually not fed to young until they were about 5 days old. This occurred in all young raised at different times during the season. As well, adults travelled the same distances to feed at all times throughout the summer months. For these reasons, adult foraging effort probably has little effect on influencing the timing of breeding.

Fluctuating water levels can have a wide array of effects on breeding waterbirds (Johnsgard 1956; Kadlec 1962; Anderson 1967). The fluctuations in water level tended to be most variable early in the season when eggs were in the nest. In some instances the fluctuations were due to precipitation. Inclement weather early in the season has been shown by some to favor breeding later in the season (Hunt and Hunt 1976b). Since water level fluctuations tended to decrease later in the season, there may be some selection pressure to favor a later start of breeding. Single storms, occurring throughout a breeding season, can cause much damage (McNicholl 1979). For this reason, birds which nest in marsh systems must face fluctuating water levels and deal with the problem as best they can (McNicholl 1985).

Predation was found to have no effect on the timing of breeding. The predation pressure in this study was relatively low. Predator abundance did not differ throughout the entire breeding season. The response to different predators, however, did change when the birds were sitting on eggs and feeding young. Corvids elicited an equal number of reactions during both the egg and chick phases and Great Blue Herons caused the most reactions during the chick phase.

In conclusion, coloniality and the timing of breeding in Black Terns cannot be explained by those factors which are usually invoked for other species. The terns nest in loose colonies, but there was no strong selection pressure found to favor the birds which nest more densely. Predation pressure was relatively low (8.6%) compared to other causes of reproductive loss in Black Terns. However, by nesting in loose colonies, the birds are better able to mob potential predators in a group of 5 or 6 birds, than a single pair can. Hence, some degree of nesting association is advantageous. Feeding on prey items which are unpredictable in distribution tend to favor colonial nesting. Nesting in colonies results in adults having to fly further distances to obtain food. For Black Terns, this may result in fewer young being produced. When Black Terns nest in loose colonies instead of a tight colony, adults may be able to obtain more food items near the nest. This would reduce the travel costs for feeding young, and result in more young produced during good weather years. No selection pressure was found that would favor Black Terns to narrowly time their breeding season. The main factors which influence timing of the breeding season are seasonal abundance of the food supply and water level fluctuations. Both of these factors are highly unpredictable and therefore provide no selective force to narrowly time the breeding season.

A FEW MANAGEMENT CONSIDERATIONS

Tilghman (1980) suggested that Black Tern populations across North America were declining and Arbib (1978) had previously expressed concern on their status. As was shown in Chapter 3, very little is actually known about the complete, continent-wide distribution of breeding Black Terns. If status maps, such as the one from B.C. (Fed. B. C. Nat. 1977), are any indication, more intense searching for breeding birds is probably needed. If this were done, perhaps the decline in numbers of Black Terns may not be as drastic as first anticipated, however populations in the eastern United States are still disappearing (Buckley pers. comm.).

One major area of concern in the reduction of Black Tern numbers is the loss of suitable marsh habitat. The natural succession of a marsh system results in the areas eventually becoming choked with vegetation and filling in (McNicholl 1985). Some management techniques for marshes have been developed. Most vegetation management consists of prescribed burning or plowing of areas. Both practices are used during the nonbreeding seasons. Plowing disrupts dead and living vegetation while burning eliminates only dead vegetation from the previous year. For many species of birds dead vegetation can provide important support for nests (Bray 1984). Black Terns benefit somewhat from dead _Typha_ stalks because they help to block waves. For these reasons, it is thought that the use of some management techniques may have a negative effect on breeding birds. If vegetation is much too dense, however, any technique which can reverse the process of succession would be most valuable. Often marsh habitats are developed for human use. Because these habitats are so unique for many animals it is important that they be preserved for all marsh nesting species.

Black Terns prefer to nest in areas where there is 25% standing vegetation, 42% matted vegetation and 33% open water. Twenty-five percent vegetation was important as a block to waves. As well, the vegetation provides suitable cover for chicks to hide in. The area occupied by these stalks of vegetation was 10-50 cm^2/m^2 at the water surface. Black Terns had the greatest hatching success when they nested in *Phalaris*. The probable reasons for this increased success was that this habitat type served as a more effective block to waves, thereby preventing eggs from washing out of nests. Unfortunately, *Phalaris* tends to suffer under constant flooding conditions. Perhaps some other type of vegetation of similar characteristics could be found to use in managed marsh systems. The 42% matted vegetation is important because it forms the mats on which Black Terns place their nests. Many other marsh nesting species such as waterfowl, American Bitterns and grebes also nest on the water. Standing and matted vegetation proportions suitable for Black Terns would also aid these other marsh nesters. Thirty-three percent of open water is also important in nesting areas as it allows the terns access to the water so they can reach their nest sites. Open water also allows them local foraging sites which they can utilize to cut down on long distance trips.

One strong factor influencing reproductive success was water level fluctuations. It is important to keep water at a fixed level over the breeding season so that nests do not wash out. In areas where water level cannot be maintained, hatching success can be improved by providing the birds with boards to nest on. Black Terns will readily nest on boards and the boards can rise and fall with water level changes. Other marsh nesting species such as grebes, will also use platforms to nest on (Ohanjanian pers. comm.).

Marsh systems can be maintained through time if the proper management techniques are applied. As well, careful consideration should be given before further marsh habitat is destroyed. These areas are important for hunted and nonhunted avian species. Proper management based on the findings of this and other studies can aid in saving crucial marsh habitat as well as Black Terns.

LITERATURE CITED

Anderson, D.R. 1967. Effects of water manipulation on waterfowl production and habitat. M.Sc. Thesis, Colorado State University, Fort Collins. 60pp.

Angles, R. 1957. A feeding method of Black Tern. Brit. Birds 50:538.

Arbib, R. 1978. The blue list for 1979. Am. Birds 32:1107-1113.

Ashkenazie, S. and U.N. Safriel. 1979. Time-energy budget of the Semipalmated Sandpiper _Calidris_ _pusilla_ at Barrow, Alaska. Ecol. 60:783-799.

Ashmole, N. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103:458-473.

Baggerman, B., Baerends, G.P., Heikens, H.S. and J.H. Mook. 1956. Observations on the behavior of the Black Tern _Chlidonias_ _niger_ _niger_ (L.), in the breeding area. Ardea 44:1-71.

Bailey, P. F. 1977. The breeding biology of the Black Tern (_Chlidonias_ _niger_ _surinamensis_ Gmelin). M. Sc. Thesis, University of Wisconsin, Oshkosk. 67pp.

Bent, A.C. 1963. Life Histories of North American Gulls and Terns. Dover Publications Inc., New York.

Bergman, G. 1980. Single-breeding versus colonial breeding in the Caspian Tern _Hydroprogne_ _caspia_, the Common Tern _Sterna_ _hirundo_ and the Arctic Tern _Sterna_ _paradisaea_. Ornis Fenn. 57:141-152.

Bergman, R.D., Swain, P. and M.W. Weller. 1970. A comparative study of nesting Forster's and Black Terns. Wilson Bull. 82:435-444.

Bochenski, Z. 1966. Nesting of Common and Black Terns. Acta. Zool. Cracov. 11:423-449.

Bourn, W.S. 1939. The effect of lowering water levels on marsh wildlife. Trans. 4th N. Amer. Wild. Conf.

Bray, M. P. 1984. An evaluation of heron and egret marsh nesting habitat and possible effects of burning. Murrelet 65:57-59.

Brewer, A. D. 1969. Black Terns feeding after ploughs. Brit. Birds 62:282.

British Museum (Natural History). 1974. Instructions for collectors: Insects. Trustees of the British Museum (Natural History), London.

Buckley F. G. and P. A. Buckley. 1974. Comparative feeding ecology of wintering adult and juvenile Royal Terns (Aves: Laridae, Sterninae). Ecol. 55:1053-1063.

Buckley, F. G. and P. A. Buckley. 1979. Do Aleutian Terns exibit extraordinary anti-predator adaptations? Proc. Colonial Waterbird Group 3:99-107.

Bundy, G. 1971. Black Terns feeding over dry land. Brit. Birds 64:32.

Burger, J. 1974. Breeding adaptations of Franklin's Gull (Larus pipixcan) to a marsh habitat. Anim. Behav. 22:521-567.

Burger, J. 1982. The role of reproductive success in colony-site selection and abandonment in Black Skimmers (Rynchops niger). Auk 99:109-115.

Burger, J. and F. Lesser. 1979. Breeding behavior and success in salt marsh Common Tern colonies. Bird-Banding 50:322-337.

Chapman, B. 1980. The comparative winter foraging ecology of gulls on southeastern Lake Erie. M. Sc. Thesis, State University of New York, Fredonia. 117pp.

Chapman, B. and L. S. Forbes. 1984. Detrimental affects of Great Blue Herons on breeding Black Terns. J. Field Ornithol. 55:271-272.

Chapman, B. and J.W. Parker. 1985. Foraging areas, techniques and schedules of wintering gulls on southeastern Lake Erie. Colonial Waterbirds 8:135-141.

Clarke, A. and P.A. Prince. 1980. Chemical composition and calorific value of food fed to Mollymauk chicks Diomedea melanophris and D. chrysostoma at Bird Island, South Georgia. Ibis 122:488-494.

Cody, M. L. 1981. Habitat selection in birds: The roles of vegetation structure, competitors and productivity. Bioscience 31:107-113.

Cook, P.P. Jr. and H.S. Horn. 1968. A sturdy trap for sampling emergent Odonata. Ann. Entom. Soc. Amer. 61:1506-1507.

Corbet, P.S. 1962. A Biology of Dragonflies. H.F. and G. Witherby, London.

Corbet, P.S. 1980. Biology of the Odonata. Ann. Rev. Entomol. 25:189-217.

Cowan, W. 1975. Impact on waterfowl breeding success of flooding in Pineimeta Lake due to regulation of water levels in Lake

Manitoba, including suggestions for management. Can. Wild. Serv. Report, Edmonton.

Crawford, D.N. 1977. Notes of the feeding of two Chlidonias terns. Emu 77: 146-147.

Cuthbert, N.L. 1954. A nesting study of the Black Tern in Michigan. Auk 71:36-63.

Dunn, E.H. 1975. Caloric intake of nestling Double-crested Cormorants. Auk 92:553-565.

Dunn, E.H. 1976. The development of endothermy and existence energy expenditure in Herring Gull chicks. Condor 78:493-498.

Dunn, E.H. 1979. Nesting biology and development of young in Ontario Black Terns. Can. Field-Nat. 93:276-281.

Dunn, E.H. 1980. On the variability in energy allocation of nestling birds. Auk 97:19-27.

Dwernychuk, L. W. and D. A. Boag. 1972. How vegetative cover protects duck nests from egg-eating birds. J. Wildl. Mgmt. 36:955-958.

Emlen, J.M. 1966. The role of time and energy in food preference. Amer. Nat. 100:611-617.

Emlen, S.T. and N. J. Demong 1975. Adaptive significance of synchronized breeding in a colonial bird: A new hypothesis. Science 118:1029-1031.

Environment Canada. 1981. Annual Meteorological Summary 1981. Vancouver, British Columbia.

Environment Canada. 1982. Annual Meteorological Summary 1982.

Vancouver, British Columbia.

Environment Canada. 1983. Annual Meteorological Summary 1983. Vancouver, British Columbia.

Erwin, R. M. 1978. Coloniality in terns: The role of social feeding. Condor 80:211-215.

Evans, R. M. 1982. Colony desertion and reproductive synchrony of Black-billed Gulls *Larus bulleri*. Ibis 124:491-501.

Faanes, C. 1978. Status of Black Terns in western Wisconsin. Pass. Pigeon 41:124-129.

Federation of British Columbia Naturalists. 1977. Newsletter 15:3.

Findlay, C. S. and F. Cooke. 1982. Synchrony in the Lesser Snow Goose (*Anser caerulescens caerulescens*). II The adaptive value of reproductive synchrony. Evolution 36:786-799.

Forbes, L. S. 1985. The feeding ecology of Western Grebes breeding at Duck Lake, British Columbia. M. Sc. Thesis, University of Manitoba, Winnipeg. 72pp.

Godfrey, W.E. 1966. The Birds of Canada. Montreal Lithographing Limited, Ottawa.

Goethe, F. 1970. Black Terns feeding after ploughs. Brit. Birds 63:34.

Goodwin, R. E. 1960. A study of the ethology of the Black Tern, *Chlidonias niger surinamensis*. Ph.D. Thesis, Cornell University, Ithaca, NY. 193pp.

Goransson, G., J. Karlsson, S. G. Nilsson, and S. Ulfstrand. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: an experimental study. Oikos 26:117-120.

Hammond, M. C. and W. R. Forward. 1956. Experiments on causes of duck nest predation. J. Wildl. Mgmt. 20:243-247.

Hammond, R. and P. McCullagh. 1978. Techniques in Geography. Clarendon Press, Oxford.

Haverschmidt, F. 1978. Die Trauerseeschwalbe. Die Neue Brehm-Bucherei 508, A. Ziemsen Verlag, Wittenberg Lutherstadt.

Higer, A. L. and M. C. Kolipinski. 1967. Pull-up trap: A quantitative device for sampling shallow-water animals. Ecol. 48:1008-1009.

Hitchcock, C. L. and A. Cronquist. 1976. Flora of the Pacific Northwest. University of Washington Press, Seattle, Wash.

Hoffman, P.W. 1926. Nesting of the Black Tern in Wisconsin. Auk 43:86-87.

Hogstad, O. 1981. Is nest predation really selecting for colonial breeding among Fieldfares _Turdus_ _pilaris_? Ibis 125:366-369.

Holmes, R.T., Black, C.P. and T.W. Sherry. 1979. Comparative population energetics of three insectivorous passerines in a deciduous forest. Condor 81:9-20.

Horn, H.S. 1968. The adaptive significance of colonial nesting in Brewer's Blackbird (_Euphagus_ _cyanocephalus_). Ecol. 49:682-694.

Hudec, K. 1979. Effects of varying water levels on nests of waterfowl. Folia Zool. 28:269-282.

Hunt, G. L. Jr. and M. W. Hunt. 1976a. Exploitation of fluctuating food resources by Western Gulls. Auk 93:301-307.

Hunt, G.L. Jr. and M.W. Hunt. 1976b. Gull chick survival: The significance of growth rates, timing of breeding and territory size. Ecol. 57:62-75.

Jenks-Jay, N. 1982. Chick shelters decrease avian predation in Least Tern colonies on Nantucket Island, Massachusetts. J. Field Ornithol. 53:58-60.

Johnsgard, P.A. 1956. Effects of water level fluctuation and vegetation change on bird populations, particularly waterfowl. Ecol. 37:689-701.

Johnson, C. G. 1950. The comparison of suction trap, sticky trap and tow net for the quantitative sampling of small airborne insects. Ann. Appl. Biol. 37:268-285.

Kadlec, J.A. 1962. Effects of a drawdown on a waterfowl impoundment. Ecol. 43:267-281.

Kahl, M. P., Jr. 1963. Technique for sampling population density of small shallow-water fish. Limnology and Oceanography 8:302-304.

King, J.R. 1974. Seasonal allocation of time and energy resources in birds. Pp.1-85 in Avian energetics (R.A. Paynter, Ed.), Publ. Nuttal Ornithological Club No. 15.

Kruuk, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull. Behaviour Suppl. XI.

Kushlan, J. A. 1974. Quantitative sampling of fish populations in shallow, freshwater environments. Trans. Am. Fish. Soc. 103:348-352.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen Press, London.

Lemmetyinen, R. 1971. Nest defense behaviour of Common and Arctic Terns and its effect on the success achieved by predators. Ornis Fenn. 48:13-24.

McNicholl, M. K. 1973. Habituation of aggressive responses to avian predators by terns. Auk 90:902-904.

McNicholl, M. K. 1975a. Larid site tenacity and group adherence in relation to habitat. Auk 92:98-104.

McNicholl, M. K. 1975b. Interactions between Forster's Terns and American Coots. Wilson Bull. 87:109-110.

McNicholl, M. K. 1979. Destruction to nesting birds on a marsh bay by a single storm. Prairie Nat. 11:60-62.

McNicholl, M. K. 1981. Interactions between Forster's Terns and Yellow-headed Blackbirds. Colonial Waterbirds 4:150-154.

McNicholl, M.K. 1985. Avian wetland habitat functions affected by water level fluctuations. Chapter 6 in Coastal Wetlands. (H.H. Prince and F.M. D'Itri, Eds.), Lewis Publishers, Michigan State University, East Lansing, Michigan.

Mittlebach, G.G. 1981. Foraging efficiency and body size: A study of optimal diet and habitat use by bluegills. Ecol 62:1370-1386.

Morse, D. H. 1980. Habitat selection. in Behavorial Mechanisms in Ecology. Harvard University Press, Cambridge, Mass.

Munro, J. A. 1950. The birds and mammals of the Creston region, British Columbia. B. C. Prov. Mus. Occ. Paper No. 8.

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

Nisbet, I.C.T. 1975. Selective effects of predation in a tern colony. Condor 77:221-226.

Nisbet, I.C.T. 1978. Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate Terns (Sterna hirundo and S. dougallii). Ibis 120:207-215.

Nol, E. and R. J. Brooks. 1982. Effects of predator exclosures on nesting success of Killdeer. J. Field Ornithol. 53:263-268.

Orians, G.H. 1980. Some Adaptations of Marsh-nesting Blackbirds. Monographs in Population Biology No. 14. Princeton Univ. Press, Princeton, N.J.

Orians, G.H. and H.S. Horn. 1969. Overlap in foods and foraging of 4 species of blackbirds in the potholes of central Washington. Ecol. 50:930-938.

Perrins, C.M. 1965. Population fluctuations and clutch-size in the Great Tit Parus major L. J. Anim. Ecol. 34:601-647.

Perrins, C.M. 1966. Survival of young Manx Shearwaters Puffinus puffinus in relation to their presumed date of hatching. Ibis 108:132-135.

Perrins, C.M. 1970. The timing of bird's breeding seasons. Ibis 112:242-255.

Peterson, A. 1964. Entomological Techniques. Edwards Brothers, Inc., Ann Arbor, Michigan.

Picozzi, N. 1975. Crow predation on marked nests. J. Wildl. Mgmt. 39:151-155.

Pienkowski, M. W. 1984. Breeding biology and population dynamics of Ringed Plovers _Charadrius_ _hiaticula_ in Britain and Greenland: Nest-predation as a possible factor limiting distribution and timing of breeding. J. Zool. 202:83-114.

Quinn, J. S. 1984. Egg predation reduced by nest covers during researcher activities in a Caspian Tern colony. Colonial Waterbirds 7:149-151.

Richardson, F. 1967. Black Tern nest and egg moving experiments. Murrelet 48:52-56.

Ricklefs, R.E. 1974. Energetics of reproduction in birds. Pp. 152-292 _in_ Avian energetics (R.A. Paynter, Ed.). Publ. Nuttall Ornithol. Club No. 15.

Ricklefs, R.E. 1979. Patterns of growth in birds. V: A comparative study of development in the Starling, Common Tern and Japanese Quail. Auk 96:10-30.

Ricklefs, R.E. and S.C. White. 1981. Growth and energetics of chicks of the Sooty Tern (_Sterna_ _fuscata_) and the Common Tern (_S._ _hirundo_). Auk 98:361-378.

Robbins, C.S., Bruun,B. and H.S. Zim. 1966. Birds of North America. Golden Press, New York.

Schartz, R.L. and J.L. Zimmerman. 1971. The time and energy budget of the male Dickcissel. Condor 73:65-76.

Schememski, D.W. 1975. Time budget and foraging site preference of the Cinnamon Hummingbird in Costa Rica. Condor 77:216-217.

Severinghaus, L. L. 1982. Nest site selection by the Common Tern *Sterna hirundo* on Oneida Lake, New York. Colonial Waterbirds 5:11-18.

Siglin, R. J. and M. W. Weller. 1963. Comparative nest defense behavior of four species of marsh birds. Condor 65:432-437.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430-455.

Spendelow, J. A. 1982. An analysis of temporal variation in, and the effects of habitat modification on, the reproductive success of Roseate Terns. Colonial Waterbirds 5:19-31.

Thompson, B. C. and R. D. Slack. 1982. Physical aspects of colony selection by Least Terns on the Texas coast. Colonial Waterbirds 5:161-168.

Tiainen, J. 1978. Nestling growth in three *Phylloscopus* warblers in Finland. Ornis Fenn. 55:1-15.

Tilghman, N.G. 1980. The Black Tern survey, 1979. Pass. Pigeon 42:1-8.

Tinbergen, N., M. Impekoven, and D. Franck. 1967. An experiment on spacing-out as a defense against predation. Behaviour 28:307-321.

Turner, E. L. 1920. The Black Tern. Brit. Birds 14:122-126.

Utter, J.M. and E.A. LeFebvre. 1973. Daily energy expenditure of Purple Martins (*Progne subis*) during the breeding season:

Estimates using D2O and time budget methods. Ecol. 54:597-604.

Veen. J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern. Behaviour Suppl. XX.

Veen, J. 1980. Waarom broeden vogels in kolonies? Limosa 53:37-48.

Verbeek, N.A.M. 1964. A time and energy budget study of the Brewer Blackbird. Condor 66:70-74.

Verbeek, N.A.M. 1970. Breeding ecology of the Water Pipit. Auk 87:423-451.

Verbeek, N.A.M. 1972. Daily and annual time budgets of the Yellow-billed Magpie. Auk 89:567-582.

Verbeek, N. A. M. 1981. Nesting success and orientation of Water Pipit Anthus spinoletta nests. Ornis Scand. 12:37-39.

Ward, P. and A. Zahavi. 1973. The importance of certain assemblages of birds as "Information Centres" for food-finding. Ibis 115:517-534.

Watanuki, Y. 1983. Predation and anti-predation behaviour in seabirds on Teuri Island, Hokkaido. J. Yamashina Inst. Ornithol. 15:167-174.

Welty, J. 1975. The Life of Birds. 2nd Edition. W. B. Saunders Company, Philadelphia.

Werner, E.E., Gilliam, J.F., Hall, D.J. and G.G. Mittlebach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecol 64:1540-1548.

Wilkinson, G. S. and G. M. English-Loeb. 1982. Predation and coloniality in Cliff Swallows (*Petrochelidon pyrrhonota*). Auk 99:459-467.

Winnett-Murray, K. 1979. The influence of cover on offspring survival in Western Gulls. Proc. Colonial Waterbirds 3:33-43.