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NEST SUCCESS AND CHICK SURVIVAL OF BLACK TERNS IN MAINE: EFFECTS OF PREDATION ON BREEDING PRODUCTIVITY

By

Shane R. Heath

B.A. Dartmouth College, 2001

A THESIS

Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Science (in Wildlife Ecology)

The Graduate School

The University of Maine

August, 2004

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NEST SUCCESS AND CHICK SURVIVAL OF BLACK TERNS IN MAINE: EFFECTS OF PREDATION ON BREEDING PRODUCTIVITY

By Shane R. Heath

Thesis Advisor: Dr. Frederick A. Servello

An Abstract of the Thesis Presented in Partial Fulfillment of the Requirements for the Degree of Master of Science (in Wildlife Ecology) August, 2004

Nest predation is a prominent cause of reproductive failure in wetland-nesting birds, including black terns. As a result, predator avoidance should play an important role in nest site selection. I examined intraspecific variation in nest success to identify factors affecting nest predation of black tern colonies in central Maine. I measured variables related to proximity of wetland features and nest aggregation for 231 successful and 124 depredated black tern nests during the period 1998-2002. I defined candidate models based on logistic regression and selected models with Akaike's Information Criterion adjusted for small sample sizes (AIC_e) to determine the best model for predicting nest outcome (success vs. depredated). Variables related to proximity to depredated nests, including the number of depredated nests within 30 meters and the number of depredated nests between 30-100 meters, were the most important factors influencing nest predation of black terns in Maine colonies during 1998-2002. Losses to predation were localized, suggesting nest predators in Maine wetlands exhibit arearestricted search behavior. Factors related to colonial nest defense, nest concealment, and proximity to wetland features were found to have little effect on the likelihood of nest predation.

Nocturnal nest absence in Laridae has been correlated with increased nest predation, prolonged incubation periods, and lowered chick survival. I monitored 45 nests in 2001-2002 with temperature monitors to determine the occurrence and duration of nocturnal nest absence in black terns and the effect of absence on nest temperature and incubation length in Maine colonies. Nocturnal absences occurred at 33 of 45 black tern nests, suggesting this behavior is common. In 2001, 36 absences lasting 60 minutes or longer were recorded, whereas only nine absences exceeded 60 minutes in 2002. Nocturnal absences among adjacent nests were rarely synchronous. The mean temperature decrease for absences greater than or equal to sixty minutes was 9.62 °C. Nest absence did not appear to influence nest predation rates or incubation length, but the indirect effects of absence on breeding productivity of black terns merits future research.

Chick survival is an important parameter of black tern population growth, but few studies have identified factors contributing to chick mortality. I utilized predator exclosures to determine whether predation and/or food resources were limiting chick survival of black terns in Maine colonies in 2001-2002. I assumed if predation were limiting, chick survival should be 100% in broods excluded from predation. Nests were also monitored in unenclosed clusters of nests to confirm that chick survival was as low as previous years. I also measured chick growth by hatch-order during the period from hatch to near-fledgling as an indicator of potential food limitation. Chick survival in the absence of predation was 88.2% in 2001 and 88.9% in 2002. Survival of chicks at unenclosed nests was 10.4% in 2001 and between 39.4-61.3% in 2002. I did not see

evidence of differential chick growth with hatch-order, suggesting food limitations were not present in 2001-2002. My results suggest predation is the primary factor limiting chick survival in Maine colonies. Additionally, I describe the design of predator exclosures utilized in this study and report on their efficacy at excluding predators.

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My research was made possible by the efforts and contributions of many people. I would like to thank Cyndy Loftin, Bill Glanz, and Mark McCollough for valuable comments, edits, and advice over the course of the past two and a half years. Cyndy provided invaluable assistance while I was learning to use ArcMap and answered countless questions I had pertaining to GIS. I am forever indebted to Bill Halteman who contributed many office hours towards answering all my statistical inquiries and offered valuable advice on several aspects of my analyses. I always left Bill's office feeling much better than went I entered and for that I am grateful. I am thankful to Don McDougal, who graciously allowed the black tern project to use his cottage over multiple summers. Don's willingness to share his knowledge of black tern ecology and his support for my research was greatly appreciated. I am grateful to Bill Hanson for contributing time and resources towards my research. I would like to thank Dan Noble, Sarah Lemin, and David Pert for their hard work and positive contributions in the field, as well as their friendship. I would like to acknowledge Andrew Gilbert and Shannon Kearny, whose previous black tern research and field methodologies were integral to the success of my own work. Lauren Hierl kept my head on straight throughout the course of my graduate study and helped me overcome countless GIS-related barriers. I'd like to thank the Wildlife Ecology graduate students, faculty, and staff for all I learned during two years in Nutting Hall. Finally, I'd like offer countless thanks to Fred Servello for giving me an opportunity to work on this project and for all the time and positive energy he has contributed to my research.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS	ii
LIST OF TABLES	vi
LIST OF FIGURES	x
Chapter	
1. FACTORS AFFECTING NEST PREDATION OF BLACK TE	RNS
IN MAINE	1
INTRODUCTION	1
STUDY SITE	4
METHODS	5
Experimental Design and Procedures	5
GIS and Statistical Analyses	8
Water Level – Nest Site Selection	10
RESULTS	10
Nest Success	12
Water Level – Nest Site Selection	16
DISCUSSION	23
2. NOCTURNAL NEST ABSENCE IN BLACK TERNS	
INTRODUCTION	
STUDY SITE	
METHODS	29
RESULTS	
DISCUSSION	40

3.	EFFECTS OF PREDATION ON BLACK TERN CHICK SURVIVAL	44
	INTRODUCTION	44
	STUDY SITE	46
	METHODS	47
	Experimental Design	47
	Field Methods	48
	Statistical Analyses	49
	RESULTS	51
	DISCUSSION	54
4.	USE OF CHICK ENCLOSURES AND PREDATOR EXCLOSURES TO	
	INCREASE CHICK SURVIVAL IN BLACK TERNS	63
	INTRODUCTION	63
	STUDY SITE	64
	METHODS	65
	Experimental Design	65
	Enclosures	66
	Exclosures	67
	RESULTS	69
	DISCUSSION	74
	RECOMMENDATIONS FOR USE OF ENCLOSURES/EXCLOSURES	78
Lľ	TERATURE CITED	80
AF	PPENDICES	87

1	APPENDIX A: Basic Statistics of Wetland-Scale Variables, Nest	
1	Aggregation Variables, and Concealment Factor Variables Used to	
۲	Validate Top-performing Logistic Regression Models Predicting Nest	
S	Success or Nest Predation for Black Tern Nests in Maine Wetlands, 1998-	
2	2002	87
1	APPENDIX B: Tables Depicting Nocturnal Absence Parameters for	
]	Individual Nests at Maine Colonies, 1998-2002	90
1	APPENDIX C: Tables Depicting Linear Growth Rates, Logistic Growth	
]	Parameters, and Mean Square Tables for Chick Growth Analyses	93
1	APPENDIX D: Figures Depicting Nest Locations and Nest Outcomes by	
S	Study Site for Maine Colonies, 1998-2002	100
BIO	GRAPHY OF THE AUTHOR	131

LIST OF TABLES

Table 1.1.	Mean and standard error estimates for continuous variables
	used in logistic regression models predicting nest success or
	nest predation for black terns nests in Maine, 1998-200211
Table 1.2.	Mean and standard error estimates for continuous variables
	used in logistic regression models predicting nest success or
	nest predation for black tern nests in Maine, 2001-200213
Table 1.3.	Candidate models for prediction of black tern nest success and
	depredation evaluated with Akaike's Information Criterion for
	small samples (AIC _c) for 265 nests from six colonies in Maine,
	1998-200214
Table 1.4.	Parameter estimates derived from the best model and variable
	importance for variables used to predict nest success and
	depredation at six colonies in Maine, 1998-200215
Table 1.5.	Candidate models for prediction of black tern nest success and
	depredation evaluated with Akaike's Information Criterion for
	small samples (AIC _c) for 119 nests from six colonies in Maine,
	2001-200217
Table 1.6.	Parameter estimates derived from the best model and variable
	importance for variables used to predict nest success and
	depredation at six colonies in Maine, 2001-200219

Table 2.1.	Mean number of absences per night, mean absence length,			
	mean percentage of nights with an absence, and mean percen-			
	tage of time absent on nights monitored at black tern colonies			
	in Maine, 2001-2002 (n = 45)	33		
Table 2.2.	Absences recorded at black tern nests less than 200 m apart			
	during the period from 18:00 – 06:00 hrs at Douglas Pond in			
	2001	37		
Table 3.1.	Chick survival estimates for unenclosed nests and nests with			
	predator exclosures that were not depredated at Carlton Pond			
	and Douglas Pond, Maine, 2001-2002	53		
Table 3.2.	Linear growth rates of black tern chicks by hatch-order for three-			
	and two-chick broods at Carlton Pond, Douglas Pond, and			
	Messalonskee Lake, Maine, 2001-2002	55		
Table 3.3.	Asymptotic mass of black tern chicks by hatch-order for three-			
	chick broods at Carlton Pond, Douglas Pond, and Messalonskee			
	Lake, Maine, 2001-2002	56		
Table 4.1.	Mean number of days prior to hatch that enclosures and			
	exclosures were constructed around black tern nests in Maine,			
	1998-2002	70		
Table 4.2.	Nest success and egg hatchability for black tern nests with			
	chick enclosures in Maine, 1998-2001	71		

Table 4.3.	Nest success, egg hatchability, and chick survival of black tern	
	nests that had both chick enclosures and predator exclosures in	
	Maine, 2001-2002	73
Table A.1.	Mean and standard error estimates for continuous variables used	
	to validate top-performing logistic regression models predicting	
	nest success or nest predation for black tern nests in Maine, 1998-	
	2002	38
Table A.2.	Frequencies of binomial variables used to validate top-	
	performing logistic regression models predicting nest success or	
	nest predation for black tern nests in Maine, 1998-2002	39
Table B.1.	Nocturnal absence parameters for 25 black tern nests monitored	
	at Douglas Pond, Carlton Pond, Messalonskee Lake, and Great	
	Moose Lake in 2001)1
Table B.2.	Nocturnal absence parameters for 25 black tern nests monitored	
	at Douglas Pond, Carlton Pond, Messalonskee Lake, and Great	
	Moose Lake in 2002	92
Table C.1.	Linear growth rates of black tern chicks between ages 2-11 days	
	in predator exclosures at Maine colonies as determined by linear	
	regression, 2001-2002	94
Table C.2.	Logistic growth parameters of black tern chicks in predator	
	exclosures in Maine colonies, 2001-2002)5

Table C.3.	Mean square error table for the general linear model on the	
	effects of colony and hatchorder on linear growth rate of black	
	tern chicks in three-chick broods in Maine, 2001-2002	.97

LIST OF FIGURES

Figure 1.1.	Relative water level (cm) measured as gauge height at Carlton
	Pond, Maine, during the period from mid-May to early-August,
	1999-2001
Figure 1.2.	Mean distance of nests to the upland edge (bars) at a subcolony
	at Carlton Pond, Maine, in relation to wetland water level
	(diamonds) at the time of nest initiation for 16 nests in 1999,
	19 nests in 2000, and 9 nests in 2001
Figure 1.3.	GPS locations of black tern nests at Carlton Pond, Maine, in 1999
	(triangles), 2000 (circles), and 2001 (crosses) on aerial photos (a)
	and National Wetland Inventory (NWI) projections
Figure 2.1.	Duration of nest absences in minutes (log-scale) at Carlton Pond,
	Douglas Pond, and Messalonskee Lake in Maine, 2001-200234
Figure 2.2.	Number of black tern nest absences by time of departure at four
	colonies in Maine, 2001-2002
Figure 2.3.	Example of temperature probe plots showing a paired absence
	during the nocturnal period of June 19-20, 2001, at Douglas
	Pond
Figure 2.4.	Linear regression of absence duration (log-scale) and temperature
	change during nest absence for 2001-2002 ($n = 113$)
Figure D.1.	NWI image of Carlton Pond, Maine, depicting nest site locations
	in 1998101

Figure D.2.	NWI image of Carlton Pond, Maine, depicting nest site locations	
	in 1999	102
Figure D.3.	NWI image of Carlton Pond, Maine, depicting nest site locations	
	in 2000	103
Figure D.4.	NWI image of Carlton Pond, Maine, depicting nest site locations	
	in 2001	104
Figure D.5.	NWI image of Carlton Pond, Maine, depicting nest site locations	
	in 2002	105
Figure D.6.	NWI image of Douglas Pond, Maine, depicting nest site locations	
	in 1998	106
Figure D.7.	NWI image of Douglas Pond, Maine, depicting nest site locations	
	in 1999	107
Figure D.8.	NWI image of Douglas Pond, Maine, depicting nest site locations	
	in 2000	108
Figure D.9.	NWI image of Douglas Pond, Maine, depicting nest site locations	
	in 2001	109
Figure D.10	NWI image of Douglas Pond, Maine, depicting nest site locations	
	in 2002	110
Figure D.11.	NWI image of Great Moose Lake, Maine, depicting nest site	
	locations in 1998	111
Figure D.12.	NWI image of Great Moose Lake, Maine, depicting additional nest	
	site locations in 1998	112
Figure D.13.	NWI image of Great Moose Lake, Maine, depicting nest site	
	locations in 1999	113

Figure D.14.	NWI image of Great Moose Lake, Maine, depicting nest site	
	locations in 2000	114
Figure D.15.	NWI image of Great Moose Lake, Maine, depicting nest site	
	locations in 2001	115
Figure D.16.	NWI image of Great Moose Lake, Maine, depicting nest site	
	locations in 2002	116
Figure D.17.	NWI image of Madawaska Pond, Maine, depicting nest site	
	locations in 1998	117
Figure D.18.	NWI image of Madawaska Pond, Maine, depicting nest site	
	locations in 1999	118
Figure D.19.	NWI image of Madawaska Pond, Maine, depicting nest site	
	locations in 2000	119
Figure D.20.	NWI image of Madawaska Pond, Maine, depicting nest site	
	locations in 2002	120
Figure D.21.	NWI image of Messalonskee Lake, Maine, depicting nest site	
	locations in 1998	121
Figure D.22.	NWI image of Messalonskee Lake, Maine, depicting nest site	
	locations in 1999	122
Figure D.23.	NWI image of Messalonskee Lake, Maine, depicting nest site	
	locations in 2000	123
Figure D.24.	NWI image of Messalonskee Lake, Maine, depicting nest site	
	locations in 2001	124

Figure D.25.	NWI image of Messalonskee Lake, Maine, depicting nest site	
	locations in 2002	125
Figure D.26.	NWI image of Plymouth Pond, Maine, depicting nest site	
	locations in 1998	126
Figure D.27.	NWI image of Plymouth Pond, Maine, depicting nest site	
	locations in 1999	127
Figure D.28.	NWI image of Plymouth Pond, Maine, depicting nest site	
	locations in 2000	128
Figure D.29.	NWI image of Plymouth Pond, Maine, depicting nest site	
	locations in 2001	129
Figure D.30.	NWI image of Plymouth Pond, Maine, depicting nest site	
	locations in 2002	130

CHAPTER 1

FACTORS AFFECTING NEST PREDATION OF BLACK TERNS IN MAINE INTRODUCTION

Nest predation is a prominent cause of reproductive failure in wetland-nesting birds (Lariviere and Messier 1998, Johnson et al. 1989, Sovada et al. 2001), including black terns (Chlidonias niger)(Dunn 1979, Mazzocchi et al. 1997, Servello 2000). As a result, predator avoidance should play an important role in nest site selection. Adaptations for decreasing predation in ground-nesting birds include reduction of nest accessibility (Jobin and Picman 1997), concealment of nest sites (Clark and Nudds 1991), nest defense (Brunton 1999, Hernandez-Matias et al. 2003), and variation in nest spacing (Lariviere and Messier 1998). While numerous studies on black terns have examined habitat selection by comparing nesting habitat with unused habitat at multiple scales (Hickey and Malecki 1997, Naugle et al. 1999, 2000), habitat variables that discriminate between successful and depredated nests have not been identified. Habitat influences on nest predation are more difficult to detect because the intensity of predation can fluctuate unpredictably between years and wetlands based on variation in the composition of predator communities (Clark and Shutler 1999, Clark and Nudds 1991). Selection of nesting habitat is further complicated by factors unrelated to predator avoidance including proximity to foraging grounds, availability of suitable substrate, wave avoidance, social structure, and site fidelity (Bergman et al. 1970, Hickey and Malecki 1997). In addition, wetland water levels during the period of nest initiation may limit the range of available, preferred habitat and thus indirectly affect nest placement and the likelihood of predation.

Reducing accessibility of nests to predators in wetlands may entail a tradeoff between avoiding both terrestrial (e.g., foxes, raccoons, ravens, raptors) and aquatic (e.g. herons, bitterns, mink) nest predators. Thus, for ground-nesting birds, distance from the nest to the upland edge and the main water body may be critical in avoiding the home ranges or travel lanes of individual predators (Boe 1993, Lariviere and Messier 1998, Garrettson and Rohwer 2001). Naugle et al. (1999) found black terns were less likely to nest in wetlands surrounded by trees and hypothesized that it may be to reduce predation risk. Water depth and proximity of nests to small water pools and channels may also influence predator activity in a nesting area. In a study utilizing artificial nests, Jobin and Picman (1997) found that water depth was the most important predictor of nest success, as declining water depth during the breeding season coincided with increased nest predation.

Several investigators have studied the potential effects of vegetation height and density (i.e., concealment value) on nest site selection in black terns (Hickey and Malecki 1997, Naugle et al. 2000, Bernard 1999), but such factors seem to have little relationship to nest success (Maxson 1994, Hickey and Malecki 1997, Bernard 1999). Waterfowl studies have produced mixed results. Numerous studies have reported greater nest success in tall and dense cover (Jimenez and Conover 2001), whereas other studies found no correlations between nest success and vegetation height or vertical cover (Maxson and Riggs 1996, Jobin and Picman 1997, Lariviere and Messier 1998). Clark and Nudds (1991) found concealment effects on duck nest success were dependent on the predator community, and concealment was more effective when avian predation was prevalent.

Black terns nest semi-colonially and commonly mob potential predators (Cuthbert 1954, Chapman-Mosher 1986). Besides mobbing, the hypothesized benefits of nest aggregation include increased vigilance and reduced predation risk as a result of the dilution effect (Hernandez-Matias et al. 2003). If dilution plays a role in nest aggregation, then the position of a nest in a cluster (interior or perimeter) may influence the likelihood of predation (Brunton 1997, Becker 1995). In studies of both common terns (Sterna hirundo.; Becker 1995, Hernandez-Matias et al. 2003) and least terns (S. antillarum; Brunton 1999) nesting on coastal beaches, nest predation was found to decline with increasing number of nests in a cluster, suggesting aggregated nests are less accessible to predators. For black terns, which typically have greater nest spacing than beach-nesting tern species (Dunn and Agro 1995), it is unclear if nest aggregation reduces nest depredation or if a threshold number of nesting pairs is necessary for effective communal defense. Colonial defense strategies also may be ineffective if nest predators are largely nocturnal. Colonial nesting may in fact increase the likelihood of predation if nest predators recognize high-density patches and exhibit area-restricted searching behavior (Lariviere and Messier 1998). Nest spacing then becomes a crucial factor affecting nest detection by predators, whereby the likelihood of a nest being depredated is related to the outcomes of neighboring nests. The presence or absence of nearest neighbor effects will be dependent on the foraging behavior of the predator species involved, as well as the effectiveness of group defense. The goal of this study was to examine intraspecific variation in nest success to identify factors affecting nest predation of black tern colonies in central Maine. Specifically, my objectives were to (1) rank the importance of factors affecting nest predation including factors related to nest

concealment, nest proximity to wetland features, and nest aggregation; and, (2) to examine the annual influence of wetland water level during nest initiation on nest site location in a black tern colony.

STUDY SITE

Our study was conducted from mid-May to late-July during 1998-2002 at six colonies in central Maine: Carlton Pond (Town of Troy, ME); Douglas Pond (Town of Palmyra, ME); Messalonskee Lake (Town of Belgrade, ME); Great Moose Lake (Town of Hartland, ME); Madawaska Pond (Town of Palmyra, ME); and Plymouth Lake (Town of Plymouth, ME). Carlton Pond and the surrounding wetland encompass 431 ha, including 75 ha of semi-permanent emergent wetland bordering 113 ha of open water. The four nesting areas at Carlton are dominated by sedge (*Carex* spp.), *Sphagnum* spp., and pickerelweed (*Pontederia cordata*), as well as sparse shrubby vegetation. Douglas Pond is an impounded wetland on the Sebasticook River and has a total area of open water and wetlands of 227 ha. There are 44 ha of semi-permanent emergent vegetation bordering 85 ha of open water. The three nesting areas at Douglas are dominated by river bulrush (*Scirpus* spp.) or sedge. Messalonskee Lake is a large lake (1786 ha) with 55 ha of semi-permanent emergent wetland at the southern end, dominated by shrub vegetation, sedge, and *Sphagnum* species. Great Moose Lake is upstream from Douglas Pond on the Sebasticook River. Great Moose Lake is 1800 ha in area and has 43 ha of semipermanent emergent wetland, primarily along the northern shore. The nesting area is dominated by sedge and pickerelweed. The remainder of the lake (1552 ha) is primarily open water with water levels controlled by a dam on the Sebasticook River. Madawaska Pond is 106 ha in area and contains 14 ha of semipermanent emergent vegetation in a

narrow strip along the edge of 21 ha of shallow open water. Plymouth Lake is 253 in area, and the nesting habitat includes 32 ha of semipermanent emergent vegetation bordering 100 ha of partially vegetated open water.

METHODS

Experimental Design and Procedures

I measured variables related to proximity of wetland features and nest aggregation for 231 successful and 124 depredated black tern nests during 1998-2002 using Geographic Positioning System (GPS) coordinates of nests concurrently with digital National Wetland Inventory (NWI) data. I defined 14 candidate models based on logistic regression and selected models with Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to determine the best model for predicting nest outcome (success vs. depredated) and to rank the predictive importance of each variable. A priori, I reserved 25% (n = 90) of nest data to use in model validation. I conducted a separate analysis of data exclusively from 2001-2002 (86 successful and 32 depredated nests) that included all the variables from the analysis described above as well as field measurements of habitat variables related to nest concealment. I defined 24 candidate models based on logistic regression, which included the 14 models from the 1998-2002 analyses and 10 additional models incorporating nest concealment factors. I performed model selection using AIC_c to determine the best model for predicting nest outcome and to rank the predictive importance of each factor. A subset of data in this analysis was not reserved a priori for model validation because of small sample size. I examined the relationship between nest placement and wetland water level at the time of nest initiation at a subcolony of nests at Carlton Pond during 1999-2001 using GPS coordinates of nests and digital NWI data.

Small nest enclosures and/or large predator exclosures were installed at a small number of nests for other studies. Forty-one small enclosures were typically placed at nests near the end of incubation, were inconspicuous, and did not influence nest success (Shealer and Haverland 2001, Chapter 4), and would not exclude predators. Nests with chick enclosures were included in all analyses. At 11 nests, predator exclosures were deployed at the end of the incubation period for other studies. I assumed that these 11 nests, which had survived through \geq 80% of the incubation period, would be successful. Of these, six exclosures were deployed four days prior to hatch, two were deployed two days prior to hatch, and three were deployed one day prior to hatch.

In 1998-2002, black tern nests were located by systematically observing adult nesting behavior as part of a comprehensive breeding productivity study for this species in Maine. Once located, each nest was marked with an inconspicuous bamboo stake placed 5 meters from the nest. If clutches contained fewer than three eggs, nests were revisited within 3 days to confirm final clutch size, which also aided in predicting hatch dates. For analyses, we designated the date the nest was found as the nest initiation date, recognizing that nests are found one or more days after the first egg is laid. Date of nest initiation (D) was recorded as early (< June 15) or late (\geq June 15). Nests were monitored for adult activity from canoes or elevated blinds every 1-4 days. Nests were classified as successful if at least one chick was observed near the nest or if adults were observed delivering food. Inactive nests were visited and classified as depredated, flooded, abandoned, or unknown loss. A nest was classified as depredated if egg fragments were located around the nest cup or if all eggs were missing prior to the anticipated hatch date and water levels had not risen substantially (>5.0 cm). Nests were classified as flooded if nest cups were found submerged following periods of rain or if eggs were found floating in the vicinity. Nests were classified as abandoned if eggs remained intact in the nest cup but adult activity was not observed for two or more days at the nest. We excluded all nests that were lost to flooding, abandonment, or unknown causes. During 1998-2002, GPS locations for each nest were recorded using a Trimble GeoExplorer GPS unit, and GPS points were corrected using the base station at the University of Maine.

During 2001-2002 a circle with 4-meter radius was established around each nest and divided into four quadrants of equal size. Within each quadrant, we estimated percentage of quadrant with standing water (PW), percentage of quadrant covered with vegetation between 0.25-0.5 m in height (PV1), and percentage of quadrant covered with vegetation between 0.51-1.0 m in height (PV2). Water depth (WD) was measured in each quadrant. Values were averaged across quadrants to determine nest site values for analyses. Rangefinders were used in 2001-2002 to measure distances from nests to main water bodies and upland edges. The main water body was defined as that portion of the wetland basin with open water and no emergent vegetation (except pickerelweed), whereas upland edge was defined as dry, forested habitat. Rangefinders were also used to measure the distance of each nest to the nearest small pool or channel, defined as a canoe-navigable water body distinct from the main water body. I used Carlton Pond water level data provided by U. S. Fish and Wildlife Service, Sunkhaze National Wildlife Refuge, during 1999-2001 to examine nest location relative to water levels.

GIS and Statistical Analyses

I used digital NWI data for wetland habitats on our study areas that had been delineated from aerial photos taken in the early 1990s. I projected nest locations from 1998-2002 on NWI maps of our six study sites after updating the NWI maps using georeferenced data from ground inspections in 2002 and 2003. I utilized ArcMap (ESRI Corp.) to determine the shortest distance (m) from each nest to forested or upland habitat (UE) and the main water body (WB), as classified in the NWI maps. I compared these values to those obtained through field observations in 2001-2002. Absolute values of the differences between the distances obtained from field and GIS measurements were calculated to validate the accuracy of NWI information. Additionally, I used ArcMap to determine nearest neighbor distance (NN) for each nest (based on GPS data), number of depredated nests within 30 m (NP1), number of depredated nests between 30-100 m (NP2), cluster size (CS), cluster area (CA), and cluster position (CP). A cluster was defined as a group of nests overlapping in incubation activity for a minimum of 5 days. For inclusion into a cluster, a nest was required to be 100 m or less to an adjacent nest in the cluster. This distance was selected based on field observations of distances between nests where adults were likely to engage in mobbing behavior of potential predators. Convex polygons were constructed around each cluster by drawing a continuous line between nests on the cluster perimeter. The area of each cluster (polygon) was determined using ArcMap. Cluster position is a binomial variable referring to whether each nest was on the cluster perimeter or in the interior.

I developed an *a priori* set of candidate, logistic models designed to predict nest success of black terns during 1998-2002 in relation to the variables D (binary), NN (continuous), NP1 (continuous), NP2 (continuous), CS (continuous); CA (continuous), CP (binary), UE (continuous), and WB (continuous). Nest outcome was the dependent variable in all analyses (binary: successful or depredated). The variables NN, CA, UE, and WB were log-transformed to approximate normality. Fourteen candidate models were examined including a global model with all variables (model number 1), models relating to wetland access (2-4), models relating to proximity of nest predation events (5-6), models related to nest aggregation (7-11), a model combining nest dispersion and nest predation proximity (12), and models combining predation proximity and wetland access variables (13-14). A priori, I randomly selected 25% of all nests from 1998-2002 to test the efficacy of the best model (Tables A.5, A.6). To assess predictability of the best models, each nest in the validation data set was classified based on logistic regression outputs as successful or depredated using 0.35 as the discriminating value. The discriminating value is the ratio of observed successful versus depredated nests across all years. In addition, successful and depredated nests in 2001-2002 were analyzed separately using the above models as well as 10 additional models incorporating the nest concealment variables PW (continuous, proportion), PV1 (continuous, proportion), PV2 (continuous, proportion), WD (continuous), and SP (continuous). The variable SP was log-transformed to approximate normality.

I selected among candidate models using Akaike's Information Criteria adjusted for small sample size (AIC_c, Burnham and Anderson 2001). Log-likelihood values were obtained for each model using logit regression in Systat 10.2. Models were tested for goodness-of-fit using Hosmer-Lemeshow statistics (p > 0.10). In addition to AIC_c, I calculated difference from the best model (Δ AIC_c) and Akaike weights for each model, as well as variable importance across all models (Burnham and Anderson 2001). Although I recognized that nest success rates differed among years and study areas, I did not include year and site variables in the candidate models as they have little predictive value (Pietz et al. 2003). My intention was to select habitat and nest dispersion variables that might help explain year and site differences in nest survival.

Water Level – Nest Site Selection

To examine the influence of wetland water level during nest initiation on nest site location, I utilized distance from upland edge (UE) as a dependent variable for all nests at a sub-colony at Carlton Pond during 1999-2001. I used a General Linear Model (SYSTAT 10.2) with year, water level, and year × water level interaction as dependent variables. I constructed a NWI map of the Carlton Pond sub-colony to visually inspect nest placement during 1999-2001.

RESULTS

During 1998-2002, the mean nearest nest distance (NN) was 58 m (n = 265, SE = 9) and ranged from 5 to 1037 m (Table 1.1). Nest clusters were comprised of 1-18 nests, and the largest nest cluster covered a total area of 38,974 m² (Table 1.1). Sixty-one nests were located on the interior of nest clusters, whereas 204 nests were located on cluster perimeters. Date of nest initiation was prior to June 15th for 181 nests, and occurred June 15th or later for 84 nests. Distances of nests to the upland edge (UE) ranged from 30 to 837 m, whereas distances to the main water body (WB) ranged from 1 to 309 m (Table 1.1). Distances from each nest to upland edge (UE), as determined from NWI maps (0 = 133.5 m, SE = 3.6, n = 177), differed by 15% (0 = 19.8 m) from those values measured in the field (0 = 153.3 m, SE = 1.35, n = 177) during 2001-2002. Distances from each

Table 1.1. Mean and standard error estimates for continuous variables used in logistic regression models predicting nest success or nest predation for black tern nests in Maine, 1998-2002.

		Successful nests ($n = 173$)		Successful nests (n = 173) Depredated nests (n = 9)		s (n = 92)	
Variable	Definition	0	SE	range	0	SE	range
NN ^a	Distance to nearest nest (m)	57	8	5 - 1037	59	10	6 - 575
NP1	No. depredated nests within 30 m	0.20	0.04	0-2	0.59	0.10	0-5
NP2	No. depredated nests between 30 – 100 m	0.72	0.10	0 – 9	1.74	0.20	0-8
CS	No. nests in colony	7.2	0.4	1 – 18	7.1	0.5	1 – 18
CA ^a	Cluster area (m ²)	6365	566	1 – 38974	7291	1115	1 – 38794
DU^{a}	Distance to upland edge (m)	248	16	30 - 837	204	17	43 - 782
WB ^a	Distance to main water body (m)	77	5	1 – 248	72	7	1 – 309

^a Variables log-transformed for use in logistic regression models.

nest to open water body (WB), as determined from NWI maps (0 = 84.2 m, SE = 4.8, n = 177), differed by approximately 25% (0 = 21.4 m) from those values measured in the field (0 = 105.6 m, SE = 2.25, n = 177) during 2001-2002. For nests exclusive to 2001-2002, the mean PV1 value was 38.9 % (n = 118, SE = 3.27), whereas the mean PV2 value was 15.9% (n = 118, SE = 3.19)(Table 1.2). The mean percentage of standing water (PW) at nests in 2001-2002 was 81.1%, whereas mean water depth at nests was 24.3 cm (Table 1.2).

Nest Success

For the 1998-2002 analyses, the best-approximating model (model 12) indicated that black tern nest success was most affected by the number of depredated nests within 30 meters (NP1), the number of depredated nests between 30-100 meters (NP2), cluster size (CS), cluster area (CA), and distance to nearest nest (NN) (Table 1.3). The Akaike weight (i.e., the weight of evidence in support) of this model was 0.54 (Table 1.3). For the best model, examination of standardized regression coefficients indicated that NP1 (β = -0.79) and NP2 (β = -0.45) were the most influential predictor variables, whereas NN (β = -0.14), CS (β = 0.03), and CA (β = 0.09) had less importance (Table 1.4). The second-best approximating model (Δ AIC_c = 2.6) had an Akaike weight value of just 0.15 (Table 1.3). The top five models accounted for almost all the Akaike weight among the entire candidate set, as all other models had Δ AIC_c values > 16.0 (Table 1.3). Each of these top five models contained the variables NP1 and NP2, and variable importance for each of these variables was 1.0. The variables NN, CA, and CS each had variable importance of 0.66, while all other variables had importance < 0.30 (Table 1.4). The best

Table 1.2. Mean and standard error estimates for continuous variables used in logistic regression models predicting nest success or nest predation for black tern nests in Maine, 2001-2002.

		Successful nests ($n = 86$)			Depredated nests $(n = 32)$		
Variable	Definition	0	SE	range	0	SE	range
NN ^a	Distance to nearest nest (m)	74	14	10 - 1037	47	7	10 – 159
NP1	No. depredated nests within 30 m	0.07	0.03	0-2	0.31	0.08	0 – 1
NP2	No. depredated nests between 30 – 100 m	0.36	0.07	0-2	0.88	0.25	0-4
CS	No. nests in colony	5.4	0.4	1 – 14	4.9	0.5	1 – 14
CA ^a	Cluster area (m ²)	4818	557	1 – 14170	2994	577	1 – 14170
DU^{a}	Distance to upland edge (m)	244	24	49 – 795	227	36	43 - 693
WB ^a	Distance to main water body (m)	85	7	1 – 247	77	11	1 – 230
PV1	Percentage vegetative cover 0.25-0.5 m in height	37.6	2.88	0 - 100	42.3	4.76	0 - 100
PV2	Percentage vegetative cover 0.5-1.0 m in height	16.1	2.83	0 – 100	15.3	5.01	0 - 100
PW	Percentage of water cover	82.3	2.57	10 - 100	77.9	4.71	3 - 100
WD	Water depth at nest (cm)	24.8	1.23	2-54	23.8	1.75	0.5 - 56
SP ^a	Distance to small pool or channel (m)	14	2	1 – 95	20	4	1 – 70

^a Variables log-transformed for use in logistic regression models.

Table 1.3. Candidate models for prediction of black tern nest success and depredation evaluated with Akaike's Information Criterion for small samples (AIC_c) for 265 nests from six colonies in Maine, 1998-2002.

Model no.	Model terms ^a	AIC _c	ΔAIC_{c}	w^b
12	NP1, NP2, NN, CS, CA	313.0	0.0	0.54
14	NP1, NP2, WB	315.6	2.6	0.15
5	NP1, NP2	315.7	2.7	0.14
1	UE, WB, NP1, NP2, CS, CA, CP, NN, D	316.0	3.0	0.12
13	NP1, NP2, UE	317.7	4.7	0.05
6	NP1	329.5	16.5	< 0.01
4	UE	346.4	33.5	< 0.01
3	UE, WB	347.2	34.2	< 0.01
11	CS	348.3	35.3	< 0.01
8	NN, CS, CA	348.4	35.4	< 0.01
7	NN, CS, CA, CP	348.6	35.6	< 0.01
2	UE, WB, D	349.2	36.2	< 0.01
10	NN, CS	350.1	37.1	< 0.01
9	NN, CS, D	352.2	39.2	< 0.01

^a Model terms: NP1 = No. depredated nests within 30 m; NP2 = No. depredated nests within between 30-100 m; UE = distance to upland edge (m), WB = distance to main water body (m); CA = cluster area (m²); CS = No. nests in colony, CP = cluster position; NN = distance to nearest nest (m); D = date of nest initiation (before or after June 15). The model terms NN, CA, UE, and WB were log-transformed for analyses.

^bAkaike weight (Burnham and Anderson 2001)

Table 1.4. Parameter estimates derived from the best model and variable importance for variables used to predict nest success and depredation at six colonies in Maine, 1998-2002.

	From b	est model	** • • • •
Variable	β	SE	Variable importance ^a
NP1	-0.79	0.26	1.00
NP2	-0.45	0.11	1.00
CS	0.03	0.05	0.66
NN	-0.14	0.22	0.66
CA	0.09	0.08	0.66
WB			0.27
UE			0.17
СР			0.12
D			0.12

^a Sum of Akaike weights for models containing the variable (Burnham and Anderson 2001).

model (12) correctly classified 66% (59/90) of all nests in the validation data set, whereas the third-best model (5), with the terms NP1 and NP2, correctly classified 69% (62/90) of all nests.

For the 2001-2002 analyses, the best-approximating model indicated nest success was most affected by NP1 and NP2 (model 5; Table 1.5). The Akaike weight for this model is 0.35 (Table 1.5), and the standardized regression coefficients (β) for NP1 and NP2, are -1.4 and -0.46, respectively (Table 1.6). The second-best model contained only the variable NP1 and had Akaike weight 0.14 (Table 1.5). Low ΔAIC_c values (< 10.0) for the top 14 models indicate uncertainty in model selection (Burnham and Anderson 2001). The top eight models constituted the 95% confidence set (based on Akaike weight), and each included the variables NP1 and NP2. Variable importance for NP1 and NP2 were 0.98 and 0.83, respectively (Table 1.6). All other variables had importance values less than 0.20 (Table 1.6).

Water Level – Nest Site Selection

Water levels at nest initiation ranged from 374 to 397 cm for 1999-2001 and declined during the nesting season (Figure 1.1). An inverse relationship was apparent between UE and water level (Figure 1.2, 1.3). Water levels at the time of nest initiation at Carlton Pond in 1999 (0 = 374 m, SE = 0.88, n = 16) were lower (p < 0.01) than in 2000 (0 = 397 m, SE = 1.27, n = 19) or 2001 (0 = 390, SE = 0.87, n = 9), and distance to upland edge (UE) was greater (p < 0.01) in 1999 (0 = 210 m, SE = 20.8) than in 2000 (0 = 126, SE = 10.8) or 2001 (0 = 112, SE = 14.2). There was no difference (p > 0.05) in distance of nests to upland edge (UE) between 2000 and 2001.

Table 1.5. Candidate models for prediction of black tern nest success and depredation evaluated with Akaike's Information Criterion for small samples (AIC_c) for 119 nests from six colonies in Maine, 2001-2002.

Model no.	Model terms ^a	AIC _c	ΔAIC_{c}	w^b
5	NP1, NP2	133.2	0.0	0.35
6	NP1	135.0	1.8	0.14
13	NP1, NP2, UE	135.2	2.1	0.12
14	NP1, NP2, WB	135.3	2.1	0.12
21	NP1, NP2, PV1, PV2	135.9	2.7	0.09
12	NP1, NP2, NN, CA, CS	136.0	2.8	0.09
23	UE, NP1, NP2, PV1, PV2	138.1	5.0	0.03
22	UE, NP1, NP2, PW, WD	138.8	5.6	0.02
10	NN, CS	139.9	6.7	0.01
20	NP1, NP2, PW, WD, PV1, PV2	140.3	7.1	0.01
8	NN, CS, CA	140.6	7.4	< 0.01
24	WB, NP1, NP2, PW, WD, SP	140.7	7.6	< 0.01
9	NN, CS, D	141.6	8.4	< 0.01
7	NN, CS, CS, CP	142.8	9.6	< 0.01
11	CS	143.6	10.5	< 0.01
4	UE	143.9	10.7	< 0.01
1	UE, WB, NP1, NP2, CS, CA, CP, NN, D	144.8	11.6	< 0.01
3	UE, WB	146.0	12.9	< 0.01
17	UE, PV1, PV2	146.7	13.5	< 0.01
19	WB, PV1, PV2	146.8	13.6	< 0.01
2	UE, WB, D	147.5	14.3	< 0.01
16	UE, SP, PW, WD	148.0	14.8	< 0.01
18	WB, SP, PW, WD	148.0	14.8	< 0.01
15	UE, WB, NP1, NP2, CS, CA, CP, NN, D, SP, PW, PV1, PV2, WD	152.0	18.8	< 0.01

^a Model terms: NP1 = No. depredated nests within 30 m; NP2 = No. depredated nests within between 30-100 m; UE = distance to upland edge (m), WB = distance to main water body (m); CA = cluster area (m²); CS = No. nests in colony; CP = cluster position; NN = distance to nearest nest (m); D = date of nest initiation (before or after June 15); PV1 = Percentage of vegetative cover 0.25-0.5 m in height; PV2 = Percentage of vegetative cover 0.5 – 1.0 m in height; PW = Percentage of water cover; WD = water depth at nest; SP = Distance to small pool or channel. The model terms NN, CA, UE, WB, and SP were log-transformed for analyses. ^b Akaike weight (Burnham and Anderson 2001) Table 1.6. Parameter estimates derived from the best model and variable importance for variables used to predict nest success and depredation at six colonies in Maine, 2001-2002.

From best model							
Variable	β	SE	Variable Importance ^a				
NP1	-1.40	0.57	0.99				
NP2	-0.46	0.24	0.83				
UE			0.18				
WB			0.13				
PV1, PV2			0.13				
CS			0.12				
NN			0.12				
CA			0.10				
PW, WD			0.04				
SP			< 0.01				
D			< 0.01				
СР			< 0.01				

^a Sum of Akaike weights for models containing the variable (Burnham and Anderson 2001).

Figure 1.1. Relative water level (cm) measured as gauge height at Carlton Pond, Maine, during the period from mid-May to early-August, 1999-2001.

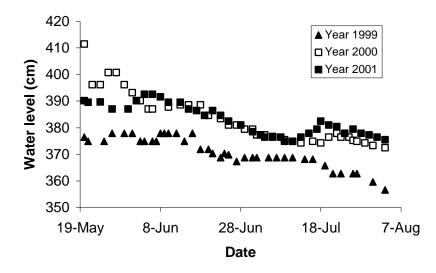


Figure 1.2. Mean distance of nests to upland edge (bars) at a sub-colony at Carlton Pond, Maine, in relation to wetland water level (diamonds) at the time of nest initiation for 16 nests in 1999, 19 nests in 2000, and 9 nests in 2001. Lines represent standard error.

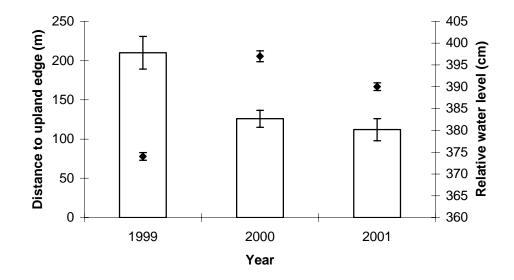
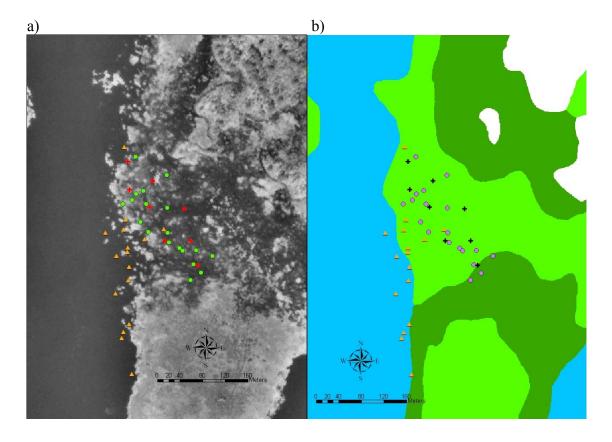


Figure 1.3. GPS locations of black tern nests at Carlton Pond, Maine, in 1999 (triangles), 2000 (circles), and 2001 (crosses) on aerial photos (a) and National Wetland Inventory (NWI) projections (b). Open water (blue), upland edge (white), scrub-shrub vegetation (dark green), emergent vegetation (light green) depicted in (b).



DISCUSSION

Variables related to proximity to depredated nests (NP30 and NP100) were the most important factors influencing nest predation of black terns in Maine colonies during 1998-2002. Predation losses were localized, indicating nest predators in Maine wetlands exhibit area-restricted search behavior. Spacing of black tern nests relative to predator foraging territories, travel lanes, and other activity centers of nest predators may thus be adaptive towards preventing nest detection by opportunistic predators (Clark and Shutler 1999). Colony size, colony area, and nearest neighbor distance appeared in the best model for 1998-2002, but the correlation coefficients of these terms had little magnitude and thus little predictive utility, suggesting that colonial nest defense plays only a minor role in predator deterrence in this species. The inclusion of these variables in the best model was likely the result of model selection bias, whereby one large colony with little predation substantially skewed the results. Models with variables related to wetland access by predators, including proximity to upland edge and main water body, were poor at predicting the occurrence of nest predation. The analysis exclusive to 2001-2002 supported proximity to depredated nests as being most important for predicting nest predation. Models incorporating nest concealment variables had little support, suggesting microhabitat features at nest sites contribute little to predator deterrence.

For the 1998-2002 analysis, the top models predicted nest outcome for the reserve data set with between 66-69% accuracy. Such accuracy is substantial given my inability to discriminate among different nest predator species. While the sample size of this study was large, it still may have been insufficient to detect variables of secondary importance, particularly variables that may be important for specific nest predator species. The

relative importance of habitat variables is likely highly variable based on whether principal nest predators were avian vs. mammalian, terrestrial vs. aquatic, or nocturnal vs. diurnal. Habitat variable influences may exist but be too subtle to detect even with a relatively large number of nests. If so, they may not be key factors in determining breeding success or influential enough to justify habitat management action or future research. Despite the large number of potential nest predator species in Maine wetlands, my results indicate that most predators behave similarly and exhibit area-restricted search behavior. The number of depredated nests within 30 m was three times greater at depredated nests relative to successful nests in 1998-2002, while the number of depredated nests between 30-100 m was nearly 2.5 times greater at depredated nests. The detrimental effects of such a trend could become amplified if black terns were forced to concentrate nests in smaller patches due to habitat constraints or if nest predators increase their foraging effort or efficiency in specific patches (Lariviere and Messier 1998). Because the Maine population of black terns is small, the effect of nest predation on breeding productivity during any given year can be affected largely by the presence of a small number of nest predators. The dynamic composition of predator communities in wetland ecosystems is a significant obstacle towards detecting the importance of secondary habitat and nest aggregation variables that may be effective at predator deterrence.

As has been reported in other studies of black terns (Maxson 1994, and Malecki 1997, Bernard 1999), habitat variables associated with nest concealment appeared to have little importance in determining nest success. I measured vegetation and water coverage variables around the nest near the time of nest initiation and recognize that vegetation growth during the breeding season likely resulted in temporal variation in concealment value. However, I contend that wetland vegetation should grow at similar rates across wetlands, and thus the relative differences in these variables would remain similar across nests. I did not include vegetation species in analyses because several studies of black tern nesting preference have concluded that structural features of vegetation are more important than actual species (Weller and Spatcher 1965, Hickey and Malecki 1997, Naugle et al. 2000). Studies utilizing artificial eggs in wetlands have reported no significant effects of vegetation height or density (Jobin and Picman 1997, Lariviere and Messier 1998) on nest depredation, although Clark and Nudds (1991) suggest concealment may be more significant if avian predators are prevalent. I was unable to differentiate between avian and terrestrial nest predation events, and thus was not able to test if nest concealment varied with predator type.

Nest predation of wetland birds in the Prairie Pothole region may have increased over the past fifty years as a result of habitat deterioration coupled with increased populations of some nest predator species that thrive in human-modified environments (Beauchamp et al. 1996, Jimenez et al. 2001). Such conditions may result in isolated patches of suitable habitat that act as ecological traps by concentrating both nests and predators in small areas where the searching efficiency of predators is high (Jimenez et al. 2001). However, habitat conditions for black terns in Maine have likely increased over the past fifty years as a result of wetland impoundments, and thus high predation levels are likely caused by different factors. Wetlands in Maine are small relative to the Prairie Pothole region and bordered by forested habitat. Therefore, Maine wetlands may still function as ecological traps for black terns and understanding factors affecting habitat availability is of critical importance. Water levels at Carlton Pond affected the distances of nests to the upland edge and thus influenced the range of favorable, nesting habitat suitable for black terns. A similar trend has been observed in ducks (Johnson and Grier 1988). Clark and Nudds (1991) hypothesized that foraging efficiency of predators is reduced with increased patch size of nesting habitats since increased spatial variation enables birds to place nests further apart. Low water levels at Carlton Pond in 1999 appeared to considerably limit the locations of nest sites relative to higher-water years (Figure 1.3). However, the influence of wetland water level would vary considerably based on geomorphic conditions and the makeup of the predator community (e.g., aquatic vs. terrestrial). Water level effects on nest location may thus be colony-specific and vary temporally with predator community. I identified evidence that the fate of individual black tern nests in Maine wetlands is related to the outcomes of nearby nests, suggesting the searching efficiency of wetland predators is a principal factor affecting nest predation rates. Such spatial correlation in nest success should result in natural selection favoring random nest placement, but such an adaptation may be negated by limited availability of suitable nesting habitat. Future research on black terns should identify factors influencing nest site location within breeding wetlands, particularly the influence of wetland water levels during nest initiation, in order to determine potential management techniques to reduce the likelihood of density-dependent nest predation.

CHAPTER 2

NOCTURNAL NEST ABSENCE IN BLACK TERNS

Temporary abandonment of nests by incubating adults during the nocturnal period has been reported in Procellariiformes (Pefaur 1974, Boersma and Wheelright 1979), Laridae (Marshall 1942, Chardine and Morris 1983), and Podicipedidae (Nuechterlein and Buitron 2002). Absences in Procellariiformes are typically attributed to the large distances adults must travel when foraging for unpredictable food resources (Boersma and Wheelright 1979), whereas nest absence in Laridae has been interpreted as a response to the presence of nocturnal predators such as great horned owls (*Bubo viginianus*) (Nisbet and Welton 1984), black-crowned night herons (*Nycticorax nycticorax*)(Hunter and Morris 1976, Shealer and Kress 1991), and raccoons (Procyon lotor)(Emlen et al 1966). Nocturnal absences in both common tern (Sterna hirundo) and ring-billed gull (Larus delawarensis) colonies are described as large-scale, synchronous departures by the entire colony in response to the presence of a predator, with synchronous return times at first light (Nisbet 1975, Chardine and Morris 1983). For Laridae, nocturnal nest absence is hypothesized as an adaptive behavior to minimize predation on adults with the tradeoff of decreasing the likelihood of breeding success. Declining breeding success could result directly from nest predation and embryonic chilling during adult absence or indirectly through extended incubation periods and lowered chick survival (Nisbet and Welton 1984). Also, extended incubation as a result of frequent nest absence may expose eggs to longer periods of predation risk.

Nest predation is a major cause of nest loss in black terns (*Chlidonias niger*) (Mazzocchi et al. 1997, Hickey 1997, Seyler 1991) and may cause significant nest absence. There have been anecdotal reports of nocturnal absence by black terns in response to avian predators (Faber 1992), but the extent and significance is unknown. Information is needed on the frequency of occurrence, length and timing of absences, and effects on nest success. As a semi-colonial nesting species, black terns frequently mob potential predators during the diurnal period suggesting that multiple terns may leave nests at night in response to a predator or disturbance. The purpose of this study was to determine the occurrence and duration of nocturnal nest absence and the effect of absence on nest temperature and incubation length for black terns in Maine colonies.

STUDY SITE

This study was conducted during mid-May to late-July, 2001-2002 at four colonies in central Maine: Carlton Pond (Town of Troy, ME); Douglas Pond (Town of Palmyra, ME); Messalonskee Lake (Town of Belgrade, ME); and Great Moose Lake (Town of Hartland, ME). Carlton Pond and the surrounding wetland have a total area of 431 ha and include 75 ha of semi-permanent emergent wetland bordering 113 ha of open water. Nesting areas at Carlton Pond are dominated by sedge (*Carex* spp.), *Sphagnum* spp., and pickerelweed (*Pontederia cordata*), as well as sparse shrubby vegetation. Douglas Pond is an impounded wetland on the Sebasticook River and has a total area of open water and wetlands of 227 ha. There are 44 ha of semi-permanent emergent vegetation bordering 85 ha of open water. Nesting areas at Douglas Pond are dominated by river bulrush (*Scirpus* spp.) or sedge. Messalonskee Lake is a large lake (1786 ha) with 55 ha of semi-permanent emergent wetland at the southern end, dominated by shrub

vegetation, sedge, and *Sphagnum* species. Great Moose Lake is upstream from Douglas Pond on the Sebasticook River. Great Moose Lake has 43 ha of semi-permanent emergent wetland, bordered by 1552 ha of open water. The nesting area is dominated by sedge and pickerelweed.

METHODS

Black tern nests were located every 1-3 days by observing adult behavior, and nests were marked with inconspicuous bamboo stakes. The number of eggs was recorded. If clutch size was less than three (common maximum), nests were re-visited within three days to determine final clutch size. This protocol was a compromise between obtaining accurate laying dates and limiting additional disturbance within colonies (Nuechterlein and Buitron 2002). Nests were monitored from elevated blinds or from canoes every 1-3 days. Hatch dates of marked nests were determined based on direct observation of hatched chicks or based on the first observation of feeding behavior by adults. Incubation periods were defined as the time the first egg was laid to the confirmation of hatch of at least one chick. Incubation periods were measured only for nests in which the lay date of the first egg was known accurately to within a 72 hour period.

Temperature monitors (Hobo Temp logger, Onset Computer Co.) were utilized during 2001-2002 to monitor nest absence. Temperature probes were arranged to protrude from the bottom of nest cups and lie at the center of clutches, extending approximately 1-3 cm from the nest bottom. Temperature monitors were utilized only on three-egg clutches. Temperature probe cords were buried under the existing marsh vegetation. Temperature monitors were attached to wooden stakes approximately 2 meters from the nest and approximately 0.25 meters aboveground. Monitors were covered with vegetation and fabric for concealment. Temperature monitors were deployed on 25 nests in 2001 and 20 nests in 2002. Nests were selected for temperature monitoring non-randomly (i.e., ease of accessibility) to reduce overall disturbance to colonies. The length of time nests were monitored ranged from 3-13 days. Some, but not all, monitoring periods were synchronous because I monitored nests throughout the nesting period. However, I attempted to monitor pairs of nests or groups of nests located within the same colony (within 200 m of each other) to determine the occurrence of paired absences. I attempted to check probe placement in nest cups every three days, but this was not possible in all cases as it may have interfered with other monitoring research. Probes found out of place were repositioned, and data from that sampling period were excluded. Temperature monitors were programmed to record nest temperature and ambient air temperature (measured at the stake) in 40 second intervals. Monitors could record nine days of temperature readings before downloading of data was required.

Absence periods were defined as periods of lowered temperature lasting a minimum of 10 minutes. Measurement of absence began at the first of three consecutive decreasing nest temperature readings and ended at the first of three consecutive increasing nest temperature readings (Nuechterlein and Buitron 2002). This study focused only on the nocturnal period, defined as 20:00 - 04:00 hrs. In addition, absences exceeding one hour in duration that were initiated prior to 20:00 hrs but extended into the nocturnal period were included in analyses to include long absences initiated during dusk and extending for much of the nocturnal period. Absences initiated during the nocturnal period and ending after 0400 hrs were also included. Nest attentiveness during the

diurnal period was not analyzed because absence during this period may have been attributed to feeding, researcher disturbance, or other human activity. Also, absences could not be positively identified during the diurnal period because exposure of temperature probes to direct sunlight when adults were absent may not have resulted in temperature declines at the nest. I recorded date, time of departure, nest temperature at time of departure, absence duration, and nest temperature at the end of absence (last reading before increase) for each nest absence. For each nest I calculated (1) the mean number of absences per night, (2) the mean absence length, (3) the percentage of nights with one or more absences, and (4) the percentage of time exhibiting absence during the total time monitored. The mean values for each nest were then used as baseline data to calculate colony and year means. For some analyses, absences were defined as short (< 60 minutes) or long (\geq 60 minutes). Group absences were defined as overlapping periods of absence at two or more nests less than 200 m apart. A distance of 200 m was selected based on field observations and was intended to represent the maximum distance paired absences would occur in response to disturbance. Departure and return times of paired absences were not required to be simultaneous. Nest absence duration (log-transformed) and change in nest temperature were analyzed using linear regression. Nest success is defined as the proportion of nests hatching at least one chick. I did not compare absence duration by colonies or years statistically because of variable sampling intensity among colonies and individuals.

RESULTS

Nocturnal absences occurred at 33 of 45 black tern nests monitored in 2001-2002. Nests were monitored for a total of 1272 nocturnal hours in 2001 and 1128 hours in 2002.

I recorded 65 absences from 19 nests in 2001 and 27 absences from 14 nests in 2002. A mean of 0.40 absences per night (0 absence length = 122 minutes) were recorded in 2001, while 0.16 absences per night (0 absence length = 36.1 minutes) were recorded in 2002 (Table 2.1). Absences occurred during 14.1% of hours monitored in 2001 and 2.4% of hours monitored in 2002 (Table 2.1). However, nearly half of the hours in absence in 2001 were attributed to two nests at Messalonskee Lake (Table B.2). In 2001, 36 absences lasting 60 minutes or longer were recorded, whereas only nine absences exceeded 60 minutes in 2002 (Figure 2.1). Only three of four nests at Messalonskee Lake underwent absences in 2001, and colony results were highly influenced by two nests. Nest #121 at Messalonskee Lake was monitored for nine nocturnal periods in late July and underwent absences in eight consecutive nights totaling 72 hours. Duration of absence exceeded 8 hours in five of these nights (Figure 2.1) and the nest was eventually abandoned. Nest #55 at Messalonskee Lake was monitored for nine nocturnal periods in mid June and underwent absences 4-8 hours in duration on six consecutive nights (Figure 2.1). Nest #98 at Douglas Pond underwent absences exceeding 2 hours on five nights, accounting for colony differences in 2002. The time of night in which nest absences occurred seemed to vary widely between years (Figure 2.2). Only two absences were recorded from 06:00 hrs to 08:59 hrs in 2002, while absences were frequent during this period in 2001 (Figure 2.2). For both years, earliest sunrise occurred at 3:50 a.m. in mid June and latest sunrise occurred at 4:22 a.m. in late July. Of 45 absences exceeding sixty minutes in 2001-2002, time at which incubation resumed was between 3:30 a.m and 5:30 a.m. for 41 of the cases.

In 2001, five clusters of nests were monitored for 38 nocturnal periods (304

Year/Site N	No. nests	Nights monitored		Absences per night		Absence length (minutes)		Percentage of nights with \geq one absence		Percentage of time absent on all nights	
		Ν	range per nest	0	SE	0	SE	0	SE	0	SE
2001											
Douglas Pond	12	71	3 – 11	0.46	0.11	127.2	35.5	39.3	8.3	13.4	3.8
Carlton Pond	7	46	4 – 9	0.25	0.10	86.9	46.8	24.8	10.0	7.3	4.1
Messalonskee Lak	e 4	27	4 - 11	0.50	0.30	182.2	105.7	41.7	24.2	30.3	17.7
Great Moose Lake	2	15	6 – 9	0.37	0.20	25.0	63.9	25.0	8.3	9.7	8.6
Total	25	159	3 – 11	0.40	0.08	122.1	26.6	34.4	6.0	14.1	3.6
2002											
Douglas Pond	6	44	3 – 11	0.25	0.11	46.9	25.5	19.9	6.8	5.1	4.1
Carlton Pond	9	51	2 - 10	0.11	0.04	24.2	11.7	11.0	4.0	1.3	0.7
Messalonskee Lak	e 4	39	5 – 13	0.20	0.04	55.6	27.4	19.8	4.3	1.7	0.4
Great Moose Lake	1	7	0	0		0		0		0	
Total	20	141	2 - 13	0.16	0.04	36.1	10.7	14.9	3.0	2.4	1.3

Table 2.1. Mean number of absences per night, mean absence length, mean percentage of nights with an absence, and mean percentage of time absent on nights monitored at black tern colonies in Maine, 2001-2002 (n=45).

Figure 2.1. Duration of nest absences in minutes (log scale) at Carlton Pond, Douglas Pond, and Messalonskee Lake in Maine, 2001-2002. For each site, symbols refer to individual nests.

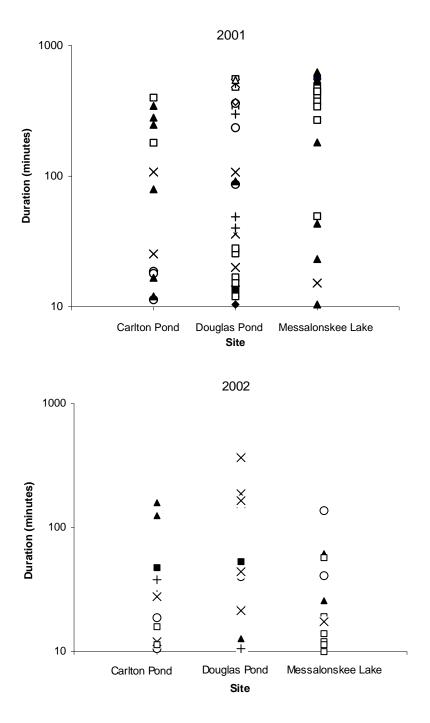
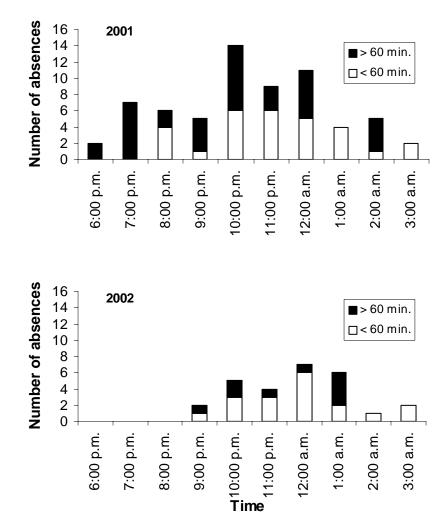


Figure 2.2. Number of black tern nest absences by time of departure at four colonies in Maine, 2001-2002. A total of 1908 hours were monitored in 2001and 1695 hours in 2002.



hours) to determine the occurrence of group absences: three pairs of nests, one cluster of seven nests, and one cluster of four nests. Thirty-three absences were recorded during this time, eleven of which constituted group absences (Table 2.2). All 11 absences occurred at Douglas Pond. In the remaining 22 cases, absences were detected at one monitored nest but not at other nests in the same cluster. An example of a temperature plot of a group absence is provided in Figure 2.3. In 2002, three pairs of nests and one cluster of three nests were monitored for a total of 25 nocturnal periods (300 hours) to determine the occurrence of group absences. Twelve absences of 12-58 minutes were recorded, but no group absences were detected. However, nocturnal nest predation occurred at two nests located 25 meters apart at Carlton Pond. On June 9th, the adult at nest #92 departed at 02:06 hrs with no subsequent return while the adult at nest #3 began absence at 02:19 hrs. Both nest cups were found empty and abandoned at 13:00 hrs on June 9th.

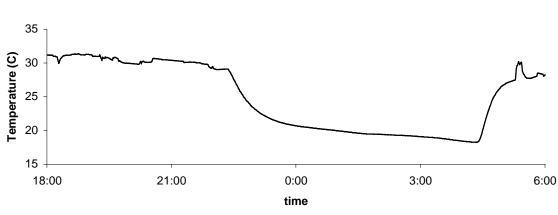
Decreases in nest temperature were correlated with the log of absence duration (linear regression, n = 92, $R^2 = 0.53$, p < 0.01)(Figure 2.4). Temperature change was dependent not only on absence duration, but ambient temperature during absence, which was naturally variable throughout the nesting season. The mean temperature decrease for absences less than sixty minutes was 4.66 °C (n = 47), whereas the mean decrease for absences greater than or equal to sixty minutes was 9.62 °C (n = 45). Thirty-three of the 45 nests monitored hatched at least one chick. Incubation length was estimated for 13 of these nests and had a range of 20-28 days, with ten nests hatching in 20-21 days. The number of nocturnal periods these nests were monitored varied from 3-13. Percentage of time in nest absence did not appear to affect incubation length; Nest #118 exhibited the

Table 2.2. Absences recorded at black tern nests less than 200 m apart during the period from 18:00 – 06:00 hrs at Douglas Pond in 2001.

Site	Date	Nest no.	Period of absence		
Douglas Pond ^a	June 19-20	54	22:27-03:26		
		24	22:22 - 04:22		
		20	22:21 - 00:08, 00:57 - 01:25		
		6	23:30 - 23:58		
Douglas Pond ^b	June 21-22	20	23:21 - 23:57		
		54	23:24 - 00:13		
Douglas Pond ^c	June 22-23	20	00:40 - 01:00		
		24	00:42 - 04:37		
Douglas Pond ^d	June 26-27	36	19:38 - 04:10		
		109	19:22 - 04:26		

^a Distance between nests ranged from 27-80 m.
^b Distance between nests was 43 m.
^c Distance between nests was 61 m.
^d Distance between nests was 107 m.

Figure 2.3. Example of temperature probe plots showing a paired absence during the nocturnal period of June 19-20, 2001, at Douglas Pond. Nests #24 (a) and #54(b) were located 55.6 m apart. The lower line in graph (b) depicts the ambient temperature.



Nest 24

Nest 54

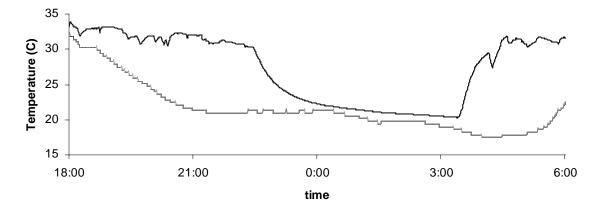
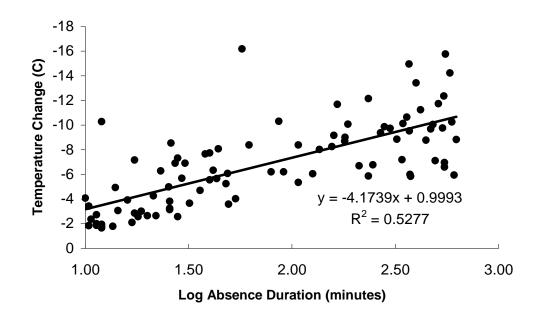


Figure 2.4. Linear regression of absence duration (log-scale) and temperature change during nest absence for 2001-2002 (n = 92).



longest incubation (28 days) but was absent only 1.5% of the time monitored (13 nocturnal periods). The three nests exhibiting the most absence (16% or greater of the nocturnal time monitored) each had incubation periods of 20-21 days.

DISCUSSION

Nocturnal nest absences were detected at four colonies during 2001-2002, suggesting this behavior is common. Longer absences (> 60 min.) were four times as frequent in 2001 compared to 2002, but the reasons for this remain unclear. My results were disproportionately affected by adults from a small number of nests exhibiting multiple, long absences (> 120 minutes) and thus merit cautious interpretation (Figure 2.2). Regardless, nest absences in black terns during the interval from 20:00-04:00 hrs were common and appeared more frequent in 2001. Nocturnal absences were rarely synchronous, as approximately three-quarters of all absences recorded while monitoring adjacent pairs or groups of nests were non-group absences. Only five group absences were recorded in 2001, and these adults may have been reacting to a common event. However, times of departure from these nests were not perfectly synchronous, ranging between 2-16 minutes. This suggests that black terns may not commonly engage in colony-wide nocturnal absence, or "mass exoduses" (Meehan and Nisbet 2002), but instead adults may remain on nests until the source of the disturbance influences them individually. Nocturnal absence may thus be an independent response influenced by risk assessment and parental quality (Meehan and Nisbet. 2002). The majority of adults exhibiting nocturnal absences between 1-10 hours in duration resumed incubation after 3:30 a.m., correlating strongly with the appearance of first light. This same pattern has

been frequently observed at common tern colonies exhibiting absences in response to nocturnal predators (Nisbet 1975).

Nest predation has been a common cause of nest failure in black tern colonies in Maine from 1997-2002 (Servello unpubl. data). Nocturnal abandonment is hypothesized to be a behavioral response to minimize predation on adults at the risk of increasing the likelihood of nest predation. Predator activity may influence attentiveness patterns during the nocturnal period and may be the cause of frequent nest absence in this study. Nocturnal absences preceded nocturnal nest predation at two adjacent nests at Carlton Pond in 2002, suggesting that predation triggered nest absence in those cases. A second hypothesis contends that nocturnal absence, besides enhancing adult survival, is a behavior that reduces the ability of olfactory predators to detect nests (Nuechterlein and Buitron 2002). Under this scenario, I would expect adults to vacate their nests synchronously upon detection of a predator to maximize time off the nest, but my data offered little evidence of synchronous departures.

The most important effects of nocturnal absence may not be direct effects on nest predation but indirect effects that decrease breeding productivity nonetheless. Nisbet (1975) reported that 12% of the 107 common tern clutches they monitored failed to hatch at a colony exhibiting high nocturnal abandonment. Frequent nocturnal absence associated with colonies of common terns resulted in extensions of the incubation period by 6-7 days (Nisbet 1975, Nisbet and Welton 1984). Similar patterns were observed in red-necked grebes (Nuechterlein and Buitron 2002). While nest temperature was inversely related with the log of absence duration, I found no relationship between the proportion of time spent in absence and incubation length. However, my sample size of

monitored nests with estimated incubation periods was small, and the frequency of absences for the non-monitored portion of incubation was unknown for individual nests. Lastly, measurement of incubation length was crude because the date of nest initiation could not be precisely measured. Given the frequency of nocturnal absence I observed at some nests, it is probable that incubation periods were extended as a result of declining nest temperatures during absence. For example, there were 12 nests in which adults were absent > 10% of the time monitored. Extended incubation also lengthens the amount of time nests are susceptible to predation or other causes of nest loss, and could also result in lowered chick survival. Chick survival declined with increasing nest absence in fork-tailed storm petrels (*Oceanodroma furcata*), and it was hypothesized that prolonged incubation and frequent embryonic chilling resulted in smaller chicks with lower probabilities of survival (Boersma and Wheelright 1979). The affect of prolonged nest absence on chick survival of black terns merits further study.

The frequent occurrence of nocturnal nest absence in black terns suggests the potential importance of interspecific interactions at night on black tern ecology. However, the causes of nocturnal nest absence are largely unknown. My observations of nest predation at monitored nests provide some support of the hypothesis that nocturnal nest absence is a response to disturbance. Disturbance could be associated with predator activity or as a result of the foraging activities of other animals (e.g., deer). Black-crowned night herons, great-horned owls, mink, and raccoons all occur in Maine wetlands utilized by black terns. Parental quality, age, the quality and quantity of eggs, and the nature of the disturbance detected all likely influence the decision of whether or not to vacate the nest (Meehan and Nisbet 2002). My research demonstrates that diurnal

observations of incubation patterns can be unrepresentative of nocturnal nest attentiveness at black tern colonies (Nuechterlein and Buitron 2002). Monitoring nocturnal attentiveness may have potential for measuring rates of disturbance at black tern colonies and contribute to assessments of factors limiting breeding productivity. However, future research needs to elucidate relationships to disturbance or predation.

CHAPTER 3

EFFECTS OF PREDATION ON BLACK TERN CHICK SURVIVAL INTRODUCTION

Black tern (*Chlidonias niger*) populations are relatively small along the southern edge of their range, and they are designated as threatened or endangered in a number of states and Canadian provinces (Peterjohn and Sauer 1997). Low breeding productivity may be limiting recovery, but there is little information on breeding success. Nest success values for black tern populations in North America range from 0.29 to 0.96, but few studies have estimated fledging production or chick survival (Servello 2000). Black terns are difficult to monitor until they reach fledging age because chicks are adept at hiding in dense wetland vegetation and often move considerable distances from the nest following hatch. Reported chick survival rates are generally low (Servello 2000), and data quantifying the causes of chick mortality are lacking. Chick survival is an important parameter of black tern population growth (Servello 2000), and identifying factors contributing to chick mortality may be critical to understanding black tern ecology and enhancing population recruitment.

Predation of black tern chicks has been reported in a number of studies where chicks were held in enclosures (Bailey 1977, Dunn 1979, Chapman and Forbes 1984, Chapman-Mosher 1986), and anecdotal reports of chick predation by numerous avian and mammalian species are common (Bailey 1977, Dunn 1979). Identifying predation rates of tern chicks under natural conditions is difficult because direct observations of predation events are rare, and little or no evidence often remains (Nisbet et al. 1990, Shealer and Haverland 2000, Maxson and Haws 2000). Black tern nests and chicks may be at high risk of predation because of habitat loss and alteration, coupled with changes in the predator community favoring medium-sized generalist predators (e.g. ravens, raccoons, foxes) (Johnson et al. 1989, Beauchamp et al. 1996a, 1996b, Jimenez et al. 2001). While the negative effects of predation on the breeding productivity of waterfowl have been well studied (for review see Sovada et al. 2001), there has been relatively little research on the effects of predation on chick survival in other ground-nesting, wetland species.

Chick mortality in black terns may also be caused by factors other than predation, including starvation, exposure to adverse weather, and disease (Langham 1972, Morris et al.1976). Limited food resources may reduce growth rates and ultimately lower chick survival. Black terns, like most larids (Erwin et al. 1999), lay their eggs asynchronously over a period of 2-4 days (Dunn and Agro 1995). Incubation begins after the first egg, resulting in hatching asynchrony and the establishment of a size-hierarchy among siblings (Bollinger et al. 1990). The brood-reduction hypothesis (Lack 1954, 1968) contends that hatching asynchrony is an adaptation that facilitates the death of the youngest chick of a brood when food availability is low or unpredictable, thus increasing the likelihood of survival for the remaining siblings. Such differential survival of chicks within broods has been observed in black terns (Beintema 1997) as well as numerous other species of Laridae (Langham 1972, Nisbet et al. 1995, Quinn and Morris 1986, Eyler et al. 1999), suggesting that food resources commonly limit chick survival amongst terns. Previous research in Maine indicated that food resources were not limiting black tern chick growth during the first half of chick growth to fledging (Gilbert 2001).

Severe weather (causing flooding, exposure) could result in direct mortality of chicks, but less severe weather conditions may depress growth and indirectly reduce

survival. Therefore inclement weather (rain, cold) may amplify effects of food limitations by depressing growth, further complicating the interpretation of limiting factors (Dunn 1975). Cold temperatures, wind-speed, and rainfall have been correlated with reduced chick growth and starvation in common and roseate terns (LeCroy and Collins 1972, Dunn 1975, Nisbet and Welton 1984, Becker and Specht 1991), and similar weather has been anecdotally linked with reduced growth in black terns (Beintema 1997, Chapman-Mosher 1986). While growth deformities linked with calcium deficiency have been reported in European black terns (Beintema 1997), occurrences of growth defects or disease have not been reported in black tern chicks in North America and are not likely limiting, although the possibility of disease (epizootics) affecting a colonial waterbird species like black terns must be recognized.

Black terns are listed as endangered in the state of Maine and exhibited low breeding success in 1997-2002 primarily because of low chick survival (Servello unpubl. data). My objective was to determine whether predation and/or food resources were limiting chick survival of black terns in Maine colonies in 2001-2002. Our study design also allowed us to account for mortality potentially due to disease and weather, but these were not the primary focus.

STUDY SITE

This study was conducted from mid-May to late-July during 2001-2002 at three colonies in central Maine: Carlton Pond (Town of Troy, ME); Douglas Pond (Town of Palmyra, ME) and Messalonskee Lake (Town of Belgrade, ME). Carlton Pond and the surrounding wetland have a total area of 431 ha and include 75 ha of semi-permanent emergent wetland bordering 113 ha of open water. The four nesting areas at Carlton

Pond are dominated by sedge (*Carex* spp.), *Sphagnum* spp., and pickerelweed (*Pantedaria cordata*), as well as shrub vegetation. Carlton Pond is part of the National Wildlife Refuge System and is managed by the U.S. Fish and Wildlife Service. Douglas Pond is an impounded wetland on the Sebasticook River and has a total area of open water and wetlands of 227 ha. There are 44 ha of semi-permanent emergent vegetation bordering 85 ha of open water. The three nesting areas at Douglas Pond are dominated by river bulrush (*Scirpus* spp.) or *Carex* spp. Messalonskee Lake is a large lake (1786 ha) with 55 ha of semi-permanent emergent wetland at the southern end, dominated by shrub vegetation, *Carex* species, and *Sphagnum* species.

METHODS

Experimental Design

Predator exclosures were used to determine the degree to which predation limits chick survival. We constructed predator exclosures around individual black tern nests to retain chicks until they reached fledging age and to reduce the potential for predation. Eliminating all predation on chicks at exclosures was the goal but was not required for the experiment. The study was designed to account for causes of mortality in the absence of predation (i.e., broods not depredated). I assumed if predation was limiting, chick survival should be 100% in broods excluded from predation. Nests were also monitored in natural, unenclosed clusters to confirm that chick survival was low as in previous years. I also measured chick growth by hatch-order during the period from hatch to nearfledgling as an indicator of potential food limitation. I assumed that food limitations in black terns, either alone or concurrently with the effects of inclement weather, would be expressed through the differential growth of chicks within broods (i.e., last-hatched chicks should exhibit the lowest growth rate), as in other birds having asynchronous hatching (Langham 1972, Beintema 1997). I tested two hypotheses: (1) predator exclusion results in chick survival near 100% if predation is the primary mortality factor and (2) growth rates of black terns chicks decrease with hatch-order and increasing brood size if food resources are inadequate.

Field Methods

I constructed predator exclosures around 13 nests in 2001 and 14 nests in 2002. Detailed descriptions of exclosure design construction and nest selection are presented in Chapter 4. I selected nests to be excluded in a non-random manner designed to reduce overall disturbance at colonies. I monitored nests every one to two days until the first egg of each nest hatched. I determined hatch-order of chicks based on direct observation of hatching or the relative degree of wetness of new chicks and chick strength. Chicks were assigned an alpha code based on hatch-order: A-chick = first hatched, B-chick = second hatched, C-chick = third hatched. Assignment of a hatch-date was to day only; thus, two chicks of a brood hatched on the same day but several hours apart were both assigned a hatch date of day zero. I applied small dots of enamel paint to chicks' heads to identify them on future visits, and weighed chicks, on average, every two days. The pre-fledging period lasts 18-24 days in black terns (Dunn and Agro 1995); therefore, I retained chicks in exclosures in 2001 until A-chicks reached age 18-19 days or until the chicks fledged from exclosures. In 2002, I released broods when A-chicks reached age 15 days to reduce predation risk in exclosures; chicks became more active in enclosures after day 15, increasing the likelihood of detection by predators. I assumed released chicks survived to fledging (Shealer and Haverland 2000).

We measured chick survival for clusters of nests without exclosures at Carlton Pond and Douglas Pond in 2001-2002 by using elevated blinds to monitor adult behavior, map chicks' locations, and to subsequently count fledgling-aged chicks. Chick survival was not measured at Messalonskee Lake in 2001. I marked all nests to be observed with inconspicuous bamboo stakes designed to resemble cattails. Trained observers monitored nests during three-hour observation periods every 1-3 days using binoculars and spotting scopes. Observers noted nests still being actively incubated, recorded when feeding activity began at nests (indicating hatch), and mapped locations where food provisioning was occurring during brood rearing periods. I assumed 100% egg hatchability at nests categorized as hatched, based on previous results for black terns in Maine (Servello unpub. data) and to avoid entering the nesting area and causing chicks to move. At the end of the monitoring period, when chicks were estimated to be 18-20 days of age, we used a flush count, conducted by a team of four observers on foot and in canoes, at all the mapped points where feeding activity had been observed to count fledglings for calculating survival rate. Broods move frequently and often separate in dense vegetation, preventing the collection of information on a per-brood basis.

Statistical Analyses

I calculated chick survival, defined as the number of chicks fledged divided by the number hatched, for experimental broods that were not depredated. I excluded chicks that escaped exclosures. Chick survival at unenclosed nests was calculated by dividing the number of fledged chicks observed during flush counts by the number of eggs in nests that hatched. Because data for enclosed nests were based on individual chicks and data for unenclosed nests were based on groups of chicks in nesting clusters, I did not statistically compare these values.

I calculated hatching intervals between chicks in a brood and mass ratio at brood completion for each exclosed nest to determine if hatching asynchrony occurred and if size hierarchies were established. Mass ratio at brood completion was defined as a chick's mass divided by the mass of the A-chick when the first measurement of the last chick of a brood to hatch was recorded (modified from Bollinger 1994). Under this definition, A-chicks always had mass ratio 1.0, but B-chicks and C-chicks could have mass ratios less than or greater than 1.0. Mass ratio is considered an index of the competitive ability of the latter-hatched chicks relative to the A-chick during the early post-hatch period (Bollinger 1994).

I calculated growth of black tern chicks using two different methods: (1) linear growth rate (LGR; Gaston et al. 1983, Emms and Verbeek 1991, Nisbet et al. 1995, Erwin et al. 1999, Robinson and Hamer 2000) and (2) asymptotic mass (AM; Bailey 1977, Dunn 1979, Einsweiller 1988, Cruz and Cruz 1990, Emms and Verbeek 1991). Linear regression analysis was used to calculate LGR for each chick during the period between ages 2-11 days, when black tern growth is approximately linear (Beintema 1997). Only chicks with a minimum of three measurements during this interval were included, and growth rates were used in analysis if p < 0.10. To estimate AM values I used iteration to fit the logistic equation,

Chick mass = $AM/(1 + exp(-K^*(age-tzero)))$,

to the growth curves of individual chicks, where K is a growth coefficient and tzero is the time of inflection (Ricklefs 1967, Starck and Ricklefs 1998). I only included chicks that

reached at least 13 days of age because weight measurements approaching the asymptote are required for accurate estimations of AM (Ricklefs 1967). All individuals of a brood must have survived the period when growth parameters were calculated to be included. I conducted separate analyses for two- and three-chick broods. Two-chick broods could only result from a two-egg clutch or the failure of the third egg of a three-egg brood to hatch, but not from the death of an individual from a three-chick brood. Growth parameters of broods that were eventually depredated within exclosures were still utilized in the analyses, as long as they met the above criteria.

I tested for a temporal trend in LGR and AM with hatch date by linear regression analysis. Effects of colony and year on LGR were first examined using General Linear Models (SYSTAT 10.2). Data were then pooled across colonies and years to examine the dependence of LGR and AM on hatch-order and brood size using a nested ANOVA. Year by colony interactions could not be examined because of small sample sizes and unequal treatment sizes, so year and colony effects were analyzed separately. Mean square error tables for analyses are presented in Appendix C.

RESULTS

Eight of the 27 exclosed broods were depredated in 2001 and 2002 and were excluded from the calculation of chick survival in the absence of predation. Additionally, one brood escaped from an exclosure and was excluded from analyses. An additional six chicks (two A-chicks, two B-chicks, and two C-chicks) from six different broods were found dead within exclosures. Four of these six chicks were less than 5 days old and are believed to have died after escaping from the chick enclosure and thus becoming separated from the brood (Chapter 4). The remaining two chicks, a 16-day-old B-chick and an 8-day-old C-chick, were both in three-chick broods and exhibited normal growth for 12 days and 6 days, respectively, before declining in weight prior to death. All other chicks in exclosures were released as planned. Including these six instances of mortality, chick survival (to age 15-18 days) in the absence of predation was 88.2% in 2001, while chick survival (to age 13-15 days) in the absence of predation was 88.9% in 2002 (Table 3.1). Survival of chicks at unenclosed nests was 10.4% in 2001 and between 39.4 and 61.3% in 2002 (Table 3.1). A range is given in 2002 because during the flush counts it was not possible to distinguish between some fledglings released from exclosures and those that came from unenclosed nests.

Of 19 nests exclosed from predation in 2001-2002, thirteen were three-chick broods and six were two-chick broods. In three-chick broods, the mean hatching interval between A- and B-chicks did not differ from zero (0 = 0.15 days; SE = 0.17; p = 0.46). However, the hatching interval between A- and C-chicks (0 = 0.85 days; SE = 0.21; p < 0.01) and between B- and C-chicks (0 = 0.70 days, SE = 0.17, p < 0.01) differed from zero. In two-chick broods, the hatching interval between A- and B-chicks differed from zero (p = 0.03) with B-chicks hatching a mean of 0.67 days (n = 6, SE = 0.21) after the A-chick.

Mass ratios differed between A-, B-, and C-chicks in three-chick broods (p < 0.05). B-chicks were on average 90.7% of the mass of A-chicks (n = 13, 95% CI = 0.83-0.98) near the time of brood completion and C-chicks were a mean of 73.1% of the mass of A-chicks (n = 13, 95% CI = 0.65-0.82) near the time of brood completion. Mass ratios differed between A- and B-chicks in two-chick broods (p < 0.05). B-chicks were on

Table 3.1. Chick survival estimates for unenclosed nests and nests with predator exclosures that were not depredated at Carlton Pond and Douglas Pond, Maine, 2001-2002.

		Unenclos	sed nests	Nests exclud			
Year/site	No. nests hatched	Total no. eggs in hatched nests ^a	No. of chicks fledged	Chick survival (%)	No. chicks released	Chick survival (%)	
2001							
Carlton Pond	8	24	1	4.2	8	88.9	
Douglas Pond	8	24	4	16.7	7	87.5	
Total	16	48	5	10.4	15	88.2	
2002							
Carlton Pond	7	21	$7 - 13^{b}$	33.0 - 61.9	15	83.3	
Douglas Pond	4	$10 - 12^{c}$	6	50.0 - 60.0	9	100	
Total	11	31 – 33	13 – 19	39.4 - 61.3	24	88.9	

^a Nests were classified as "hatched" when adults were observed bringing food to the nest. Hatchability in hatched nests was assumed to be 100%.

^b Range is given because it was not possible to distinguish between some fledglings released from enclosures and those from unenclosed nests.

^c Range is given because one nest was discovered after it had hatched and the number of eggs was not known.

Feeding by adults was observed at the nest site, so a minimum of one chick hatched, but potentially three.

average 72.4% of the mass of A-chicks (n = 6, 95% CI = 0.59-0.86) near brood completion.

Neither LGR (p = 0.102, n = 51, $r^2 = 0.034$) nor AM (p = 0.483, n = 43, $r^2 = 0.000$) were affected by hatch date. Estimates of LGR for individual chicks ranged from 3.22 g/day to 5.87 g/day (Table B.1). Colony (n = 39, F = 1.08, p = 0.392) and year (n = 39, F = 2.43, p = 0.115) did not affect LGR, so data were pooled across years and colony for analysis while retaining nest as a nested factor (n = 39, F = 6.33, p = 0.001). Linear growth rates were not affected by hatch-order for either three-chick broods (n = 39, F = 2.13, p = 0.140) or two-chick broods (n = 12, F = 1.06, p = 0.350) (Table 3.2). Growth rates also did not differ (n = 51, F = 1.33, p = 0.258) with brood size. Estimates of AM for individual chicks ranged from 39.01 g to 73.49 g (Table B.2). Asymptotic masses (AM) did not differ (n = 33, F = 1.36, p = 0.292) among colonies and were pooled, but year effects were present with AM values for 2002 greater than 2001 (n = 33, F = 4.07, p = 0.035) (Table 3.3). The effect of hatch-order on AM was not significant for either year (n = 33, F = 0.55, p = 0.584). I did not compare AM estimates by hatch-order for two-chick broods given the small sample sizes per year.

DISCUSSION

The study design for this experiment assumes that enclosing chicks does not decrease chick survival or growth. It has been proposed that exclosed broods do not mimic natural conditions and that such an experimental design significantly affects black tern behavior (Shealer and Haverland 2000). Unenclosed black tern broods are often observed to separate, and Shealer and Haverland (2000) hypothesize that "containment of the entire brood prevents chicks from scattering and keeps the smaller chick in the

	Linear growth rate ^a (g/day)		
Hatch-order	n	0	SE
Three-chick broo	ods		
A-chick	13	4.59	0.08
B-chick	13	4.44	0.08
C-chick	13	4.38	0.08
All chicks	39	4.47	0.07
Two-chick brood	ds		
A-chick	6	4.79	0.16
B-chick	6	4.55	0.16
All chicks	12	4.67	0.19

Table 3.2. Linear growth rates of black tern chicks by hatch-order for three- and twochick broods at Carlton Pond, Douglas Pond, and Messalonskee Lake, Maine, 2001-2002.

^a Data pooled by colony and year. Linear growth rate (LGR) for individual chicks determined by linear regression analysis.

		Asymptotic Mass ^a	(g)	
Hatch-order	n	0	SE	
2001				
A-chick	7	61.82	1.36	
B-chick	7	56.98	1.36	
C-chick	7	59.48	1.36	
All chicks	21	59.43	1.81	
2002				
A-chick	4	60.86	1.79	
B-chick	4	64.59	1.79	
C-chick	4	65.38	1.79	
All chicks	12	63.61	1.21	

Table 3.3. Asymptotic mass of black tern chicks by hatch-order for three-chick broods at Carlton Pond, Douglas Pond, and Messalonskee Lake, Maine, 2001-2002.

^a Asymptotic Mass (AM) for individual chicks determined by fitting the logistic equation to growth data using iteration.

vicinity of its larger siblings, where it may be better able to compete for food." However, an alternate hypothesis proposes larger chicks in asynchronously hatching broods may act aggressively toward smaller siblings or keep them away from parents during feeding, as has been observed in other species (Jenni 1969, Milstein et al. 1970, Hahn 1981). Such behavior would depress growth of C- chicks retained in predator exclosures. I did not see evidence of differential growth with hatch-order indicating that food did not limit survival in 2001-2002.

Higher survival observed in experimental broods relative to unenclosed broods may be affected by the earlier release of chicks from exclosures (ages 13-18 days) relative to unenclosed chicks during flush counts (18-20 days). Differences in ranges of chick ages at the time of release compared with those at the time of flush counts were a result of protocols to minimize losses of chicks to predation. Chicks older than 15 days were observed to become more conspicuous in exclosures (increased wing flapping, vocalizations)(Dunn 1979) thus broods were removed from exclosures when the A-chick reached age 15 days to reduce detection by predators. At unenclosed broods, we waited until the youngest chick(s) in the cluster was ready to fledge (~age 18 days) to minimize disturbance (scattering chicks) at the colony and thus potentially increase loss to predation. While I cannot quantify rates of chick losses over time at unenclosed nests, anecdotal observations indicate that most chick loss occurred in the first ten days after hatch. This suggests the higher chick survival recorded in exclosures was not likely attributable to the shorter interval. Comparisons between survival rates for enclosed and unenclosed were not a goal of this study and thus should be interpreted cautiously. My design was based on testing for 100% survival in the absence of predation. Chick

survival rates at unenclosed clusters were measured to confirm that rates were as low as in previous years (Servello unpubl. data).

My results indicate that in the absence of predation, nearly all chicks survive. Chick survival was greater than 88% in both years at nests excluded from predation. If I excluded the four instances of chick mortality potentially related to investigator disturbance, chick survival in non-predated exclosures would have been 95%. In contrast, chick survival of unenclosed broods varied between years but was lower overall, as has been consistently observed in these colonies. Chick survival estimates in Maine colonies in 1997 and 1999-2000 have all been low, ranging 8-36% (Servello unpubl. data). Low chick survival (< 0.50) is not unique to Maine and has also been reported in western New York (0.48; Hickey 1997) and Wisconsin (0.12; Bailey 1977). High variability in chick survival across years and study sites may be the result of variation in predator communities. Black terns are considered semi-colonial nesters and the presence of only one or a few predators may have a significant effect on chick survival rates. Although direct observations of chick predation are relatively rare, enough anecdotal reports exist to suggest predation is a common factor influencing chick survival throughout the range of this species. Great blue heron (Ardea herodias, Chapman and Forbes 1984, Shealer and Haverland 2000), mink (Mustela vison, Dunn 1979, Hickey 1997, Servello pers. comm.), northern harrier (*Circus cyaneus*, pers. obs.), great horned owl (Bubo virginianus, Einsweiller 1988, Bailey 1977), black-crowned night heron (Nycticorax nycticorax, Bailey 1977), raccoon (Procyon lotor, Servello pers. comm.), raven (*Corvux corax*, this study), and fish (Don McDougal pers. comm.) have all been directly observed or else implicated by physical evidence to be responsible for predation

of black tern chicks. Other potential chick predator species that commonly occur in marshes utilized by black terns include American bitterns, crows, magpies, striped and spotted skunks, snapping turtles, great egrets, bullfrogs, and northern water snakes (Bailey 1977, Hickey 1995, this study).

My results offer no support for the hypotheses that food resources, disease, or inclement weather reduce chick survival in black terns at more than marginal levels. I observed significant differences in the mass ratios of chicks within broods, thus demonstrating that a size hierarchy was established during the early post-hatch period. Despite this size inequality, differential growth (LGR and AM) with hatch-order was not observed for either two-chick or three-chick broods. Furthermore, neither LGR nor AM were found to significantly decrease with increasing brood size, as would be expected if food resources were scarce. Sample sizes may have been inadequate for tests on twochick broods; however, considering the mean tended to be higher in three-chick broods, a larger sample size would not likely have resulted in statistically significant differences. Mass ratios are dependent on egg mass (biological factor), the hatching intervals between chicks (biological factor) as well as the age of the last-hatched chick when its first weight measurement was recorded (sampling factor), and thus merit cautious interpretation. Because logistic equations require growth measurements approaching asymptotic mass for accurate estimations of that variable, greater AMs reported for 2002 may be the result of differences in sampling protocol between years and not environmental differences. The differences in AM by year are likely the result of a small sample size for 2002 coupled with the fact that growth measurements during this year extended at most to 15 days, and often less for B- and C-chicks. This conclusion is supported by the fact that

mean AM values increase with hatch-order in 2002, which is the opposite trend for the corresponding LGR values. Regardless, my finding that C-chicks did not grow slower than A-chicks does not support the brood reduction hypothesis and suggests that food resources were not limiting to black tern chicks in Maine colonies during 2001-2002.

Mean LGR and AM values for Maine black tern chicks were within ranges reported in other studies of black tern growth (Bailey 1977, Dunn 1979, Chapman-Mosher 1986, Beintema 1997, Starck and Ricklefs 1998, Gilbert 2001). Six chicks from three broods in 2001 had LGRs below 4.0 g/day, and two of these chicks exhibited LGRs below the 3.32 g/day rate reported for starved black tern chicks in Europe (Beintema 1997). Of these six chicks, four were depredated prior to release, one chick was found dead, apparently of starvation, and one chick was released on schedule. Two of these broods occurred in the same colony as broods exhibiting normal and even high LGRs, suggesting factors other than food limitation were responsible for depressed growth in the former. Starvation of chicks can be a direct result of insufficient food resources (poor foraging environment) or an indirect result caused by low "parental quality," whereby there is ample food but the parents are inadequate at providing sufficient food for their young (Langham 1972, Nisbet and Cohen 1975, Parsons 1975, Gaston et al. 1983, Bollinger 1994, Nisbet et al. 1995). In the case of the latter, the breeding adults may have been young or inexperienced parents or else were affected by investigator disturbance associated with exclosure construction. I observed no anecdotal evidence that inclement weather resulted in either reduced chick growth or survival. In early July 2002 severe thunderstorms occurred on several days, but no mortality of exclosed chicks

resulted. Likewise, no mortality clearly resulting from disease or stunted growth was detected.

Results from the present study in conjunction with previous research offer clear evidence that predation is the primary factor limiting chick survival in Maine colonies. During 1998-2002 no associations between chick mortality and inclement weather or disease were observed (Gilbert 2001, this study). Chick mortality resulting from starvation has been uncommon and is likely the result of poor parental quality and not limited food resources (Gilbert 2001, this study). Numerous factors attributed to a high quality foraging environment have been observed over the course of this study: (1) average clutch sizes near three, the typical maximum (Servello unplubl. data); (2) hatchability near 100% in all years (Servello unplubl. data); (3) a lack of differential growth with hatch-order or brood size (this study, Gilbert 2001); and, (4) LGR (Gilbert 2001, this study) and AM (this study) values within the ranges typically reported for normal growth in this species. Cumulatively, these results suggest food resources do not limit black tern productivity in Maine wetlands. Predation significantly affects waterfowl breeding productivity in the prairie pothole region of Canada and the United States (Sovada et al. 2001), which is core black tern habitat (Dunn and Agro 1995), so my conclusion that predation significantly influences recruitment should not be surprising. Chick predation rates of 61.5% (Bailey 1977) have been reported for black tern chicks retained in enclosures in Wisconsin, and predation has been hypothesized as the cause of low fledging success in Forster's terns nesting in Minnesota wetlands (Cuthbert and Louis 1993). The wetland habitat utilized by black terns throughout their range is rich in potential chick predators given the high productivity of the large emergent wetlands they

inhabit or as a result of habitat alteration or shifts in the distribution of predator species (Johnson et al. 1989). Predation should be considered a principal limiting factor on the breeding productivity of black terns in Maine wetlands, and predation effects should be examined throughout the breeding range of the species to increase our understanding of factors limiting population growth.

CHAPTER 4

USE OF CHICK ENCLOSURES AND PREDATOR EXCLOSURES TO INCREASE CHICK SURVIVAL IN BLACK TERNS

INTRODUCTION

Predator exclosures have been utilized as a management tool to increase breeding productivity in piping plovers (Charadrius melodus) (Rimmer and Deblinger 1990, Melvin et al. 1992, Vaske et al. 1994, Larson et al. 2002, Maxson and Haws 2000, Mabee and Estelle 2000), snowy plovers (C. alexandrinus) (Mabee and Estelle 2000), killdeer (C. vociferus) (Nol and Brooks 1982, Mabee and Estelle 2000), and pectoral sandpipers (Calidris melanotos) (Estelle et al. 1996). Exclosures are typically constructed around individual nests to prevent access by medium- to large-sized predators (mammalian and avian) during the egg-stage. Adults shorebirds, such as those listed above, can easily enter and exit exclosures by walking through fence openings, and chicks readily leave the exclosures after hatching (Rimmer and Deblinger 1990). Smaller enclosures designed to confine chicks for research purposes (monitoring growth, survival, feeding behavior, etc.) rather than predator deterrence are also common. Such enclosures have commonly been used with tern species, including black terns (Chlidonias niger; Bailey 1977, Dunn 1979, Chapman Mosher 1986, Hickey 1997, Shealer and Haverland 2000), common terns (Sterna hirundo; Nisbet and Drury 1972, Morris et al. 1976), arctic terns (S. paradisaea; Robinson and Hamer 2000), gull-billed terns (S. nilotica; Eyler et al. 1999), roseate terns (S. dougallii; Nisbet and Drury 1972, LeCroy and Collins 1972, Burger et al. 1996), and Caspian terns (S. caspia; Quinn and Morris 1986).

Black terns are a federal species of concern and are endangered, threatened, vulnerable, or of special concern in 21 states and three Canadian provinces (Shuford 1999). Shealer and Haverland (2000) evaluated the use of nest enclosures as a research tool for measuring reproductive success of black terns and found that enclosures had no detrimental effects on either nest success or fledging success. The relatively unstable wetland substrates characteristic of black tern nesting areas are a challenge for use of larger predator exclosures. I investigated the use of chick enclosures concurrently with predator exclosures at individual black tern nests. My objectives were to develop an enclosure/exclosure design that would (1) allow unimpeded feeding and brooding by the adults; (2) retain chicks for a period of 15-19 days (or until fledging); and, (3) prevent chick predation by terrestrial and aerial predators. Black terns differ from other species for which nest exclosures have been constructed in that adults fly rather than walk into exclosures, and our design had to accommodate this behavioral difference. Development and use of enclosures/exclosures was part of a study of chick growth and survival (Chapter 3). I describe here the design and field methods for utilizing exclosures in a marsh habitat and report on their efficacy at excluding predators.

STUDY SITE

Our study was conducted from mid-May to late-July during 1998-2002 at four colonies in central Maine: Carlton Pond (Town of Troy, ME); Douglas Pond (Town of Palmyra, ME) Messalonskee Lake (Town of Belgrade, ME); and Madawaska Pond (Town of Palmyra, ME). The Carlton Pond site was 431 ha in area and included 75 ha of semi-permanent emergent wetland bordering 113 ha of open water. Nesting areas are dominated by sedge (*Carex* spp.), *Sphagnum* spp., and pickerelweed (*Pantedaria*

cordata), as well as sparse shrubby vegetation. Douglas Pond is an impounded wetland on the Sebasticook River and has a total area of open water and wetlands of 227 ha. There are 44 ha of semi-permanent emergent vegetation bordering 85 ha of open water. Nesting areas at Douglas Pond are dominated by river bulrush (*Scirpus* spp.) or *Carex* species. Messalonskee Lake is a large lake (1786 ha) with 55 ha of semi-permanent emergent wetland at its southern end, dominated by shrub vegetation, *Carex* species, and *Sphagnum* species. Madawaska Pond is 106 ha in area and nesting areas contains 14 ha of semi-permanent emergent vegetation dominated by *Carex* species.

METHODS

Experimental Design

I documented nest success, hatchability, and chick survival using small enclosures at 59 nests from 1998-2001 for the period from hatch to day 3-10. I used large predator exclosures concurrently with chick enclosures at 31 nests from 2001-2002 for the period from hatch to day 15-19. I compared chick survival in enclosures and exclosures with survival at unenclosed nests monitored from elevated blinds (Chapter 3). I selected nests for enclosure/exclosures in a non-random method. The substrate immediately surrounding the nest had to support an enclosure and an exclosure as well as a researcher without sinking or otherwise damaging the nest. Enclosed nests also must have been greater than 50 m from the nearest unenclosed nest. I determined the hatch order of chicks from direct observation of hatching or else based on the degree of wetness of the chick. I placed dots of enamel paint on the head of each chick to differentiate among them, and recorded the date the nest was found, the number of eggs, the date the enclosure was deployed, the outcome of each nest (hatch, predation, flooding by water level changes, abandonment, unknown), and the fate of the chicks (predation, escape, released, unknown). Nest predation was indicated by the presence of shell fragments or pecked eggs or was assumed if eggs were missing prior to their estimated hatch date. Chicks missing from exclosures prior to their anticipated fledge date were considered depredated if there was no evident means of escape from the exclosure. Dead chicks were removed from the exclosures to avoid attracting predators.

Enclosures

I placed enclosures around nests estimated to be in the latter half of incubation. Circular chick enclosures were made of hardware cloth and were 95-105 cm in diameter and 30 cm tall. A band of black landscaping cloth was stapled around the inside of the enclosures from the bottom to a height of 15 cm. Landscaping cloth provided concealment and protected chicks from sharp wire edges. Two pieces of chicken wire wrapped with landscaping cloth attached to the inner portion of the enclosure provided overhead protection for chicks. These were designed to extend towards the center of the enclosure at a height of 15 cm and had a width of approximately 10-15 cm. These overhead wire covers were raised in place after hatch and provided a place for chicks to hide when adults gave alarm calls. Enclosures were painted green and were held tightly to the substrate with three wooden stakes. Enclosures were erected quickly in the field (2-4 minutes), which included attachment to three wooden stakes pressed into the substrate to be level with the top of the enclosure. After clutches hatched, pieces of shrub or aquatic vegetation were placed in and around the enclosure to provide additional cover. Strips of camouflage netting 30 - 40 cm in height and supported by four small bamboo stakes were also used in 2002 to attempt to avoid predation such as those

instances in 2001 that were thought to be associated with inadequate cover. Camouflage had a diameter approximately equal to the enclosures, provided additional overhead concealment, and increased the effective height of the enclosures twofold. Chicks were released when the eldest chick (hereafter referred to as "A-chick") of each brood was between the ages of 3 and 10 days. In 1998, 30 enclosures were used (15 at Douglas Pond, 6 at Carlton Pond, 6 at Messalonskee Lake, and 3 at Madawaska Pond), and broods were released after the last chick hatched. Eleven enclosures were used at Douglas Pond in 1999, and a total of 14 enclosures were used in 2000 (8 at Douglas Pond and 6 at Carlton Pond). Broods in 1999 and 2000 were released when the A-chick was 8-10 days old.

Exclosures

Predator exclosures were circular and constructed from one roll of green fencing 1.5 m in height and 15.24 m in length. Exclosures were 4.5 - 4.8 m in diameter. Exclosures were wrapped in landscaping cloth (attached by wire or plastic ties) to a height of 0.85 m with a 0.35 m skirt of cloth hanging loosely below the fencing. The landscape cloth was painted green and brown to blend with the wetland vegetation. Exclosures were placed around nests with enclosures on days with fair weather (no rain, temperatures near 65-75° and calm winds) to prevent the eggs from becoming either too cool or too hot while adults were off the nest. Eggs were placed in a closed, padded container during exclosure placement to prevent damage or heat stress. Two to four people were required to erect exclosures and construction time was 10 - 25 minutes (depended on water depth). Eight to ten wooden stakes were used to secure the exclosure flush to the ground. Stakes did not extend beyond the top of the fencing to discourage

birds from perching. Four rope guidelines were attached near the top of four of the wooden stakes and secured to the ground using smaller stakes to add tension to exclosures and to prevent blowdown by strong winds. The skirt of landscaping cloth was submerged under the extant water along with the lower portion of the exclosure wire to serve as an additional ground-level barrier. The two ends of the exclosure fencing, overlapped and fastened together so no gap remained, served as the entrance for researchers. The exclosure was observed from a distance to ensure that at least one adult tern landed within exclosures for at least 30 seconds following placement.

Predator exclosures were constructed at 17 nests in 2001 (6 at Douglas Pond, 6 at Carlton Pond, and 5 at Messalonskee Lake). Exclosures were typically constructed several days after enclosures and when eggs were estimated to be close to hatch or, in a few cases, when one or more chicks had already hatched. I staggered construction of enclosures and exclosures to minimize disturbance at any one time and reduce the likelihood of nest abandonment. Staggering construction allowed adults to acclimate to enclosures prior to placement of exclosures. However, in four cases early in the study, enclosures and exclosures were constructed around nests on the same day. Following hatch, exclosures were visited, on average, every two days to weigh chicks and perform minor maintenance. Chicks were retained in exclosures until A-chicks reached 18-19 days of age or until chicks fledged (i.e., flew) from exclosures. Chicks that did not fledge were released outside of exclosures. Exclosures were constructed around 14 nests in 2002 (9 at Carlton Pond and 5 at Douglas Pond). Field methods were similar to 2001, with three exceptions: (1) no exclosures were constructed on the same day that corresponding nests were enclosed; (2) chicks of a brood were released when A-chicks

reached 15 days of age; and, (3) additional artificial camouflage (as described above) and copious dense vegetation were added to enclosures after hatch to enhance concealment.

Enclosure and exclosure days are defined as the number of days prior to hatch that each structure was placed around a nest. Nest success is the proportion of nests hatching at least one chick. Hatchability is the ratio of hatched eggs to total number of eggs incubated to full term. Eggs from abandoned nests were excluded. Chick survival is the proportion of hatched chicks that survived to day 18 (2001) or day 15 (2002).

RESULTS

On average, enclosures were put in place 6.8-8.7 days prior to hatch dates of eggs and exclosures 3.1-3.6 days prior to hatch (Table 4.1). Following enclosure construction, adults generally landed at the nest 2-10 minutes after researchers withdrew. Only one nest was abandoned following erection of a chick enclosure during the study; the adults initially resumed incubation but later abandoned the nest, possibly because of additional researcher disturbance. Adults generally returned to the nest 15-30 minutes after exclosures were erected, but in one instance the interval from the time exclosure construction was complete to the potential resumption of incubation 1-3 days following exclosure construction, and a fourth nest failed to hatch despite apparent resumption of incubation. Two of these four cases of abandonment occurred at nests where the chick enclosures and predator exclosures were constructed on the same day. In 2002 no nests were abandoned in the interval between exclosure construction and hatch.

Annual nest success for nests with enclosures (no exclosures) ranged from 43 to 79% for 1998-2001 (Table 4.2). In 1998 flooding from heavy rains was the primary

cause of failed nests in enclosures (Table 4.2) and losses to flooding were not influenced by enclosures. There were eight instances of nest depredation in 1998-2001 at nests with Table 4.1. Mean number of days prior to hatch that enclosures and exclosures were constructed around black tern nests in Maine, 1998-2002.

		Enclosures			Exclosures			
Year	n	0	Range	n	0	Range		
1998	13	6.8	1 – 11					
1999	7	8.6	0 – 16					
2000	11	7.5	0 - 11					
2001	14	7.1	0-17	13 ^a	3.6	0-12		
2002	14	8.7	4 – 16	14 ^b	3.1	-2 - 7		

^a Four of these exclosures were constructed on the day the first chick of a brood hatched.

^b One exclosure was constructed on the day the first chick of a brood hatched and one exclosure was constructed post-hatch and exclosure days were negative.

Year	No. nests enclosed	Nest Success ^a (%)	Hatchability (%)
1998	30	43.3 ^b	100
1999	11	63.6 ^c	100
2000	14	78.6 ^d	100
2001	4	50.0 ^e	100

Table 4.2. Nest success and egg hatchability for black tern nests with chick enclosures in Maine, 1998-2001.

^a Successful nest defined as hatching at least one chick.
^b 17 failed nests: 16 nests were flooded and one nest was depredated.
^c 4 failed nests: two was depredated, one was abandoned, and one was flooded.
^d 3 depredated nests.
^e 2 depredated nests.

enclosures (no exclosures). Hatchability of eggs incubated to full term at enclosed nests was 100% from 1998-2001.

In 2001, nine chicks were released from five hatched nests (60% chick survival) with predator exclosures at Carlton Pond (Table 4.3). At Douglas Pond, seven chicks were released from four hatched nests (63.4% chick survival) with predator exclosures (Table 4.3). No chicks were released from four hatched nests at Messalonskee Lake (Table 4.3). Chick survival at exclosed nests across all three colonies was 44.4%. Predators entered seven different exclosures and depredated 17 chicks. All four hatched nests at Messalonskee were depredated within a three-day period. These four depredated exclosures contained three 15-day-old chicks, three 16-day-old chicks, two 10-day-old chicks, and two 6-day-old chicks, respectively. No evidence remained to identify the predator(s), although odor in the vicinity suggested mink (Mustela vison). Of the two depredated exclosed nests at Carlton Pond, feathers remaining at one nest suggested the predator was a northern harrier (*Circus cyaneus*), as a nesting pair was frequently observed flying over the colonies. The two depredated exclosures at Carlton Pond contained three 16-day-old chicks, and one 14-day-old chick, respectively. The depredated exclosure at Douglas Pond contained three chicks less than a week old. In addition to the 17 depredated chicks, three chicks from three different broods escaped their respective enclosures and were found dead in their exclosures, apparently from exposure. Overall hatchability of eggs at exclosed nests was 97.3%.

In 2002, 15 chicks were released from nine hatched nests (83.3 % chick survival) with predator exclosures at Carlton Pond (Table 4.3). At Douglas Pond, nine chicks were released from five hatched nests (75.0% chick survival) with predator exclosures (Table

Year (Colony	No. nests exclosed	No. nests hatched	No. chicks hatched	Hatchability (%)	No. chicks depredated (no. of nests)	No. chicks released	Chick survival (%)
2001 ^a	Carlton	6	5 ^c	15	100	4 (2)	9 ^h	60.0
	Douglas	6	4^d	11	92 ^f	3 (1)	7^{i}	63.6
	Messalonskee	5	4 ^e	10	100	10 (4)	0	0
	Total	17	13	36	97	17 (7)	16	44.4
2002 ^b	Carlton	9	9	18	69 ^g	0	15 ^j	83.3
	Douglas	5	5	15	100	3 (1)	9 ^k	75.0
	Total	14	14	33	81	3 (1)	24	80.0

Table 4.3. Nest success, egg hatchability, and chick survival of black tern nests that had both chick enclosures and predator exclosures in Maine, 2001-2002.

^a In 2001, chicks were released from exclosures when the A-chick reached age 18-19 days.

^b In 2002, chicks were released from exclosures when the A-chick reached age 15 days.

^c One nest was abandoned following exclosure construction and failed to hatch.

^d One nest was abandoned following exclosure construction and failed to hatch. The other nest was incubated by adults past the expected hatch date and was eventually abandoned.

^e One nest was abandoned following exclosure construction and failed to hatch.

^f One egg of a four-egg brood failed to hatch.

^g Eight eggs failed to hatch: 3 were cases where the 3rd egg of three-egg clutches failed to hatch, one nest with 2 intact eggs was abandoned, and two nests experienced high water levels that likely resulted in 3 eggs not hatching.

^h In addition to the depredated chicks, one chick escaped its enclosure and was found dead, and another chick died for unknown reasons.

ⁱ In addition to the depredated chicks, one chick escaped its enclosure and was found dead.

^j 3 chicks died for reasons unrelated to predation: a two-day-old chick was abandoned, a one-day-old chick was not brooded and found dead, and an 8-day old chick died for unknown reasons.

^k In addition to the depredated chicks, 3 chicks escaped their exclosure and were excluded from the calculation of chick survival.

4.3). Chick survival of exclosed nests across both colonies was 80.0%. One exclosure containing three chicks (less than a week old) was depredated at Douglas Pond. Additionally, one chick died from abandonment; one chick died because it was separated from its brood when it escaped from the enclosure; and, another 8-day-old chick died for unknown reasons. Two broods escaped their respective enclosures when water levels increased nearly 20 cm in one day, but were found and returned. Two days later when water level dropped, the same two broods escaped again (this time by going underneath the raised enclosures), but were found and returned. Three chicks escaped an exclosure and were not found (predation was ruled out since one of the chicks was observed outside the exclosure); these chicks were excluded from estimates of survival. Hatchability of exclosed nests at Carlton Pond was 69.2%, compared to 100% at Douglas Pond. At Carlton Pond, the 3rd egg of three-egg clutches failed to hatch at three nests, and another nest containing one chick and two intact eggs was abandoned. Additionally, three eggs from two adjacent exclosed nests failed to hatch because of high water levels flooding the nest.

DISCUSSION

Our enclosure/exclosure design was generally effective in achieving our objectives of chick retention, predator exclusion during incubation, and not impeding normal adult behavior, with some exceptions. Most adult terns adopted both enclosures and exclosures and resumed seemingly normal incubation and feeding patterns as long as exclosures were not constructed too early in the incubation period. After nest enclosures were erected, adults typically flew over the nest a number of times and hovered low to the ground inspecting the nest. Adults responded more variably to the construction of predator exclosures; adults exhibited similar flying and hovering behavior but took longer to resume incubation. The willingness of adults to leave their nests for extended periods was anecdotally observed to decrease as the incubation period lengthened (Cuthbert 1954). Therefore, we would expect enclosures constructed towards the latter half of incubation to be accepted more readily than those constructed earlier in incubation. Shealer and Haverland (2000), in a study of investigator disturbance on black tern reproductive success, recommended that enclosures should not be constructed until the first egg is pipping. We typically constructed enclosures 7-8 days prior to hatch and noted only one instance where adults abandoned their nest, suggesting that adults tolerate the presence of enclosures during this phase of incubation. The 100% hatchability of eggs during 1998-2001 demonstrates that enclosures did not change adult incubation behavior. In 2001, the first year we used exclosures, hatchability was nearly 100%, but there were four cases where adults abandoned nests prior to hatch. In 2002, hatchability was 100% at Douglas Pond but was less than 70% at Carlton Pond. The decrease in hatchability of exclosed nests between 2001 and 2002 was attributed to the addition of dense vegetation and artificial camouflage in enclosures following the hatch of the first and/or second chick of an exclosed nest. These measures were designed to increase concealment in the enclosure. However, at three of these nests, the third egg of a threeegg clutch failed to hatch and another nest with one chick and two intact eggs was abandoned altogether. In the case of the former, we hypothesize the addition of dense vegetation to the enclosures resulted in adults' failure to properly incubate the remaining egg, and, in the case of the latter, was responsible for abandonment. Placement of dense vegetation in the enclosure following the hatch of the first two chicks may have resulted

in the refusal of adults to incubate the remaining egg. Adults may have landed in enclosures only to feed chicks. Overall, detrimental effects to black tern behavior were observed when (1) enclosure/exclosures were constructed in the earlier stages of incubation and (2) when dense vegetation was applied in enclosures prior to complete hatch of the brood. The fact that only a small percentage of unsuccessful nests were lost to predation, suggest experimental nests were not highly vulnerable while in enclosures. Overall, these nest success rates are typical of rates in the literature for nesting colonies (Servello 2000).

Chick enclosures with predator exclosures successfully retained the majority of chicks during 2001-2002, but fluctuating water levels at some sites (most notably Douglas Pond) resulted in chicks escaping under enclosures when water levels dropped or climbing/swimming over the top of enclosures when water levels increased. Daily fluctuations of 10-20 cm in water depth were not uncommon during some times of the year. Because the height of enclosuress is only 30 cm, daily adjustments would be required during these periods. Taller enclosures could potentially alleviate this problem, but it may increase rates of nest abandonment. I found that broods could escape enclosures with fluctuating water levels. Vegetation added for overhead cover in the enclosures must thus be selected carefully to prevent escape.

The efficacy of predator exclusures varied dramatically between 2001 and 2002. Predators successfully entered 41% of the predator exclosures in 2001, including all four exclosed nests with chicks at Messalonskee Lake. Black tern chicks in enclosures may become more conspicuous as they approach fledging, engaging in behavior such as wing posturing and vocalization that could attract predators. Increased susceptibility with age was supported by our data, as ten of the 17 depredated in 2001 were between the ages of 14 and 17 days. When researchers approached enclosures, chicks were often well hidden around the inside perimeter of enclosures or else under vegetation remaining immobile. In the absence of cover chicks moved continuously in the enclosures looking for places to hide, thus increasing their visibility. As a result I altered the field methodology in 2002 by (1) increasing concealment in enclosures using natural and artificial vegetation and (2) by releasing all chicks of a brood when A-chicks reached 15 days of age, thus allowing chicks the freedom to select escape cover. I believe that change accounted for the greater proportion of chicks released in 2002. It is unknown whether chicks released earlier would ultimately survive to fledging at a similar, greater rate.

Chick survival at exclosed nests was greater than estimated survival of natural nests in both 2001 and 2002. In 2001, chick survival at exclosed nests (44.4%) was approximately four times greater than chick survival (10.4%) observed at unenclosed nests at Douglas and Carlton Ponds (Chapter 3). In 2002, chick survival at exclosed nests was 80.0% compared to an estimate of 39.4 - 61.3% for unenclosed nests (Chapter 3). Given the apparent increase in chick survival between years at unenclosed nests, I cannot conclude that changes in protocols between years improved the efficacy of exclosures.

With small numbers of birds nesting in colonies, significant losses could result from the actions of one predator. In 2001, a nesting pair of northern harriers was frequently observed flying over Carlton Pond whereas in 2002, there were no harriers. In 2001 a mink was suspected to be responsible for all four cases of depredation at exclosed nests that all occurred within three days of one another. Knowledge of the predator community is thus very helpful in designing an exclosure protocol.

RECOMMENDATIONS FOR USE OF ENCLOSURES/EXCLOSURES

I advocate the use of chick enclosures concurrently with predator exclosures as a research technique, but would only cautiously recommend their use as a conservation tool. Enclosures and exclosures were utilized in the present study strictly for research purposes and the methodology was altered from 1998-2002 as priorities shifted. The design and field methodology described here are time and labor intensive and require almost daily visits to exclosed nests. The use of exclosures for research purposes (chick survival and growth) at small scales may justify labor and time requirements. Exclosures may be useful as a conservation tool only for small, high-risk populations of black terns, as labor and time requirements at large colonies would be large.

I would discourage the construction of enclosures and exclosures at sites that typically have large daily water level fluctuations, as well as sites with highly unstable substrate. I recommend the construction of enclosures up to seven days prior to expected hatch and construction of exclosures one or two days prior to expected hatch to minimize the likelihood of abandonment. Enclosures and exclosures should not be constructed during the same day, and events that would stress adult birds (such as capture) should not take place the same day as enclosure construction. Using vegetation and artificial camouflage is cautiously encouraged for enclosed chicks. Vegetation should not be added (and concealment structures) until all eggs are hatched and the youngest chick reaches three days of age. Vegetation should be added sparingly initially, but the amount can be steadily increased each subsequent visit. Artificial camouflage used to increase the effective height of enclosures should only be added when the oldest chick reaches age 10 days. I recommend that chicks be released from exclosures when the A-chick reaches

15 days of age in order to reduce the likelihood of predation within the exclosures.

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Appendix A

Basic Statistics of Wetland-Scale Variables, Nest Aggregation Variables, and Concealment Factor Variables Used to Validate Top-performing Logistic Regression Models Predicting Nest Success or Nest Predation for Black Tern Nests in Maine Wetlands, 1998-2002.

Table A.1. Mean and standard error estimates for continuous variables used to validate top-performing logistic regression models predicting nest success or nest predation for black tern nests in Maine, 1998-2002.

		Successful nests ($n = 58$)			Depredated nests $(n = 32)$		
Variable	Definition	0	SE	range	0	SE	range
NN ^a	Distance to nearest nest (m)	56	6	7.5 – 232	53	19	5 - 604
NP1	No. depredated nests within 30 m	0.16	0.05	0-2	0.59	0.17	0-4
NP2	No. depredated nests between 30 – 100 m	0.81	0.19	0-9	1.47	0.32	0-8
CS	No. nests in colony	6.8	0.7	1 – 18	6.7	0.9	1 – 18
CA ^a	Cluster area (m ²)	5968	943	1 – 38794	6824	1733	1 - 38794
DU^{a}	Distance to upland edge (m)	269	27	55 - 827	234	33	55 - 698
WB^a	Distance to main water body (m)	69	8	1 – 251	78	11	1 – 205

^a Variables log-transformed for analyses

Table A.2. Frequencies of binomial variables used to validate top-performing logistic regression models predicting nest success or nest predation for black tern nests in Maine, 1998-2002.

Variable	Successful nests ($n = 58$)	Depredated nests $(n = 32)$
Date (D)		
Before June 15	38	27
June 15 or later	20	5
Cluster Position (CP)		
Interior	12	6
Perimeter	46	26

Appendix B

Tables Depicting Nocturnal Absence Parameters for Individual

Nests at Maine Colonies in 2001-2002

Colony	Nest	No. nocturnal periods monitored	No. absences	0 departures per night	0 absence length (min.)	Percentage of nights with absence	Percentage of time absent on nights monitored
Douglas	3	8	8	1.0	184.1	87.5	38.4
e	6	3	1	0.33	27.2	33.3	1.9
	20	5	4	0.80	47.8	40.0	8.0
	23	3	1	0.33	16.8	33.3	1.2
	24	6	3	0.50	226.9	50.0	23.6
	36	7	2	0.29	262.0	28.6	15.6
	44	6	1	0.17	28.4	16.7	1.0
	54	3	4	1.33	100.4	100.0	27.9
	85	8	2	0.25	302.0	25.0	15.7
	101	6	1	0.17	13.6	16.7	0.5
	109	5	2	0.40	317.6	40.0	26.5
	117	11	0	0	0	0	0
Carlton	110	6	4	0.67	14.8	66.7	2.1
	7	9	4	0.44	237.7	44.4	22.0
	18	4	0	0	0	0	0
	29	9	2	0.22	66.3	22.2	3.1
	35	6	0	0	0	0	0
	57	5	2	0.40	289.7	40.0	24.1
	38	7	0	0	0	0	0
Messalonskee	59	4	0	0	0	0	0
	121	11	9	1.22	390.9	88.9	66.6
	55	9	7	0.78	337.8	77.8	54.7
	66	5	0	0	0	0	0
Great Moose	81	9	5	0.56	158.1	33.3	18.3
	116	6	1	0.17	30.4	16.7	1.1

Table B.1. Nocturnal absence parameters for 25 black tern nests monitored at Douglas Pond, Carlton Pond, Messalonskee Lake, and Great Moose Lake in 2001.

Colony	Nest	No. nocturnal periods monitored	No. absences	0 departures per night	0 absence length (min.)	Percentage of nights with absence	Percentage of time absent on nights monitored
Douglas	78	6	1	0.17	10.0	16.7	0.3
C	42	9	1	0.11	10.7	11.1	0.2
	54	3	1	0.33	53.3	33.3	3.7
	61	8	1	0.13	40.2	12.5	1.0
	66	7	0	0	0	0	0
	98	11	8	0.73	167.4	46.0	25.4
Carlton	92	3	0	0	0	0	0
	3	2	0	0	0	0	0
	49	6	0	0	0	0	0
	16	10	3	0.30	104.9	30.0	6.6
	108	5	1	0.20	38.0	20.0	1.6
	37	4	0	0	0	0	0
	47	4	1	0.25	48.0	25.0	2.5
	60	8	1	0.13	16.0	12.5	0.4
	115	9	1	0.11	11.3	11.1	0.3
Messalonskee	68	10	1	0.10	136.0	10.0	2.8
	110	11	2	0.18	44.0	18.2	1.7
	118	13	4	0.31	25.2	30.8	1.6
	119	5	1	0.20	17.3	20.0	0.7
Great Moose	17	7	0	0	0	0	0

Table B.2. Nocturnal absence parameters for 20 black tern nests monitored at Douglas Pond, Carlton Pond, Messalonskee Lake, and Great Moose Lake in 2002.

Appendix C

Tables Depicting Linear Growth Rates, Logistic Growth Parameters,

and Mean Square Tables for Chick Growth Analyses

Year	Colony	Nest	Clutch Size	Hatch Order	n	Growth Rate	r ²	р
2001	MS	104	3	А	4	4.405	0.997	0.001
				В	4	4.113	0.991	0.003
				С	4	4.408	0.956	0.015
2001	MS	66a	3	А	5	5.042	0.995	0.000
				В	5	4.678	0.993	0.000
				С	5	4.480	0.981	0.001
2001	MS	102	2	А	4	4.356	0.960	0.014
				В	4	3.250	0.870	0.044
2001	СТ	71	3	А	4	4.886	0.994	0.006
				В	4	5.158	0.990	0.003
				С	4	4.849	0.999	0.000
2001	СТ	48	3	А	4	3.958	0.957	0.014
				В	4	3.219	0.915	0.029
				С	4	4.083	0.969	0.010
2001	СТ	38	3	А	5	4.781	0.993	0.000
				В	5	4.176	0.978	0.001
				С	4	4.196	0.932	0.023
2001	СТ	40	3	Α	4	3.940	0.984	0.005
				В	4	3.688	0.954	0.015
				С	4	3.886	0.993	0.002
2001	DG	401	3	А	4	4.474	0.996	0.001
				В	4	4.501	0.998	0.001
				С	4	4.617	0.996	0.001
2001	DG	16	2	А	4	4.531	0.982	0.006
				В	4	4.460	0.987	0.004
2002	СТ	18	3	А	5 5	4.823	0.966	0.000
				В	5	4.498	0.997	0.000
				С	5	4.590	0.963	0.002
2002	СТ	49	2^{a}	Α	5	5.215	0.989	0.000
				В	4	5.867	0.992	0.003
2002	СТ	1	2^{a}	Α	5	5.261	0.997	0.000
				В	4	5.069	0.969	0.010
2002	СТ	7	3	А	3	4.707	0.989	0.047
				В	3	4.825	0.981	0.063
				С	3	4.683	0.982	0.060
2002	СТ	81	2	А	5	4.846	0.992	0.000
	-			В	5 5	4.569	0.988	0.000
2002	СТ	47	2^{a}	А	5	4.542	0.962	0.002
				В	4	4.098	0.991	0.000
2002	DG	78	3	А	4	5.090	0.994	0.002
				В	4	4.875	0.998	0.001
				С	4	4.721	0.986	0.005
2002	DG	66b	3	Α	5	4.717	0.992	0.000
				B	4	5.234	0.999	0.000
		. ·	-	С	5	4.317	0.985	0.001
2002	DG	54	3	A	4	4.742	0.962	0.013
				В	4	4.126	0.950	0.017
• • • • •			-	С	3	3.915	0.964	0.085
2002	DG	61	3	Α	5	4.108	0.995	0.000
				В	5	4.597	0.997	0.000
				С	5	4.162	0.973	0.001

Table C.1. Linear growth rates of black tern chicks between ages 2-11 days in predator exclosures at Maine colonies as determined by linear regression, 2001-2002.

2001 2001 2001	MS MS CT	104 66a 71	3 3 3	A B C A B C	7 7 7 7 7	64.922 57.304 59.265 59.763	(58.534 - 71.310) (51.931 - 62.677) (51.086 - 67.445) (54.921 - 64.606)	0.317 0.331 0.340	(0.249 - 0.386) (0.255 - 0.407) (0.232 - 0.449)	6.076	(5.823 - 7.638) (5.218 - 6.935) (5.475 - 7.941)
				C A B C	7 7 7	59.265 59.763	(51.086 - 67.445)		(
				A B C	7 7	59.763	(0.340	(0.232 - 0.449)	6.708	(5475 - 7941)
				B C	7		(54921 - 64606)				(3.175 7.511)
2001	СТ	71	3	С		(2.2.2)	(21.721 01.000)	0.388	(0.281 - 0.496)	5.310	(4.578 - 6.043)
2001	СТ	71	3			63.205	(57.394 – 69.016)	0.322	(0.242 - 0.401)	6.272	(5.411 – 7.134)
2001	СТ	71	3		7	59.965	(55.063 – 64.866)	0.332	(0.260 - 0.405)	6.495	(5.740 - 7.250)
2001				А	9	69.179	(64.333 - 74.024)	0.303	(0.226 - 0.379)	5.610	(4.734 – 6.487)
				В	9	69.544	(62.017 – 77.071)	0.316	(0.191 – 0.440)	5.817	(4.476 – 7.158)
				С	9	66.280	(62.076 - 70.784)	0.301	(0.236 – 0.366)	6.130	(5.337 – 6.923)
2001	СТ	48	3	А	9	47.901	(45.160 - 50.642)	0.448	(0.295 - 0.601)	4.056	(3.328 - 4.784)
				В	7	39.014	(31.837 – 46.191)	0.465	(0.050 - 0.880)	3.841	(1.988 – 5.694)
				С	9	44.592	(41.463 – 47.720)	0.485	(0.292 - 0.677)	3.830	(2.952 - 4.709)
2001	СТ	38	3	А	7	65.980	(61.819 – 70.140)	0.336	(0.261 - 0.411)	5.325	(4.696 – 5.953)
				В	8	59.943	(54.344 – 65.541)	0.316	(0.195 – 0.438)	5.321	(4.243 – 6.399)
				С	9	57.734	(53.180 - 62.289)	0.311	(0.217 - 0.405)	6.057	(5.050 - 7.065)
2001	СТ	40	3	А	8	57.469	(45.846 - 69.092)	0.284	(0.124 - 0.444)	5.662	(3.244 - 8.079)
				В	8	49.455	(42.908 - 56.001)	0.347	(0.182 - 0.512)	4.975	(3.409 – 6.541)
				С	8	59.659	(47.490 - 71.828)	0.264	(0.145 - 0.382)		(4.440 – 9.252)
2001	DG	401	3	А	9	67.526	(65.016 – 70.036)	0.305	(0.266 - 0.343)	6.474	(6.014 – 6.933)
				В	9	60.371	(58.647 – 62.095)	0.346	(0.306 – 0.386)		(5.433 – 6.132)
				С	9	68.863	(63.010 – 74.662)	0.335	(0.239 – 0.431)		(5.078 – 7.116)
2001	DG	16	2	А	9	56.642	(54.698 - 58.587)	0.426	(0.350 - 0.501)	3.515	(3.107 – 3.924)
				В	8	64.051	(61.378 - 66.725)	0.338	(0.284 – 0.393)	4.945	(4.462 - 5.428)
2002	СТ	18	3	А	7	60.722	(56.360 - 65.084)	0.364	(0.279 - 0.448)	4.955	(4.323 – 5.587)
				В	7	62.491	(57.012 - 67.970)	0.316	(0.242 - 0.390)	5.560	(4.765 – 6.355)
				С	7	59.456	(57.074 – 61.838)	0.393	(0.348 - 0.437)	5.097	(4.761 – 5.432)
2002	СТ	49	2^{a}	А	8	63.112	(60.222 - 66.002)	0.381	(0.333 – 0.429)	5.875	(5.459 – 6.292)
				В	7	68.745	(64.640 - 72.851)	0.368	(0.315 – 0.421)		(5.850 - 6.863)
2002	СТ	1	2^{a}	А	8	69.170	(66.298 - 72.042)	0.344	(0.309 – 0.378)		(5.937 – 6.709)
				В	8	66.588	(60.500 - 72.677)	0.330	(0.269 - 0.392)	6.459	(5.627 – 7.292)
2002	СТ	81	2	А	8	65.120	(62.751 – 67.489)	0.346	(0.311 – 0.381)	5.448	(5.092 - 5.804)
				В	8	58.263	(56.533 – 59.992)	0.389	(0.352 - 0.425)	5.247	(4.960 – 5.534)

Table C.2. Logistic growth parameters of black tern chicks in predator exclosures in Maine colonies, 2001-2002.

Year	Colony	Nest	Clutch Size	Hatch Order	n	А	(95% Weld C.I.)	Κ	(95% Weld C.I.)	tzero	(95% Weld C.I.)
2002	СТ	47	2 ^a	А	8	60.051	(56.916 - 63.186)	0.378	(0.291 – 0.465)	4.570	(4.085 - 5.054)
				В	8	66.607	(58.931 - 74.283)	0.278	(0.227 - 0.330)	7.801	(6.754 - 8.847)
2002	DG	78	3	А	7	56.680	(48.222 - 65.139)	0.445	(0.218 - 0.673)	4.957	(3.569 - 6.345)
				В	7	67.160	(61.348 - 72.973)	0.315	(0.261 - 0.369)	7.271	(6.492 - 8.049)
				С	6	65.511	(57.558 - 73.463)	0.350	(0.252 - 0.447)	5.559	(4.581 - 6.536)
2002	DG	66b	3	А	8	62.187	(50.127 - 74.247)	0.319	(0.162 - 0.475)	5.675	(3.764 - 7.587)
				В	8	64.743	(51.748 - 77.738)	0.311	(0.178 - 0.445)	5.767	(3.859 - 7.674)
				С	7	73.494	(51.824 - 95.163)	0.280	(0.158 - 0.402)	7.058	(4.396 - 9.721)
2002	DG	61	3	А	8	63.869	(58.727 - 69.011)	0.297	(0.239 - 0.354)	5.332	(4.503 - 6.160)
				В	8	63.969	(57.963 - 69.976)	0.314	(0.250 - 0.379)	6.187	(5.262 - 7.111)
				С	7	63.053	(50.142 - 75.964)	0.287	(0.188 - 0.386)	6.814	(4.898 - 8.730)

Table C.2. continued

Source	df	MS	F	Р
Colony	2	0.115	1.597	0.227
Hatchorder	2	0.154	2.130	0.145
Colony*Hatchorder	4	0.078	1.081	0.392
Nest(Colony)	10	0.488	6.760	0.000
Error	20	0.072		

Table C.3. Mean square error table for the general linear model^a on the effects of colony and hatchorder on linear growth rate of black tern chicks in three-chick broods in Maine, 2001-2002.

^a General linear model run on SYSTAT 10.2.

Table C.4. Mean square error table for the general linear model^a on the effects of year and hatchorder on linear growth rate of black tern chicks in three-chick broods in Maine, 2001-2002.

Source	df	MS	F	Р
Year	1	0.545	8.315	0.009
Hatchorder	2	0.160	2.433	0.111
Year*Hatchorder	2	0.156	2.387	0.115
Nest(Year)	11	0.415	6.328	0.000
Error	22	0.066		

^a General linear model run on SYSTAT 10.2.

Table C.5. Mean square error table for the general linear model^a on the effect of hatchorder on linear growth rate of black tern chicks in three-chick broods in Maine, 2001-2002.

Source ^b	df	MS	F	Р
Hatchorder	2	0.156	2.139	0.140
Nest	12	0.426	5.821	0.000
Error	24	0.073		

^a General linear model run on SYSTAT 10.2.

^b Data pooled by colony and year.

Source ^b	df	MS	F	Р
Hatchorder	1	0.172	1.064	0.350
Nest	5	3.819	4.717	0.057
Error	5	0.162		

Table C.6. Mean square error table for the general linear model^a on the effect of hatchorder on linear growth rate of black tern chicks in two-chick broods in Maine, 2001-2002.

^a General linear model run on SYSTAT 10.2. ^b Data pooled by colony and year.

Table C.7. Mean square error table for the general linear model^a on the effects of brood size on linear growth rate of black tern chicks in Maine, 2001-2002.

Source ^b	df	MS	F	Р
Broodsize	1	0.126	1.326	0.258
Nest	17	0.525	5.510	0.000
Error	32	0.095		

^a General linear model run on SYSTAT 10.2.

^b Data pooled by colony and year.

Table C.8. Mean square error table for the general linear model^a on the effects of colony and hatchorder on asymptotic mass of black tern chicks in three-chick broods in Maine, 2001-2002.

Source	df	MS	F	Р
Colony	2	155.396	9.901	0.002
Hatchorder	2	7.506	0.478	0.628
Colony*Hatchorder	4	21.313	1.358	0.292
Nest(Colony)	8	127.954	8.153	0.000
Error	16	15.695		

^a General linear model run on SYSTAT 10.2.

Source	df	MS	F	Р
Year	1	133.797	10.395	0.005
Hatchorder	2	7.129	0.554	0.584
Year*Hatchorder	2	52.336	4.066	0.035
Nest(Year)	9	133.403	10.364	0.000
Error	18	12.872		
Year	LS Mean	S	SE	Ν
2001	59.425	0.7	783	21
2002	63.611	1.036		12

Table C.9. Mean square error table for the general linear model^a on the effects of year and hatchorder on asymptotic mass of black tern chicks in three-chick broods in Maine, 2001-2002.

^a General linear model run on SYSTAT 10.2.

Appendix D

Figures Depicting Nest Locations and Nest Outcomes by Study Site

for Maine Colonies from 1998-2002.

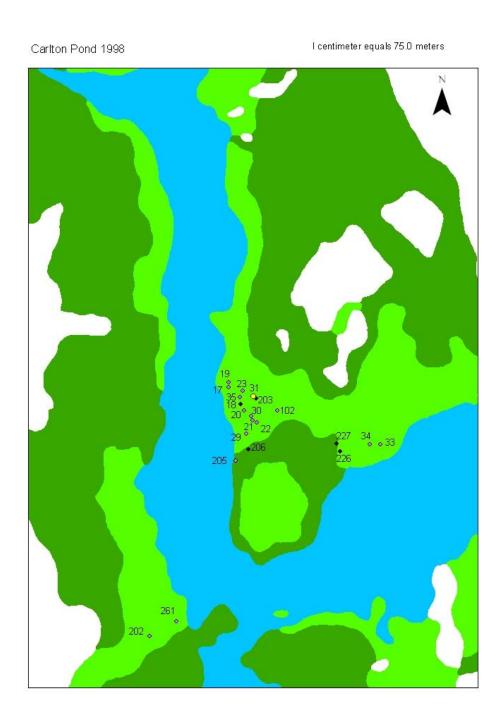


Figure D.1. NWI image of Carlton Pond, Maine, depicting nest site locations in 1998. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).



Figure D.2. NWI image of Carlton Pond, Maine, depicting nest site locations in 1999. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

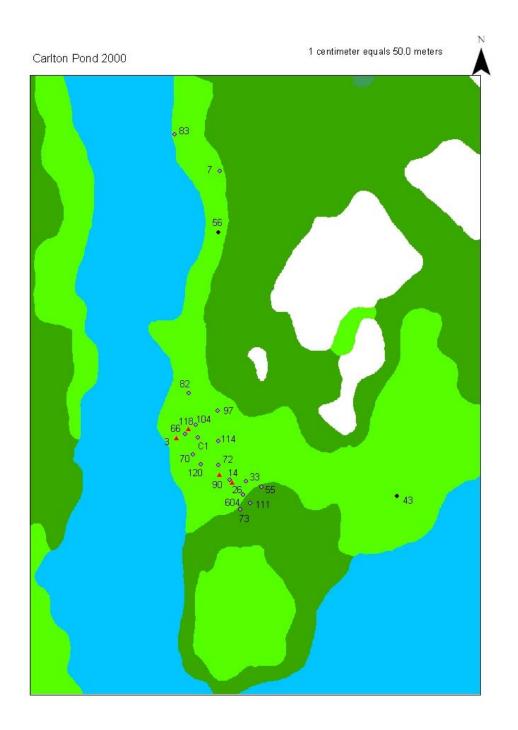


Figure D.3. NWI image of Carlton Pond, Maine, depicting nest site locations in 2000. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

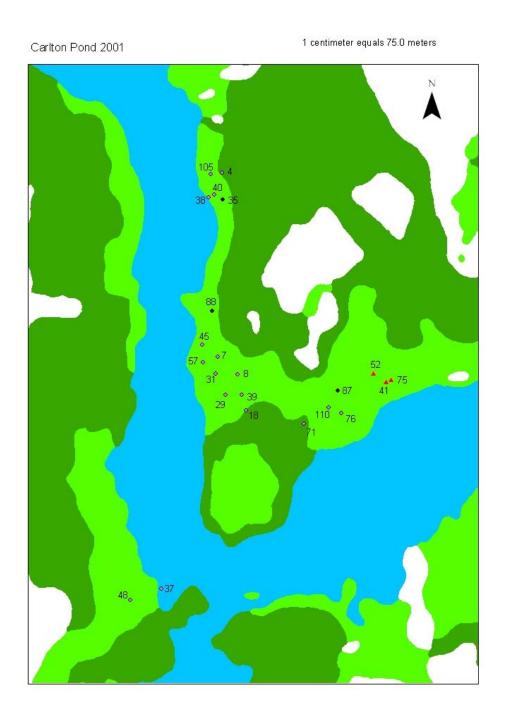


Figure D.4. NWI image of Carlton Pond, Maine, depicting nest site locations in 2001. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

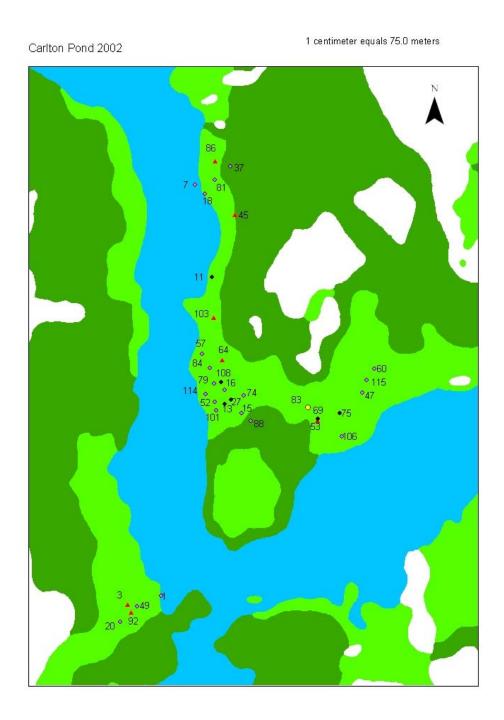
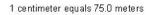


Figure D.5. NWI image of Carlton Pond, Maine, depicting nest site locations in 2002. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).





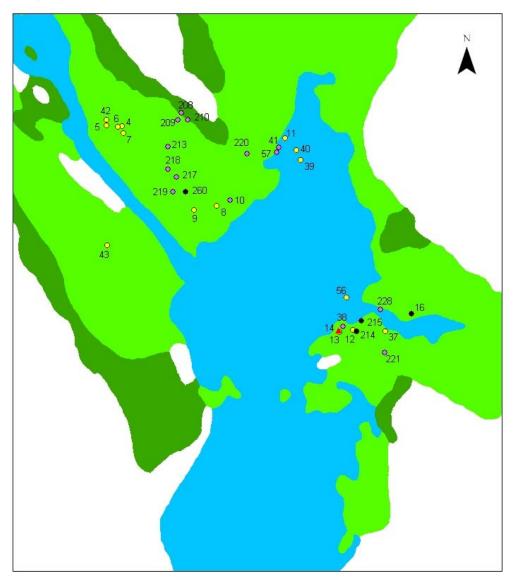


Figure D.6. NWI image of Douglas Pond, Maine, depicting nest site locations in 1998. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

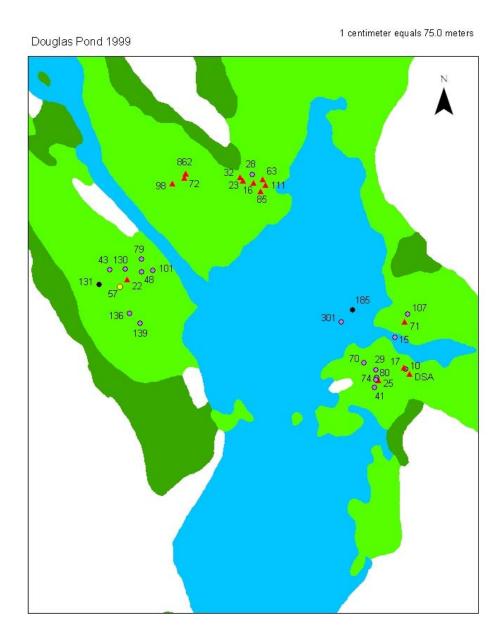


Figure D.7. NWI image of Douglas Pond, Maine, depicting nest site locations in 1999. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

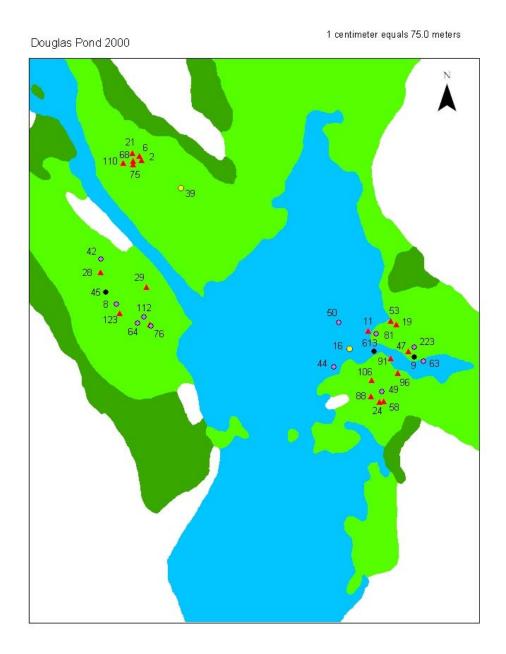


Figure D.8. NWI image of Douglas Pond, Maine, depicting nest site locations in 2000. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

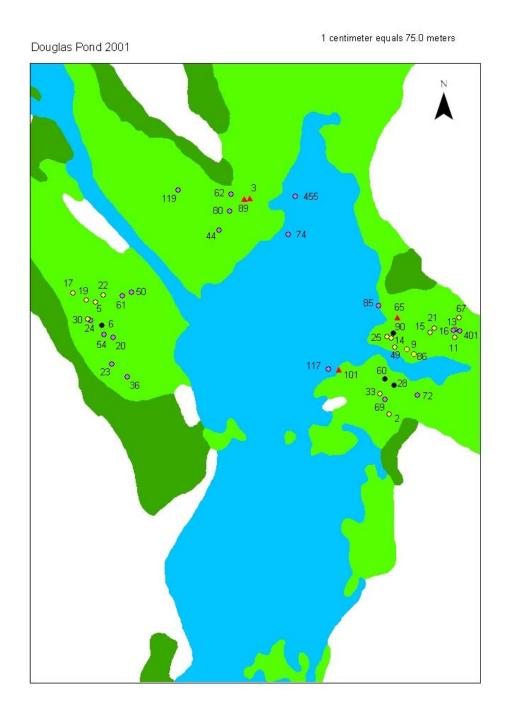


Figure D.9. NWI image of Douglas Pond, Maine, depicting nest site locations in 2001. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

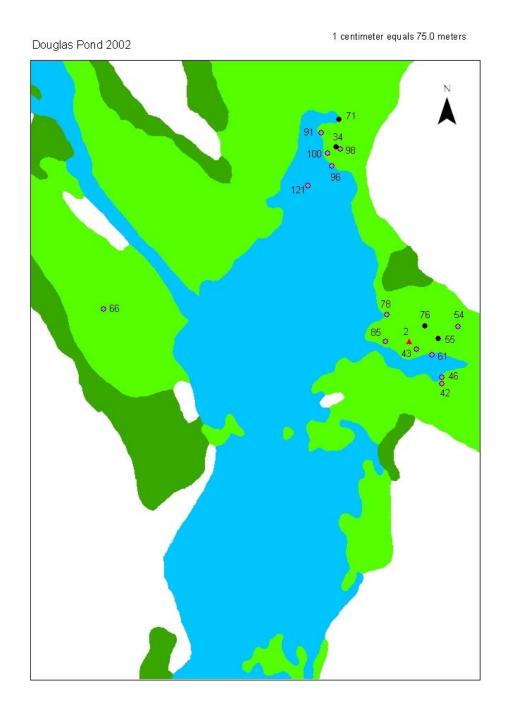


Figure D.10. NWI image of Douglas Pond, Maine, depicting nest site locations in 2002. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

Great Moose Lake 1998a

1 centimeter equals 100.0 meters

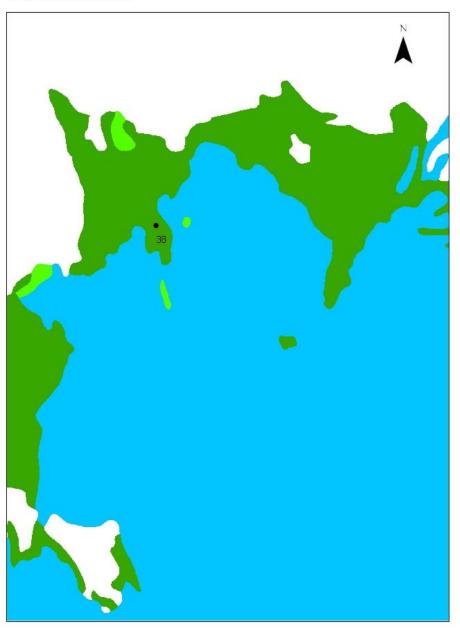


Figure D.11. NWI image of Great Moose Lake, Maine, depicting nest site locations in 1998. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

1 centimeter equals 75.0 meters

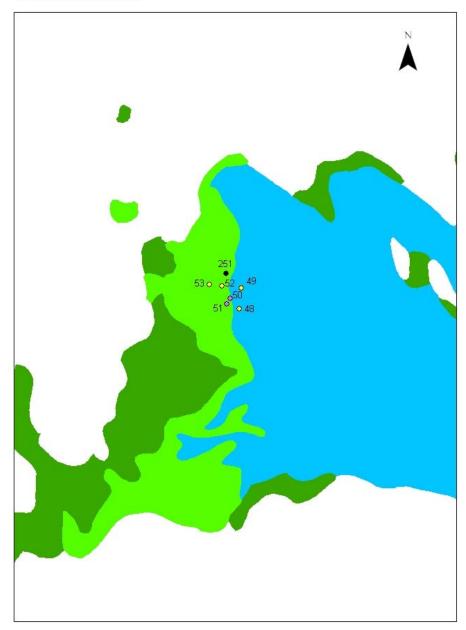


Figure D.12. NWI image of Great Moose Lake, Maine, depicting additional nest site locations in 1998. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

Great Moose Lake 1999

1 centimeter equals 100.0 meters

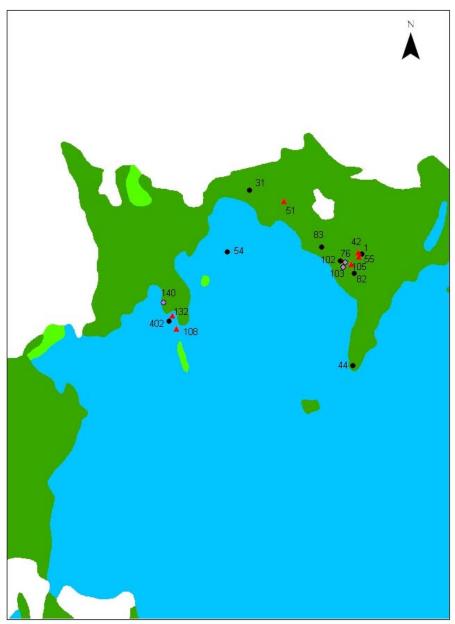


Figure D.13. NWI image of Great Moose Lake, Maine, depicting nest site locations in 1999. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

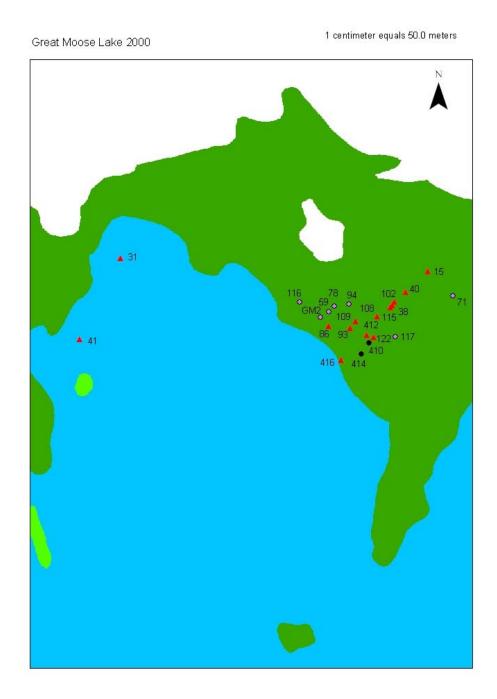


Figure D.14. NWI image of Great Moose Lake, Maine, depicting nest site locations in 2000. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

Great Moose Lake 2001

1 centimeter equals 100.0 meters

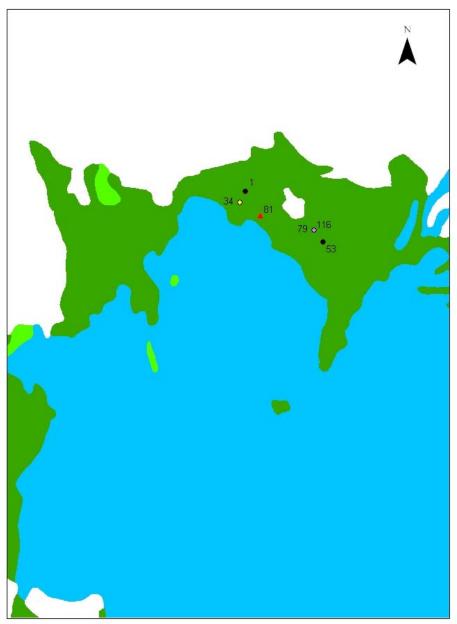


Figure D.15. NWI image of Great Moose Lake, Maine, depicting nest site locations in 2001. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

Great Moose Lake 2002

1 centimeter equals 100.0 meters

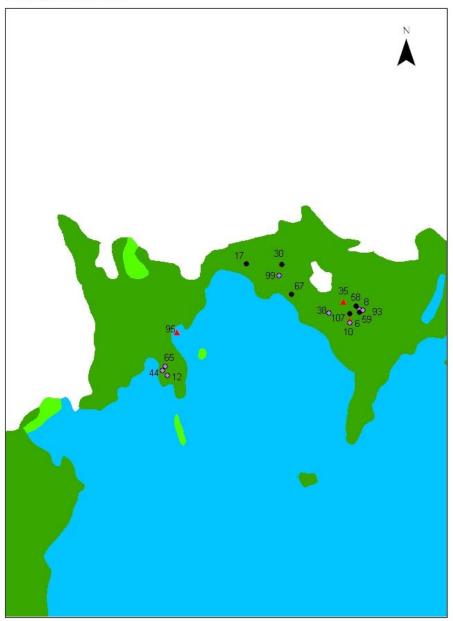


Figure D.16. NWI image of Great Moose Lake, Maine, depicting nest site locations in 2002. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

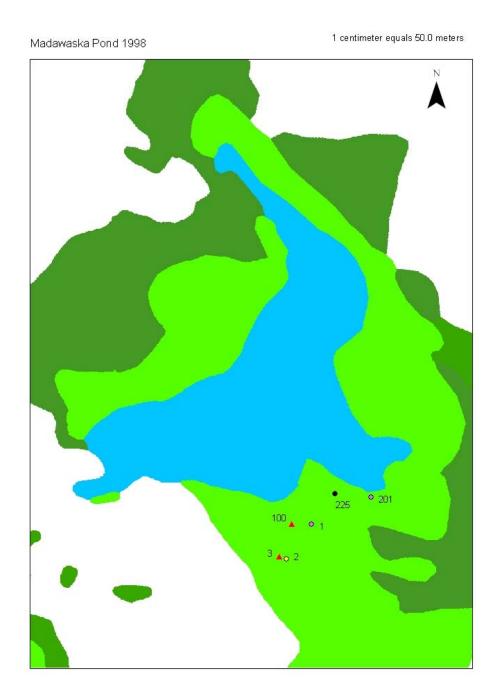


Figure D.17. NWI image of Madawaska Pond, Maine, depicting nest site locations in 1998. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

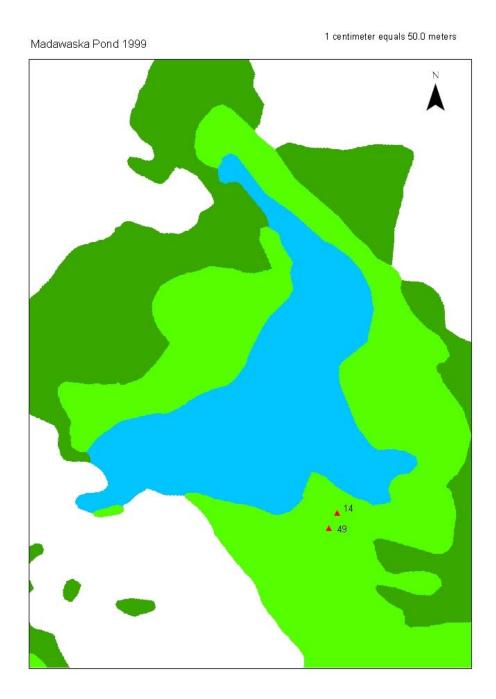


Figure D.18. NWI image of Madawaska Pond, Maine, depicting nest site locations in 1999. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

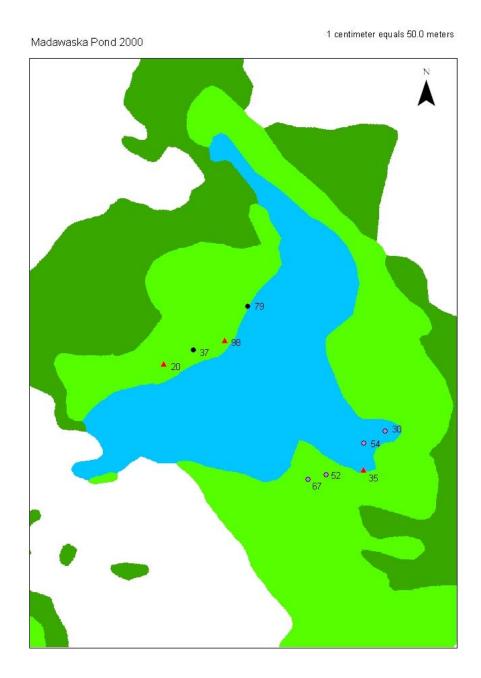


Figure D.19. NWI image of Madawaska Pond, Maine, depicting nest site locations in 2000. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

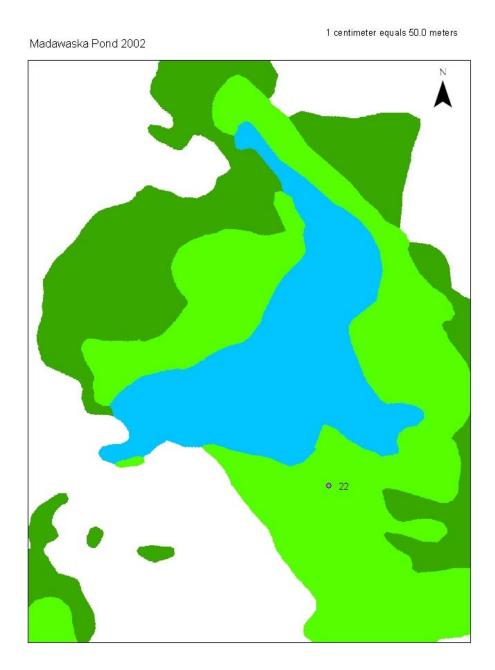


Figure D.20. NWI image of Madawaska Pond, Maine, depicting nest site locations in 2002. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

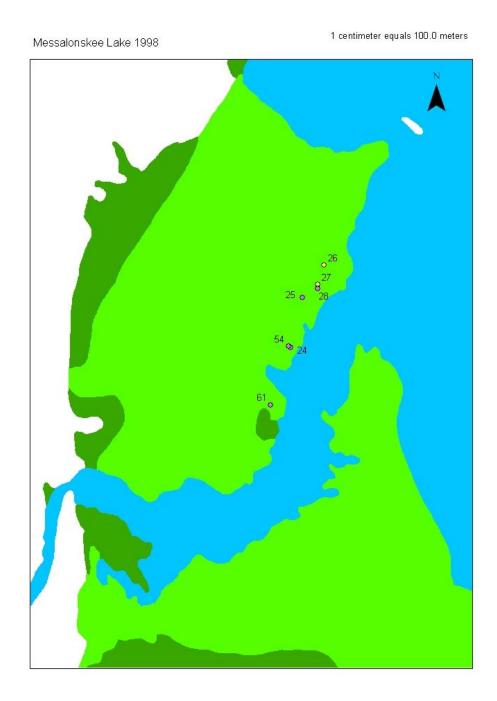


Figure D.21. NWI image of Messalonskee Lake, Maine, depicting nest site locations in 1998. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

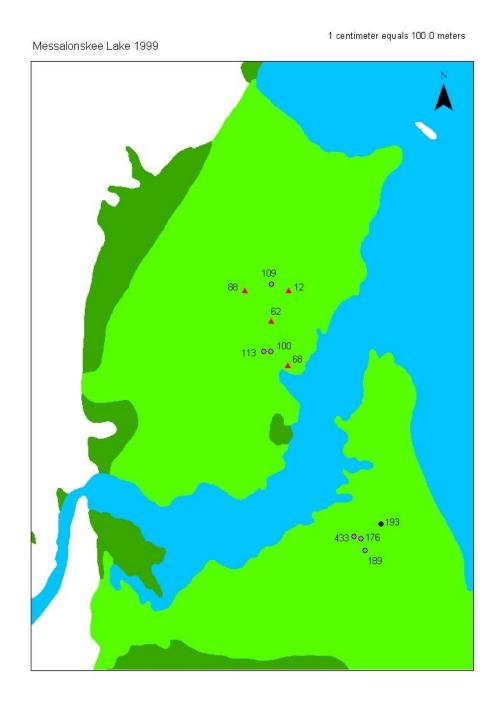


Figure D.22. NWI image of Messalonskee Lake, Maine, depicting nest site locations in 1999. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

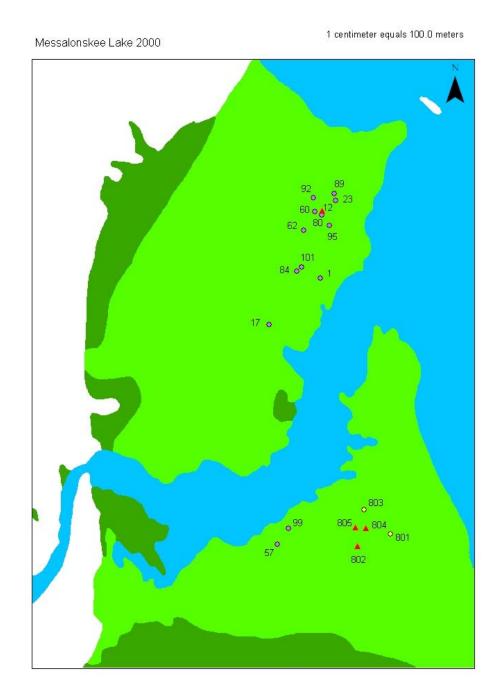


Figure D.23. NWI image of Messalonskee Lake, Maine, depicting nest site locations in 2000. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

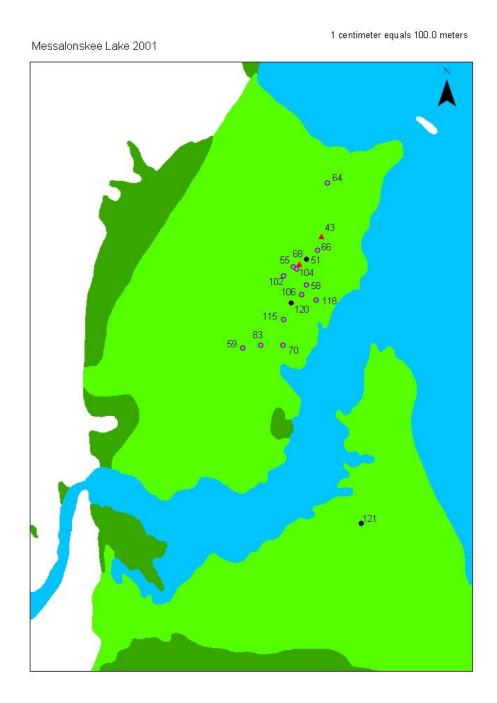


Figure D.24. NWI image of Messalonskee Lake, Maine, depicting nest site locations in 2001. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

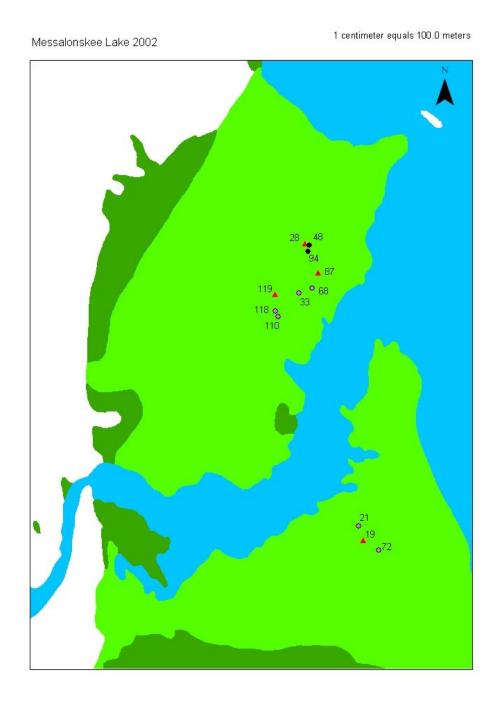


Figure D.25. NWI image of Messalonskee Lake, Maine, depicting nest site locations in 2002. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

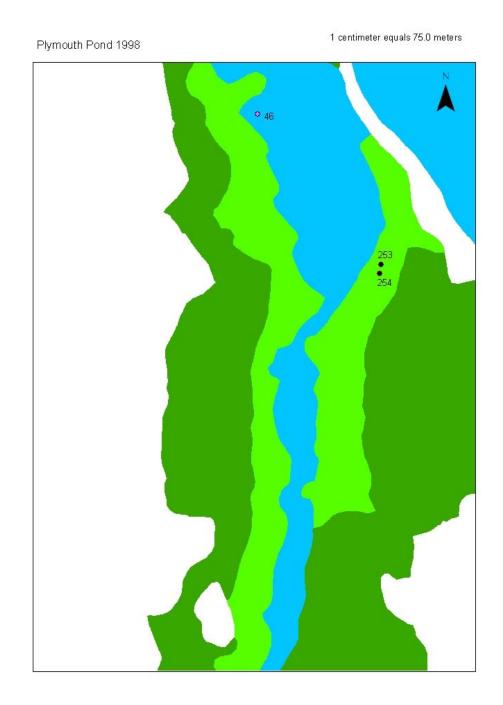


Figure D.26. NWI image of Plymouth Pond, Maine, depicting nest site locations in 1998. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

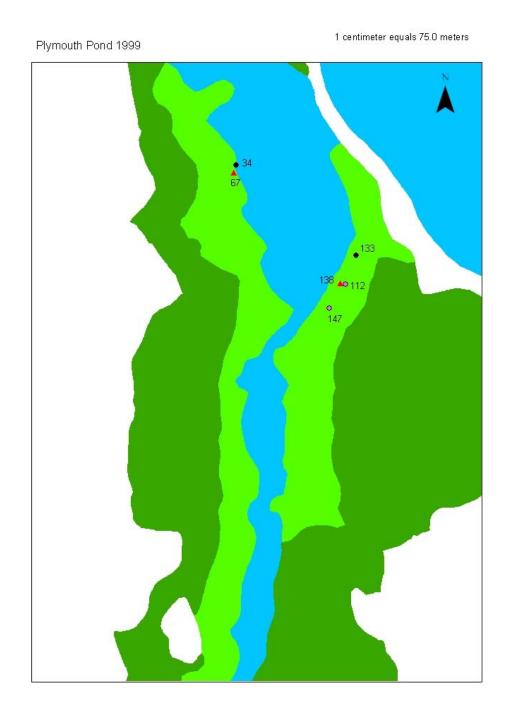


Figure D.27. NWI image of Plymouth Pond, Maine, depicting nest site locations in 1999. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

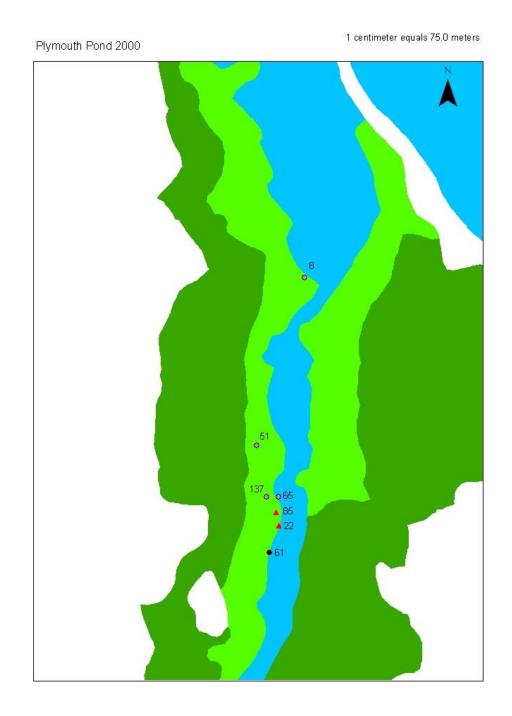


Figure D.28. NWI image of Plymouth Pond, Maine, depicting nest site locations in 2000. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

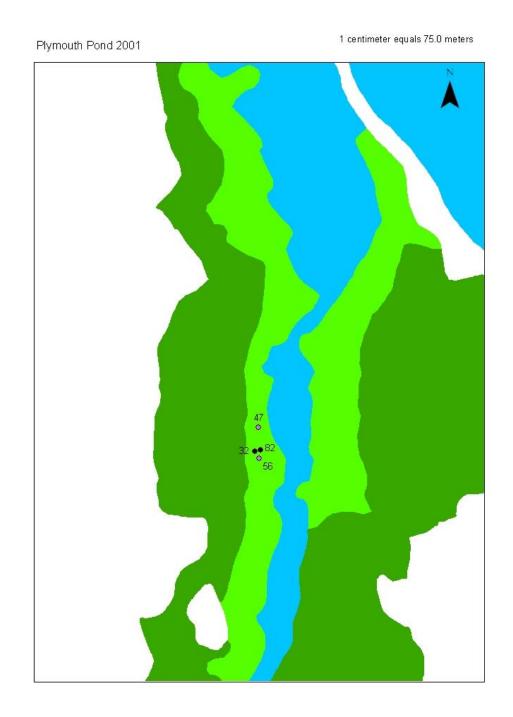


Figure D.29. NWI image of Plymouth Pond, Maine, depicting nest site locations in 2001. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

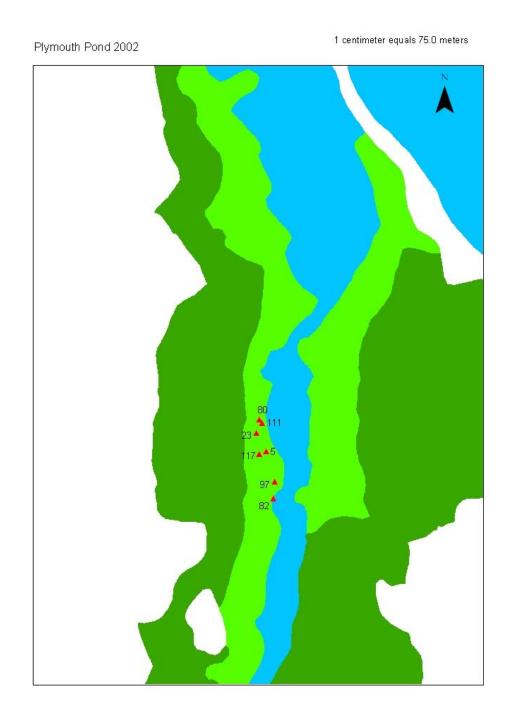


Figure D.30. NWI image of Plymouth Pond, Maine, depicting nest site locations in 2002. Successful (purple circles), depredated (red triangles), flooded (yellow circles), and other (black circles) outcomes are depicted along with nest number. Land area is classified as forested upland (white), scrub-shrub (dark green), emergent (light green), or water (blue).

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Shane Richard Heath was born in Morrisville, Vermont on 23 February, 1979. He was raised in North Hyde Park, Vermont and graduated in 1997 from Lamoille Union High School, Hyde Park, Vermont. He attended Dartmouth College, Hanover, New Hampshire and graduated with a Bachelor of Arts degree, double-majoring in Environmental and Evolutionary Biology <u>and</u> Environmental Studies. Upon graduation, Shane was employed by the Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts and conducted nutrient cycling research in northern Alaska. Shane also volunteered at Pocosin Lakes National Wildlife Refuge in Creswell, North Carolina. He entered the graduate program in the Department of Wildlife Ecology at the University of Maine in January, 2002. Since January of 2004, Shane has been a wildlife biologist and project supervisor for the Institute for Wildlife Studies, San Diego, California. Shane is a candidate for the Master of Science degree in Wildlife Ecology from The University of Maine in August, 2004.