

EFFECTS OF PREDATION AND FOOD PROVISIONING ON BLACK TERN CHICK SURVIVAL

SHANE R. HEATH^{1,2,3} AND FREDERICK A. SERVELLO¹

ABSTRACT.—We placed predator exclosures around 31 Black Tern (*Chlidonias niger*) nests in Maine in 2001–2002 to measure growth and survival of chicks. Fifty-four percent of exclosed nests that hatched young were depredated in 2001 and four exclosed nests were abandoned prior to hatch. We modified our exclosure design in 2002 and only one nest (7%) was depredated and no nests were abandoned prior to hatch. Kaplan-Meier estimates of chick survival in the absence of predation were 0.87 to 18 days in 2001 and 0.90 to 15 days in 2002. Mass ratios among first, second, and third-hatched chicks indicated that size hierarchies were present in broods near time of brood completion, but linear growth rates and asymptotic mass were not affected by hatch order in 2- or 3-chick broods. Predation was the primary determinant of chick survival in Black Tern colonies studied and food availability was not limiting chick growth. Predator exclosures did not prevent all depredation, but our exclosure design was effective at protecting and retaining chicks until fledgling age at 70% of nests; the majority of adults readily accepted predator exclosures. Received 23 December 2006. Accepted 19 April 2007.

Black Terns (*Chlidonias niger*) are listed as endangered, threatened, or a species of concern in multiple states (USA) and Canadian provinces (Shuford 1999), and populations declined 3.1% annually during 1966–1996 in North America (Peterjohn and Sauer 1997). Low breeding productivity may be a key factor limiting population growth (Servello 2000), especially among small, isolated populations along the southern portion of this species' range. Nest success in this species is well studied (reviewed in Servello 2000), but chick survival estimates are lacking. Monitoring chick survival for wetland-nesting terns is problematic because chicks use dense vegetation for cover and leave nests soon after hatching (Hall 1988, Cuthbert and Louis 1993). Thus, few studies have reported chick survival rates or investigated factors contributing to chick mortality (Servello 2000). Fewer than 100 pairs of Black Terns nest annually in Maine and chick survival appears to be the primary cause of low breeding success (F. A. Servello, unpubl. data). Identifying factors contributing to chick mortality is critical for understanding Black Tern ecology and devel-

oping management strategies for increasing recruitment.

Black Terns nest in wetlands where a wide variety of predators commonly occur. Reports of predation on Black Tern chicks have been limited to chicks held in small enclosures (Dunn 1979, Chapman and Forbes 1984) or anecdotal observations (Shealer and Haverland 2000). Low food availability or inadequate provisioning by adults may be a common cause of chick mortality in Black Terns (Mosher 1986, Beintema 1997) as in other tern species (Safina et al. 1988, Monaghan et al. 1989, Nisbet et al. 1998, Eyler et al. 1999). However, food limitation in Maine colonies has not previously been observed (Gilbert and Servello 2005). Black Terns exhibit laying and hatching asynchrony (Dunn and Agro 1995), which produces a size hierarchy among siblings and can result in lower growth and survival rates for the youngest chicks in broods when food resources are scarce (Langham 1972, Skagen 1988, Bollinger et al. 1990, Brown and Morris 1996). We hypothesize that predation is the primary factor contributing to chick mortality of Black Terns in Maine, but annual or local variation in food availability may also have a contributing role.

Predator exclosures have been successfully used with shorebirds to prevent egg depredation (Rimmer and Deblinger 1990, Estelle et al. 1996, Mabee and Estelle 2000, Larson et al. 2002), but have not been designed to protect chicks. With terns, smaller retention fenc-

¹ Department of Wildlife Ecology, 5755 Nutting Hall, University of Maine, Orono, ME 04469, USA.

² Current address: Institute for Wildlife Studies, 2515 Camino del Rio S, Suite 334, San Diego, CA, 92108, USA.

³ Corresponding author; e-mail: shaneheath1@gmail.com

es have frequently been used to confine chicks, including those of Black Terns, for research purposes (e.g., monitoring growth, survival, feeding behavior) but not for predator deterrence (Morris et al. 1976, Burger et al. 1996, Robinson and Hamer 2000, Shealer and Haverland 2000, Gilbert and Servello 2005). We sought to develop a predator enclosure that would hold chicks until fledging, deter mammalian and avian predators, and be suitable for wetland substrates while simultaneously allowing unimpeded feeding and brooding by adults. A useful enclosure would also provide opportunities for research on chick predation and growth. We report on the efficacy of our predator enclosures and test two hypotheses: (1) predator exclusion would result in chick survival near 100% if predation was the principal mortality factor and (2) growth rates of Black Tern chicks would decrease with hatch order and increasing brood size if food provisioning was inadequate.

METHODS

Study Area.—This study was conducted at three Black Tern breeding colonies (Carlton Pond, Douglas Pond, and Messalonskee Lake) in Maine, USA, in May–July 2001–2002. Carlton Pond (44° 40' N, 69° 15' W) had a total area of 431 ha and included 75 ha of semi-permanent emergent wetland bordering 113 ha of open water with dense mats of floating-leaf vegetation. Nesting areas were dominated by sedges (*Carex* spp.), *Sphagnum* spp., and pickerelweed (*Pantedaria cordata*). Douglas Pond (44° 50' N, 69° 21' W) was an impounded wetland on the Sebasticook River and had a total area of 227 ha, which included 44 ha of semi-permanent emergent vegetation bordering 85 ha of open water. Nesting areas at Douglas Pond were dominated by river bulrush (*Scirpus* spp.) or sedges. Messalonskee Lake (44° 26' N, 69° 49' W) was a large lake (1,786 ha) with 55 ha of semi-permanent emergent wetland at one end; nesting areas were dominated by sedges and *Sphagnum* spp.

Field Procedures.—We constructed 17 predator enclosures around individual nests in 2001 and 14 enclosures around nests in 2002. Black Terns differ from other species for which nest enclosures have been constructed in that adults fly rather than walk into enclosures, and our design had to accommodate this

behavioral difference. Predator enclosures consisted of two primary parts: (1) a circular fence 1 m in diameter and 0.3 m in height placed around the nest (chick retention fence), and (2) a circular fence 4.6 m in diameter and 1.4 m in height, placed concentrically around the retention fence (predator exclusion fence; Fig. 1). Landscaping cloth was attached to the inside of the chick retention fences to a height of 0.15 m and to the outside of the predator exclusion fences to a height of 0.9 m prior to deployment (Fig. 1). In addition, the retention fences had a 10–15 cm wide flap of chicken wire wrapped with landscaping cloth (“concealment flap”) attached inside the retention fence at a height of 0.15 m to provide overhead concealment. The purposes of the retention fence were to reduce predation risk by limiting movements of chicks, keeping chicks from enclosure fences, and providing a location for horizontal and overhead concealment of chicks. The landscaping cloth in retention fences also prevented chicks from climbing out of the enclosure. The purposes of the exclusion fence were to reduce predator access and reduce visibility of chicks to ground predators. We deployed retention fences around nests during the second half of incubation, and installation took less than 3 min. Retention fences were held tightly to the substrate with three wooden stakes. The “concealment flaps” were initially pressed flat against the retention fence until clutches hatched.

We avoided hot sunny days when deploying enclosures to avoid egg heating while adults were acclimating to the structure. We removed eggs and placed them in an insulated container during erection of the exclusion fence. Exclusion fencing was typically deployed 3–4 days after the retention fencing, but before eggs hatched to allow terns to acclimate to these structures. However, retention and exclusion fences in 2001 were installed simultaneously at four nests and exclusion fencing was installed after hatch at two nests in 2002. Two to four people were required to erect predator exclusion fencing and construction time was typically 15–25 min depending on water depth. Water depths were typically 0.2 to 1.0 m. Eight to 10 wooden stakes (2 m in length) were used to support exclusion fences and hold them flush to the substrate, and four rope guidelines attached to smaller stakes were

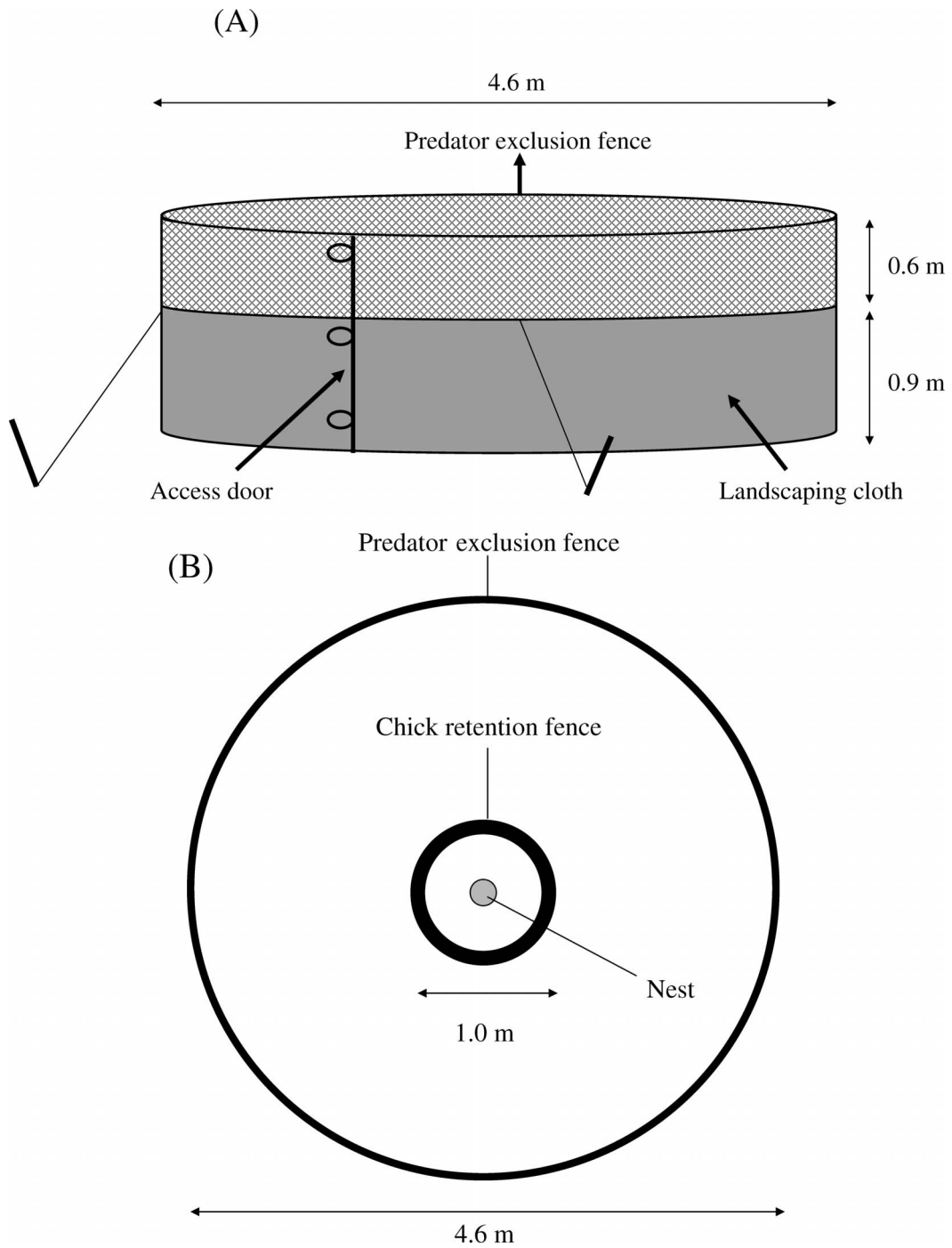


FIG. 1. (A) Predator exclusion fence including landscaping cloth, rope and stakes, and researcher access door, and (B) diagram showing predator enclosure around Black Tern nest, including predator exclusion and chick retention fences.

used to add tension and reduce movement by strong winds (Fig. 1). The skirt of landscaping cloth was partially submerged under the extant water along with the lower portion of the fence to serve as an additional ground-level barrier. The two ends of the exclusion fencing, overlapped and fastened together with removable wires, served as the entrance for researchers.

We selected entire clusters of nests or individual nests on colony edges for predator exclosures to allow repetitive access to nests without major disturbance to colonies. We visited exclosures approximately every 1–2 days to document hatching and to inspect exclosures. Chicks at each nest were assigned an alpha code based on hatch order: A-chick = first hatched, B-chick = second hatched, C-chick = third hatched. We visited exclosures to weigh chicks every 2 days following hatch, on average. Chicks missing from exclosures prior to the anticipated fledge dates were considered depredated if no means of escape were evident. Dead chicks were removed from the exclosures to avoid attracting predators. We retained broods in 2001 until A-chicks reached an approximate fledging age of 18 days (Dunn and Agro 1995) except when they flew from exclosures. We released broods in 2002 when A-chicks reached 15 days of age to reduce potential losses of older chicks to predators. Chicks became more active (increased wing flapping, vocalizations) at this age (Dunn 1979) and appeared to be more vulnerable to predators at older ages in exclosures during 2001.

Statistical Analyses.—We calculated Kaplan-Meier survival estimates for non-depredated chicks by censoring depredated, escaped, or released chicks in analyses (Pollock et al. 1989). We compared survival rates between years using log-rank tests (Pollock et al. 1989). We calculated mass ratios of chicks for each nest with a predator exclosure to examine if size hierarchies were established by hatch order. Mass ratio is an index of the competitive ability of the latter-hatched chicks relative to the A-chick during the early post-hatch period (Bollinger 1994). We defined mass ratio as a chick's mass divided by the mass of the A-chick following brood completion (modified from Bollinger 1994). Brood completion occurred when the final chick of

each brood hatched. Mass ratios of B- and C-chicks were compared using ANOVA. B- or C-chicks were assumed to differ from A-chicks if 95% CIs for their mass ratios did not include 1.0. We used linear regression analysis to calculate linear growth rate (LGR; Emms and Verbeek 1991) for each chick for the age period 2–11 days when Black Tern chick growth is approximately linear (Beintema 1997). Only chicks with a minimum of three mass measurements during this interval were included. We iteratively fit the logistic equation,

Chick mass

$$= AM / \{1 + \exp[-K \cdot (\text{age} - t_0)]\},$$

to growth curves of individual chicks to estimate asymptotic mass (AM), where K is a growth coefficient and t_0 is time of inflection (Starck and Ricklefs 1998). We only calculated AM for chicks that reached 13 days of age because weight measurements approaching the asymptote are required (Ricklefs 1967). Chick weights from broods that were eventually depredated were included if meeting the above criteria for all growth analyses (mass ratio, LGR, AM).

We analyzed data for 2- and 3-chick broods separately. We only included 2-chick broods if they resulted from a 2-egg clutch or the failure of the third egg to hatch; broods that lost a chick from a 3-chick brood were excluded. We used linear regression to examine relationships of LGR and AM with hatch date. We first examined effects of colony and year on LGR using ANOVA, and then pooled data across colonies and years to separately examine the dependence of LGR and AM on hatch order and brood size using nested ANOVA (with brood as the nested term). Year and colony effects were analyzed separately because small sample sizes precluded tests of year by colony interactions.

RESULTS

Predator Exclosures.—Four nests did not hatch in 2001 and were abandoned (Table 1). Three of these nests were abandoned immediately after exclusion fencing was erected, while the fourth nest was incubated past the expected hatch date and eventually abandoned. Hatching success of nests incubated to

TABLE 1. Success of Black Tern nests with predator exclosures in Maine wetlands, 2001–2002. Hatching success is defined as the proportion of eggs hatched.

Year	Colony	Nests exclosed	Nests hatched (eggs)	Eggs hatched	Hatching success (%)
2001	Carlton	6	5 (15)	15	100
	Douglas	6	4 (12)	11	92
	Messalonskee	5	4 (10)	10	100
	Totals	17	13 (37)	36	97
2002	Carlton	9	9 (26)	18	69
	Douglas	5	5 (15)	15	100
	Totals	14	14 (41)	33	81

term was 97% in 2001 and 36 eggs hatched (Table 1). Seven (54%) of 13 nests with young were depredated with 17 chicks lost (Table 2). The two depredated exclosures at Carlton contained three 16-day-old chicks and one 14-day-old chick, respectively, while the depredated exclosure at Douglas contained three chicks less than a week old. All four nests that hatched at Messalonskee were depredated within a 3-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. Overall, three chicks from three different broods died of causes unrelated to predation (Table 2). Sixteen chicks were released from exclosures in 2001 (Table 2).

No nests were abandoned prior to hatch in 2002. Hatching success of nests incubated to term was 81% in 2002 and 33 eggs hatched (Table 1). Hatching success of exclosed nests at Carlton was 69%, but 100% at Douglas (Table 1). At Carlton, the third egg of a 3-egg clutch failed to hatch at three nests, and another nest containing one chick and two intact eggs was abandoned. One nest (7%) was depredated at Carlton in 2002 resulting in loss of three chicks <1 week of age. Three chicks from three different broods died of causes unrelated to predation, while one brood of three chicks escaped their exclosure prior to fledging age (Table 2). Twenty-four chicks were released from exclosures in 2002 (Table 2). Predators entering exclosures were not identified in either year.

Survival of Non-depredated Chicks.—Six chicks from six different broods died within exclosures in a manner unrelated to predation. Two of these chicks were <5 days of age and were found dead outside of the retention fencing. These chicks may have escaped from the retention fence and perished after becoming separated from their respective broods, or may have died and been removed from the nest by the adults. Two other chicks died after apparent abandonment by adults, most likely as a result of investigator disturbance associated with predator exclosures. The remaining two chicks, a 16-day-old B-chick and an 8-day-old C-chick, were both in 3-chick broods and exhibited normal growth for 12 and 6 days, respectively, before declining in mass prior to

TABLE 2. Fate of Black Tern chicks in predator exclosures, including cause of loss, 2001–2002.

Year	Colony	Chicks depredated (nests)	Chicks died of other causes (nests)	Chicks escaped from exclosure (nests)	Chicks released from exclosures (nests)
2001	Carlton	4 (2)	2 ^a (2)	0	9 (3)
	Douglas	3 (1)	1 ^b (1)	0	7 (3)
	Messalonskee	10 (4)	0	0	0
	Totals	17 (7)	3 (3)	0	16 (6)
2002	Carlton	0	3 ^c (3)	0	15 (8)
	Douglas	3 (1)	0	3 (1)	9 (3)
	Totals	3 (1)	3 (3)	3 (1)	24 (11)

^a One chick was found dead outside of retention fencing and one chick died of apparent starvation.

^b Chick found dead outside of retention fencing.

^c Two chicks from two separate broods died after apparent abandonment by adults, while the third chick died of apparent starvation.

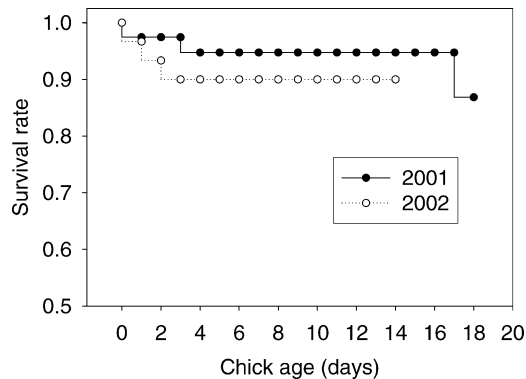


FIG. 2. Kaplan-Meier survival rates for Black Tern chicks not depredated in predator exclosures in 2001–2002 at Douglas Pond and Carlton Pond, Maine. Estimates were based on 17 chicks from six broods in 2001 and 27 chicks from 13 broods in 2002.

death. Including the above instances of mortality, chick survival (\pm SE) to 18 days in 2001 in the absence of predation was 0.87 ± 0.08 (95% CI: 0.71–1.03) and 0.90 ± 0.05 (95% CI: 0.80–1.00) to 15 days in 2002 (Fig. 2) and did not differ among years ($P = 0.46$).

Growth Analyses.—Nineteen broods (3-chick broods, $n = 13$; 2-chick broods, $n = 6$) were used in growth analyses. Mass ratios differed ($F_{1,24} = 11.38$, $P = 0.003$) between B- and C-chicks in 3-chick broods. B-chicks were on average 91% of the mass of A-chicks ($n = 13$, 95% CI = 0.83–0.98) near time of brood completion and C-chicks were 73% of the mass of A-chicks ($n = 13$, 95% CI = 0.65–0.82). In 2-chick broods, B-chicks were on average 72% of the mass of A-chicks ($n = 6$, 95% CI = 0.59–0.86) near brood completion.

Neither LGR ($P = 0.10$, $n = 51$, $r^2 = 0.034$) nor AM ($P = 0.48$, $n = 43$, $r^2 = 0.001$) were affected by hatch date. Estimates of LGR for individual chicks ranged from 3.22 to 5.87 g/day, with a mean of 4.47 g/day. Colony ($F_{2,10} = 0.24$, $P = 0.79$) and year ($F_{1,11} = 1.31$, $P = 0.28$) did not affect LGR; therefore, data were pooled across years and colonies to test hatch order effects. Linear growth rates were not affected by hatch order for either 3-chick broods ($F_{2,24} = 2.13$, $P = 0.14$) or 2-chick broods ($F_{1,5} = 1.06$, $P = 0.35$). Growth rates did not differ ($F_{1,32} = 1.33$, $P = 0.26$) with brood size. Estimates of AM for individual chicks ranged from 39.0 to 73.5 g, with a

mean of 61.6 g. Asymptotic mass did not differ among colonies ($F_{2,8} = 1.21$, $P = 0.35$) or years ($F_{1,9} = 1.00$, $P = 0.34$) and data were pooled across years and colonies to test for hatch order effects. Asymptotic mass did not differ by hatch order for 3-chick broods ($F_{2,20} = 0.71$, $P = 0.50$). We did not test effects of hatch order on AM for 2-chick broods because of small sample sizes.

DISCUSSION

Predator Exclosures.—Our predator exclosure design was not effective in excluding predators in 2001, but after our modifications we observed lower predation in 2002. However, it is unknown if this lower predation (7%) resulted from our modifications or from changes in predator abundance between years. Adult terns generally accepted the small retention fences relatively quickly (3–15 min), but were more hesitant to initially enter the larger exclosures. Adults frequently circled the structure for >20 min. Once acclimated, adults appeared to travel normally to and from the nest during incubation and chick feeding. Four nests in 2001 were abandoned prior to hatch following deployment of predator exclosure fencing. Retention and exclosure fencing were erected simultaneously at two of these nests, resulting in immediate abandonment. The predator exclosure fences at all four abandoned nests were erected ≥ 6 days prior to hatch, which may have been too early. The willingness of adult Black Terns to leave their nests for extended periods decreases as the incubation period lengthens (Cuthbert 1954) suggesting that adult acceptance of exclosures may increase closer to hatching. Nests where exclosure fences were constructed just before or immediately following hatch were not abandoned and we conclude this is the optimal time for deployment. We do not recommend deploying retention fencing and predator exclosure fencing on the same day.

Predators successfully entered more than half of all exclosures where eggs hatched in 2001. A high proportion of depredated chicks were relatively old (58% at 14–17 days of age) suggesting that older chicks in exclosures may be susceptible to loss as they approach fledging. Chicks may become more conspicuous as they approach fledging as a result of wing posturing behaviors and increased vo-

calization rates that could attract predators. We observed that chicks were often well hidden around the inside perimeter of retention fences or remained immobile under vegetation when we visited exclosures. However, in 2001 when we used less physical or vegetative cover, chicks moved continuously in the retention fence seeking escape cover, which increased their visibility to potential predators. We modified our techniques in 2002 by adding additional vegetation and/or artificial camouflage netting in and around retention fences, as well as releasing broods at earlier ages. Only one exclosed nest was depredated in 2002 suggesting our modifications were highly effective. However, placement of additional vegetation and camouflage in 2002 likely resulted in lower hatching success of exclosed nests relative to 2001. The third egg of a 3-egg clutch failed to hatch in three nests in 2002. We hypothesize the addition of dense vegetation within retention fences following hatch of the first two chicks impeded the view of the nesting adults and resulted in their failure to properly incubate the remaining egg. Adults may have only landed in exclosures to feed chicks or brood chicks for short periods. We recommend waiting several days after all chicks have hatched before gradually adding vegetation/camouflage to the retention fence over the course of several visits.

Chick Survival.—Nearly 90% of chicks survived in the absence of predation to 13–18 days in 2001–2002. We observed only six cases of mortality due to other causes and four of these were most likely influenced by investigator disturbance. These results suggest that predators were a primary cause of chick mortality in these wetlands and that weather, food resources, or disease were not significantly influencing chick survival at these sites in the 2 years studied. We cannot assess the magnitude of natural mortality due to predation without data on chick survival for unexclosed broods; however, the difficulty we had in preventing predation of broods attests to a significant level of predator activity in these wetlands. We could not identify the primary predators of chicks in this study. Many species occurring in Maine have been directly observed preying on Black Tern chicks and nests, or else have been implicated by indirect evidence in other studies: Great Blue Heron

(*Ardea herodias*) (Chapman and Forbes 1984, Shealer and Haverland 2000), mink (*Mustela vison*) (Dunn 1979; Hickey 1997; F. A. Servello, pers. obs.), Northern Harrier (*Circus cyaneus*) (this study), Great Horned Owl (*Bubo virginianus*) (Bailey 1977, Einsweiler 1988), Black-crowned Night-heron (*Nycticorax nycticorax*) (Bailey 1977), common raccoon (*Procyon lotor*) (F. A. Servello, pers. obs.), Common Raven (*Corvus corax*) (this study), and fish (Don McDougal, pers. comm.).

Inadequate food provisioning was not a significant cause of chick mortality during the 2 years of study. Despite the presence of a size hierarchy within broods during the early post-hatch period, differential growth (LGR and AM) with hatch order was not observed for either 2- or 3-chick broods. Furthermore, neither LGR nor AM decreased with increasing brood size, as would be expected if food provisioning was inadequate. Gilbert and Servello (2005) similarly found little evidence of food limitation during the 2 years prior to this study. Mean LGR and AM values for chicks were within ranges reported in other studies (Bailey 1977, Dunn 1979, Mosher 1986, Beintema 1997). 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). Four of these six chicks were depredated prior to release, one chick was found dead, apparently of starvation, and one chick was released. Two of these broods occurred in the same colony as broods exhibiting average to high LGRs suggesting factors other than food limitation may have been responsible for depressed growth. Starvation of chicks can be a direct result of insufficient food resources (poor foraging environment) or an indirect result of low “parental quality,” whereby there is ample food but the parents do not provide sufficient food for their young (Nisbet et al. 1995).

Predator exclosures may be a useful conservation tool for increasing breeding productivity of small, high-risk populations of Black Terns. Our predator exclosures allowed adults to successfully raise broods of fledglings within a fenced structure and, therefore, we recommend the design as a research tool to obtain chick growth and survival data. Before

exclosures are implemented as a management tool, we recommend that Black Tern chick predators be identified regionally to assess if our exclosure design would be effective. Predator control (most commonly mammal trapping) has increased nest success for ducks (Sovada et al. 2001, Drever et al. 2004) and duckling survival (Pearse and Ratti 2004) in prairie pothole wetlands, but it is unclear if such control would be effective in Maine wetlands because the primary predators of Black Tern nests and chicks are not known. Predation should be considered a primary factor contributing to mortality of Black Tern chicks in Maine, and predation effects should be examined throughout the breeding range of the species to increase our understanding of factors limiting population growth.

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