Effects of Gull Predation and Predator Control on Tern Nesting Success at Eastern Egg Rock, Maine

CHRISTINA E. DONEHOWER[1,2], DAVID M. BIRD[1], C. SCOTT HALL[3] AND STEPHEN W. KRESS[4]

[1]Avian Science and Conservation Centre, MacDonald Campus, McGill University
21,111 Lakeshore Road, Ste-Anne-de-Bellevue, QC H9X 3V9, Canada

[2]Corresponding author. Internet: christina.donehower@mail.mcgill.ca

[3]Seabird Restoration Program, National Audubon Society, 41 Northport Avenue, Belfast, ME 04915, USA

[4]Seabird Restoration Program, National Audubon Society, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA

Abstract.—Gull predation is an important source of egg and chick mortality for many seabirds. From 2003-2005, the effects of gull predation and a predator control program on tern nesting success were studied at Eastern Egg Rock, Maine. In 2003, gull predation was uncontrolled, and in 2004 and 2005, attempts were made to shoot Herring (*Larus argentatus*), Great Black-backed (*L. marinus*), and Laughing (*L. atricilla*) gulls that preyed on Common (*Sterna hirundo*), Arctic (*S. paradisaea*), and Roseate (*S. dougallii*) tern adults, eggs, and chicks. To evaluate the effectiveness of gull removal, daily watches were performed from an observation tower and tern hatching and fledging success were measured annually. Despite shooting efforts in 2004-2005, many known predators could not be removed. Great Black-backed Gull predation was a function of year, tidal state, and visibility, while Herring Gull predation depended only on the stage of the tern breeding cycle. Using disappearance of eggs and chicks from monitored nests as a proxy for gull predation pressure, an estimated 23% of Common, 32% of Arctic, and 6% of Roseate tern nests were depredated by gulls during the study period. Predation risk depended on nest position within the colony, but not year, with some areas consistently more vulnerable to gulls than others. We discuss the difficulty of removing predatory gulls from a tern colony lacking nesting Herring and Great Black-backed gulls and suggest the importance of human presence and associated research activities for reducing gull predation at this site.
Received 25 April, accepted 29 October 2006.

Key words.—Arctic Tern, Common Tern, Great Black-backed Gull, Gulf of Maine, gull control, gull predation, Herring Gull, Laughing Gull, Roseate Tern.

Waterbirds 30(1): 29-39, 2007

Larus gull populations in Europe and North America grew dramatically in the last century, benefiting from increased food and reduced hunting pressure (reviewed in Mudge 1978; Pierotti and Good 1994; Good 1998). In the Gulf of Maine, Herring (*L. argentatus*) and Great Black-backed (*L. marinus*) gull increases in the early- to mid- 1900s coincided with tern (*Sterna* spp.) declines (Drury 1973, 1974; Nisbet 1973). These declines were linked to displacement from preferred breeding grounds and depredation of tern offspring by gulls (Hatch 1970; Drury 1973, 1974; Nisbet 1973; Kress *et al.* 1983; Kress 1998). Some gulls often 'specialize' as seabird predators, preying heavily on seabird adults, eggs, and young (Pierotti and Annett 1990, 1991; Spear 1993; Guillemette and Brousseau 2001).

Many studies have shown that gull predation can limit the breeding success of terns and other colonial waterbirds (e.g., Vermeer 1968; Hatch 1970; Dwernychuk and Boag 1972; Becker 1995; Guillemette and Broussard 2001). In two recent gull-tern studies, estimated egg and chick losses to gulls exceeded 70%. Whittam and Leonard (1999) reported that gulls depredated 77% of Roseate Tern (*Sterna dougallii*) chicks on Country Island, Nova Scotia in 1996 and that Roseates abandoned the colony the following year. O'Connell and Beck (2003) suggested that gulls took as many as 73% of all eggs produced by *Sterna* terns and Black Skimmers (*Rynchops niger*) in the Virginia barrier islands. Small and declining seabird colonies may be particularly vulnerable to gull predation due to compromised group defense (Gilchrist 1999).

To reestablish former seabird colonies and to improve nesting opportunities for small seabirds, gull control programs have been implemented in some areas (Kress 1983, 1998; Anderson and Devlin 1999;

Kress and Hall 2002). Typically, adult Herring and Great Black-backed gulls are removed in the early stages of restoration through harassment and nest removal or large-scale poisoning/shooting. Thereafter, efforts are made to keep the area free of breeding or territorial gulls through the establishment of seasonal research camps, nest destruction, harassment, and shooting of individuals or territorial pairs. It is clear that terns can respond favorably to management since 96% of all Common (*S. hirundo*), Arctic (*S. paradisea*), and Roseate terns breeding in the Gulf of Maine nested at managed sites in 2005 (GOMSWG 2005).

At many managed tern colonies, gulls seen preying on tern eggs and chicks are shot. The rationale is that a few 'specialist' gulls usually consume the majority of tern prey and that removing these individuals is a practical, inexpensive means of controlling predation (Guillemette and Brousseau 2001; Kress and Hall 2002). Some managers also perceive the removal of a small number of predatory gulls as an ethical alternative to broad-scale culling (CED, pers. obs.).

It has generally been assumed that shooting gulls effectively reduces predation pressure on terns and thereby enhances productivity, but few studies have quantified gull predation rates or examined gull-tern dynamics before and after implementation of a shooting program. Guillemette and Brousseau (2001) found that the disappearance rate of Common Tern chicks was lower and the lifespan of broods higher in a year when predatory gulls were shot than in other years. However, their study occurred at a tern colony where predatory gulls bred on the same island as the terns and could be easily identified and removed. Many tern colonies are located at sites that lack nesting gulls but continue to experience high levels of gull predation (GOMSWG 2005), presumably due to non-breeding, resident gulls and/or gulls traveling from nearby gull colonies. The main objective of this study was to compare tern nesting success and losses to gulls in years with and without a shooting program at a site lacking nesting Herring and Great Black-backed gulls. A secondary objective was to identify factors affecting gull predation rates.

METHODS

Study Area

Our study was conducted from 2003-2005 during the tern breeding season (early June-mid August) at Eastern Egg Rock (43°52'N, 69°23'W), a 3 ha island located 10 km east of New Harbor in Muscongus Bay, Maine, USA. The island has a central meadow of grasses (*Phleum pratensis* and *Agropyron repens*) and shrubs (mostly raspberry *Rubus idaeus* and elderberry *Sambucus canadensis*) surrounded by a rocky coastline. It is managed by the National Audubon Society, and several researchers/wardens occupy a seasonal field camp from late May to mid August. Since the 1970s, gull control, captive-rearing, and social attraction efforts have restored a mixed-species seabird colony (see Kress 1998 for a detailed site history and description). Common, Arctic, and Roseate terns nest on the island as do Atlantic Puffins (*Fratercula arctica*), Black Guillemots (*Cepphus grylle*), Common Eiders (*Somateria mollissima*), Leach's Storm-petrels (*Oceanodroma leucorhoa*), and Laughing Gulls (*L. atricilla*). Over one hundred Herring and Great Black-backed gulls reside on the island daily but are not permitted to breed; their nests and eggs are destroyed upon discovery. Several unmanaged Herring and Great Black-backed gull colonies are located <10 km from Eastern Egg Rock. Lethal control (shooting with a .22 caliber rifle) of gulls preying on terns has been practiced since 1984 but was prohibited in 2003 so that predation could be monitored. Shooting resumed in 2004 and continued in 2005. There are no mammalian predators, and other avian predators rarely visit the site.

Tern Census and Productivity

An island-wide tern nest census was conducted annually in mid-late June. Arctic and Roseate tern population estimates were generated from direct counts of incubating adults from blinds, while the Common Tern estimate was obtained from a "walk-through" ground count and adjusted using a Lincoln mark-recapture index to correct for missed nests (Kress and Hall 2002). The general location (block) of each tern nest was recorded, so that nesting density (no. nests per block) could be determined. Blocks were delineated by mapping available tern nesting habitat (National Audubon Society Seabird Restoration Program, unpubl. data) and dividing the area into 16 sections using census markers (Fig. 1).

To assess tern productivity (fledglings $nest^{-1}$), a sample of nests of each species was monitored (Table 1). Individual nests were numbered and marked. Common Tern nests were monitored in four fenced enclosures (three enclosures in 2003), hereafter plots, and in unfenced habitat. All Arctic and Roseate tern nests were located in unfenced habitat. Nests were checked daily until all eggs hatched and every 2-5 days thereafter; all chicks were banded at hatching. Because of the difficulty of following older chicks, chicks surviving 15 days were considered fledged (Kress and Hall 2002). Clutch sizes, hatch dates, and fates of eggs (hatched, failed, or disappeared) and chicks (fledged, died, or disappeared) were also recorded.

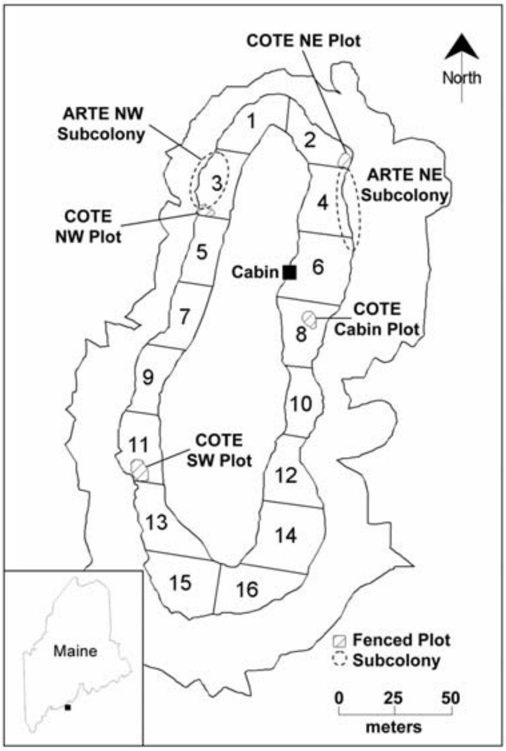

Figure 1. Available tern nesting habitat at Eastern Egg Rock, Maine, was mapped and divided into 16 blocks. Nest density (no. tern nests per block) was recorded during annual censuses. Locations of Common Tern (COTE) fenced plots and Arctic Tern (ARTE) subcolonies referred to in the text are also indicated.

Losses to Gulls

Disappearance of tern eggs and chicks from nests was used as a proxy for gull predation pressure. Whenever an egg or chick went missing from a nest, observers spent up to five min carefully searching the vicinity for dead chicks or failed eggs in an attempt to rule out other sources of mortality. Only after a chick or its remains could not be located for three consecutive nest checks did we presume that it had been depredated. Nevertheless, we were concerned that the occasional dead chick or failed egg may have escaped our detection in unfenced habitat, since our search area was unconfined. Therefore, for tern nests in unfenced habitat only, a nest was considered depredated only if all of its contents disappeared. Since all Arctic and Roseate tern nests were in unfenced habitat, partial predation was not examined for these species. For Common Terns, an estimate of partial predation was generated using nests in the fenced plots only (N = 145). It is unlikely that any Common Tern chicks escaped from the plots since fencing was checked regularly for holes, and chicks capable of flight were not followed; our cut-off for fledging was 15 days.

All nests were grouped by location (plot for Common Terns, subcolony for Arctic and Roseate terns) for analysis. Nests in locations that were not sampled in all years were excluded from analyses but included in productivity estimates. Exact logistic regression (PROC LOGISTIC; SAS Institute 2002) was used to compare 1) the number of depredated nests in each location and year for all species and 2) the number of partially depredated nests in each plot and year for Common Terns only. Since some plots/subcolonies experienced little or no predation, exact conditional estimates were used; exact methods are preferable for sparse data and can handle contingency tables with low/zero cell counts (Stokes *et al.* 2000). Models with the dichotomous response variable ‘nest depredated’ (1 = nest contents disappeared, 0 = no evidence of predation) and two explanatory variables, location and year, were considered.

Factors Affecting Gull Predation

CED observed the tern colony daily for a total of 160 h in 2003 (15 June-2 August), 257 h in 2004 (11 June-4 August), and 300 h in 2005 (22 June-5 August). Predation watches generally lasted 2-4 h ($\bar{x}$ = 2.5) and were conducted from a 5 m platform overlooking the majority of tern nesting habitat. Watches could not be performed under adverse weather conditions (heavy rain, winds >30 km h^{-1}) and were done opportunistically during daylight hours. All gull intrusions (successful and unsuccessful) were recorded.

Table 1. Breeding parameters for Common (COTE), Arctic (ARTE), and Roseate (ROST) terns on Eastern Egg Rock, Maine in 2003-2005. Data are shown as $\bar{x}$ ± SD.

Species	Year	Nests[1]	Clutch size	N	Hatch day	N	Productivity[2]	N
COTE	2003	992	2.0 ± 0.6	50	26 Jun ± 4	78	1.06 ± 0.88	49
	2004	873	1.9 ± 0.6	83	30 Jun ± 5	78	0.62 ± 0.65	78
	2005	758	2.0 ± 0.7	69	1 Jul ± 6	54	0.60 ± 0.59	62
ARTE	2003	77	1.8 ± 0.4	44	28 Jun ± 7	58	0.81 ± 0.83	42
	2004	84	1.7 ± 0.6	26	27 Jun ± 3	25	0.62 ± 0.75	26
	2005	81	1.8 ± 0.4	26	30 Jun ± 4	20	0.54 ± 0.58	26
ROST	2003	164	1.6 ± 0.5	50	29 Jun ± 5	62	0.93 ± 1.00	30
	2004	110	1.3 ± 0.5	46	30 Jun ± 4	49	0.91 ± 0.00	22
	2005	136	1.7 ± 0.6	90	3 Jul ± 4	121	0.92 ± 0.29	12

[1]No. nests found on the island during the annual census in mid-late June.
[2]Fledglings $nest^{-1}$, assumes that chicks surviving 15 days fledged.

For each gull intrusion, the location (block), quantity and type of prey consumed, and the species, age class (adult or subadult), and identity of the predatory gull were noted. Attempts were made to uniquely color-mark each predatory gull to facilitate individual recognition (see Donehower and Bird 2005 for details on the color-marking procedure). However, some predatory gulls could not be marked, so a combination of natural plumage characteristics (e.g., feather pigmentation, molt) and behavioral patterns (fidelity to particular loafing or hunting areas) was used to establish identity. Tidal state (low, mid, or high) and visibility (>1600 m or <1600 m) were recorded at 30 min intervals.

The probability of observing gull predation (1 = at least one gull entered the tern colony to take prey, 0 = no predatory activity observed) was modeled in relation to year, tern breeding period, tidal state, and visibility using logistic regression (PROC LOGISTIC; SAS Institute 2002). Separate analyses were performed for Herring Gulls and Great Black-backed Gulls. Laughing Gull predation was seldom observed and was not modeled. A 2-h interval was used as the sampling unit because predation was usually detected within this period and because this allowed examination of tidal state and visibility. Tide and visibility levels seldom changed within 2 h, but when applicable, average values were used.

We confined our analysis to a single 2-h interval per day collected between 05:00 and 09:00 to control for the confounding effects of human disturbance that occurred irregularly throughout the remainder of the day. Human activities (e.g., research and gull control activities, persons walking to and from blinds, etc.) clearly affected gull behavior, and consequently, predation. Predatory gulls temporarily left usual hunting or loafing areas upon the approach of a human, retreating to undisturbed parts of the island or even sitting in the water offshore until human activity subsided (CED, pers. obs.).

Following Dinsmore *et al.* (2002), a small set of eight candidate models based on the following *a priori* hypotheses were developed: *Year.* We predicted that probability of gull predation would be higher in 2003 than in 2004-2005 since predatory gulls were shot in the latter two years. *Tern breeding period.* We reasoned that predation could depend on the stage of the tern breeding cycle if parental defense (e.g., Whittam and Leonard 2000) and/or gull preferences or food demands (e.g., Pierotti and Annett 1990) changed seasonally. We divided the season into three 18-day periods: 1) egg-laying/incubation, 2) hatching/chick-rearing, and 3) chick-rearing/fledging, defining periods around the mean hatch date for all tern species in a given year. *Tidal state.* If predatory gulls depended on marine invertebrates in the intertidal zone for additional food, we predicted that they would prey more heavily on terns at high or mid tides when these items were less available. *Visibility.* We reasoned that visibility could affect predation if gulls were unable to locate or feed at lobster boats during fog; discarded fish offal is an important food source for gulls in some parts of Maine (Goodale 2001).

Models with each of the main effects, year and tern breeding period (Models 1 and 2; Table 2) were fitted first. To each of the main effects, tidal state and visibility covariates were added separately (Models 3, 4, 6, and 7; Table 2) and together (Models 5 and 8; Table 2). An information-theoretic approach for model selection based on Akaike's Information Criterion corrected for small sample size (AIC_c) was used. After applying the model with all explanatory variables, goodness-of-fit was assessed using the variance inflation factor, c, where $\hat{c} = \chi^2/\text{df}$ and overdispersion is suggested when $\hat{c} > 1$ (Burnham and Anderson 2002). Akaike weights, w_i, were used to evaluate the strength of evidence in support of each model and to calculate relative variable importance, w_+ (Burnham and Anderson 2002). For the best model only, the odds ratio was examined for different levels of each explanatory variable (Stokes *et al.* 2000).

All data are reported as $\bar{x} \pm$ SD, unless otherwise indicated. With the exception of information-theoretic analyses, we set $\alpha = 0.05$.

RESULTS

Tern Census and Productivity

Altogether, 1233, 1067, and 975 tern nests were found in 2003, 2004, and 2005, respectively. The majority of nests belonged to

Table 2. Summary of model-selection results for factors affecting probability of Great Black-backed Gull (left) and Herring Gull (right) predation at Eastern Egg Rock, Maine in 2003-2005. Models examined the effects of year, tern breeding period, tidal state, and visibility on gull predation. *K* is the number of parameters, ΔAIC_c is the difference between the model with the lowest AIC_c value (best-fitting model) and the current model, and w_i is the model weight.

		Great Black-backed Gull		Herring Gull	
Model	*K*	ΔAIC_c[1]	w_i	ΔAIC_c[2]	w_i
1) *P*(year)	3	6.54	0.03	16.71	0.00
2) *P*(period)	3	26.00	0.00	0.00	0.56
3) *P*(year + tide)	5	5.03	0.06	19.83	0.00
4) *P*(year + visibility)	4	2.71	0.19	16.99	0.00
5) *P*(year + tide + visibility)	6	0.00	0.73	19.98	0.00
6) *P*(period + tide)	5	25.41	0.00	2.22	0.18
7) *P*(period + visibility)	4	25.84	0.00	2.07	0.20
8) *P*(period + tide + visibility)	6	24.61	0.00	4.39	0.06

[1]AIC_c for the best model was 103.56.
[2]AIC_c for the best model was 112.07.

Common Terns (758-992 nests), with small numbers of Roseate (110-164 nests) and Arctic (77-84 nests) terns (Table 1). Clutch sizes (eggs nest^{-1}) were consistent among years and species, ranging from 1.9-2.0 for Common Terns, 1.7-1.8 for Arctic Terns, and 1.3-1.7 for Roseate Terns (Table 1). Peak hatching occurred in the last week of June/first week of July in all years for all species (Table 1). Productivity (fledglings nest^{-1}) ranged from 0.60-1.06 for Common Terns, 0.54-0.81 for Arctic Terns, and 0.91-0.93 for Roseate Terns (Table 1). All species experienced highest productivity in 2003.

Losses to Gulls

For Common Terns, 11-25% of eggs and 13-33% of chicks disappeared from nests in the plots (Table 3). Overall, we estimate that 23% (33 of 145 nests) of Common Tern nests were completely depredated during the study period, while 42% (61 of 145 nests) suffered partial predation. The proportion of depredated nests differed significantly among plots (Score test statistic = 57.6, P < 0.001) but not years (Score test statistic = 3.1, n.s.) (Fig. 2A). Terns nesting in the 'SW' plot consistently suffered high predation, while those in the 'Cabin' plot never experienced complete nest predation (see Fig. 1 for plot locations). Similarly, the proportion of Common Tern nests experiencing partial predation differed significantly among plots (Score test statistic = 44.5, P < 0.001) but not years (Score test statistic = 1.0, n.s.) (Fig. 2B).

For Arctic Terns, 11-32% of eggs and 16-35% of chicks disappeared from nests (Table 3). Overall, 32% (27 of 84 nests) of Arctic Tern nests were completely depredated during the study period. The proportion of depredated Arctic Tern nests differed significantly among subcolonies (see Fig. 1 for subcolony locations; Score test statistic = 15.9, P < 0.001) but not years (Score test statistic = 5.0, n.s.) (Fig. 3).

For Roseate Terns, 0-4% of eggs and 0-6% of chicks disappeared from nests (Table 3). Overall, only 6% (4 of 64 nests) of Roseate Tern nests were completely depredated during the study period. Since nest predation was negligible, subcolony and year effects were not examined.

Nest location, as indicated by the highly significant plot and subcolony effects, was clearly important for Common and Arctic terns. This was further evident by examining the frequency of gull intrusions in each block of the tern colony. The number of intrusions per tern nest per block in 2004 was significantly correlated with the number of intrusions per tern nest per block in 2005 (r_s = 0.68, P < 0.01, N = 16) (Fig. 4). The number of intrusions in a block was also significantly correlated with the number of tern nests in that block (r_s = 0.49, P < 0.01, N = 32).

Factors Affecting Gull Predation

Adult Herring and Great Black-backed gulls were the principal predators (Fig. 5, Table 4), consuming all tern life stages. Great

Table 3. Egg and chick fates of Common (COTE), Arctic (ARTE), and Roseate (ROST) terns nesting on Eastern Egg Rock, Maine in 2003-2005.

Species	Year	Nests	Eggs	Chicks	% Eggs hatched	% Eggs failed	% Eggs missing	% Chicks fledged	% Chicks dead	% Chicks missing
COTE	2003	39	79	64	81	8	11	59	8	33
	2004	50	94	68	72	9	19	56	25	19
	2005	56	113	69	63	12	25	49	38	13
ARTE	2003	32	59	51	86	3	32	65	0	35
	2004	26	44	29	68	0	32	55	17	28
	2005	26	46	25	57	33	11	56	28	16
ROST	2003	30	47	35	74	21	4	80	14	6
	2004	22	30	26	87	17	0	77	19	0
	2005	12	20	17	85	15	0	65	29	0

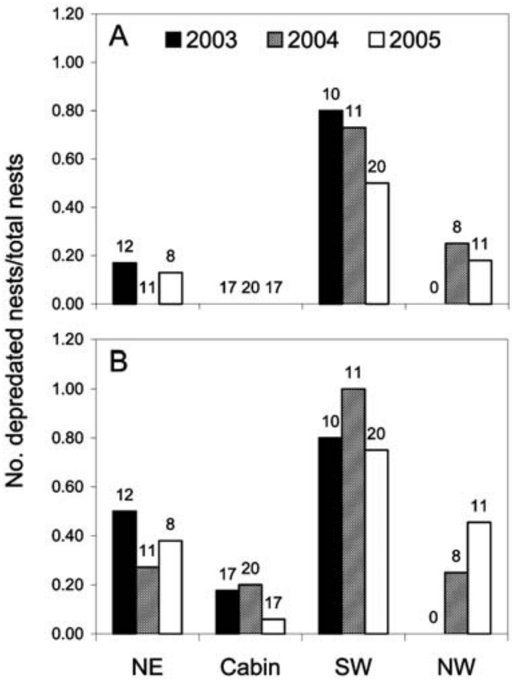

Figure 2. A) Ratio of completely depredated nests to total nests and B) ratio of partially depredated nests to total nests for Common Terns breeding in four plots (NE, Cabin, SW, and NW) on Eastern Egg Rock, Maine in 2003-2005. Note that the NW plot was not monitored in 2003. Sample sizes (no. nests monitored) are given above bars.

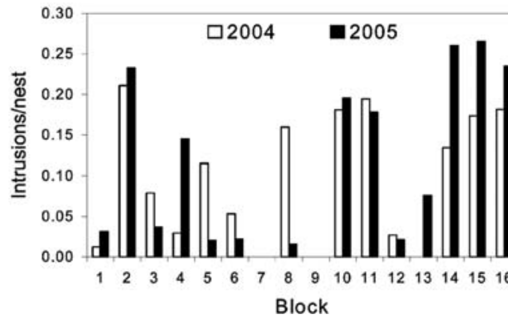

Figure 4. Gull predation pressure according to tern nest location at Eastern Egg Rock, Maine in 2004-2005. The relative number of observed gull intrusions per tern nest was calculated for each habitat block (2004: N = 79 intrusions, 2005: N = 195 intrusions).

Black-backed Gulls preyed heavily on eggs and chicks (73% eggs, 20% chicks, 6% fledglings, and 1% adults; N = 160 prey items identified), while Herring Gulls fed almost exclusively on chicks and fledglings (6% eggs, 68% chicks, 21% fledglings, and 5% adults; N = 99 prey items identified). It is possible that some very young chicks (0-2 days old) were misclassified as eggs (and vice versa) since gulls swallowed these items quickly. Herring Gulls frequently lost kills to piracy by Great Black-backed Gulls and returned to the colony repeatedly to replace stolen items. One Herring Gull took three adult terns in 50 min, losing all but the last prey item to Great Black-backed Gulls. Laughing Gulls were rarely observed taking tern prey and were seen eating only downy chicks and eggs. Laughing Gulls, unlike Herring and Great Black-backed gulls, were tolerated by terns in tern nesting areas, so detection of predation by this species was extremely difficult, and predation was likely underestimated. In 2005, one color-marked Laughing Gull took at least 20 tern chicks in 136 h (0.15 chicks h^{-1}) before it was shot.

In total, 13, 19, and 13 predatory gulls were identified in 2003, 2004, and 2005, respectively (Table 4). Many gulls favored particular loafing and hunting areas. High rock ledges, blinds, and signs at the colony periphery were used as 'hunting stations', presumably because they provided good views of the tern colony yet offered refuge from mobbing terns. Despite the shooting program in 2004-2005, many predatory gulls were never removed. In both years combined, a total of seven Herring Gulls, one Laughing Gull, and ten Great Black-backed Gulls were killed (Fig. 5B, C, Table 4).

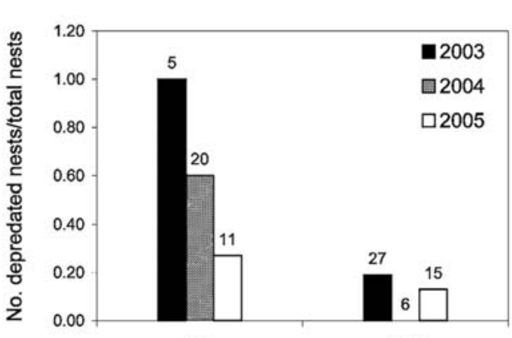

Figure 3. Ratio of completely depredated nests to total nests for Arctic Terns breeding in two subcolonies (NE and NW) on Eastern Egg Rock, Maine in 2003-2005. Sample sizes (no. nests monitored) are given above bars.

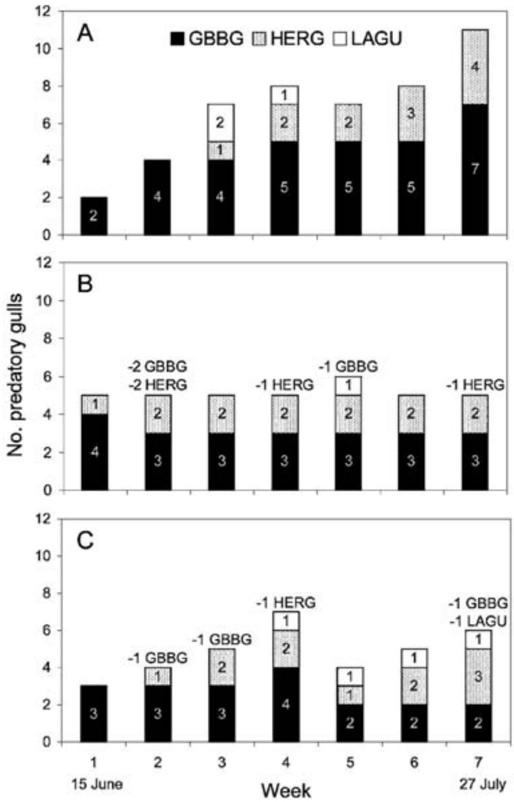

Figure 5. Weekly number of predatory Laughing (LAGU), Herring (HERG), and Great Black-backed (GBBG) gulls at Eastern Egg Rock, Maine in A) 2003, B) 2004, and C) 2005. Values on bars denote the contribution of each species to the total. Numbers and species of gulls removed are indicated with "-" above bars. Note that four additional GBBG and two HERG were removed prior to 15 June 2004 (not shown).

The best model for probability of Great Black-backed Gull predation included year, tide, and visibility (Tables 2 and 5). The odds of Great Black-backed Gull predation were 51.3 times higher in 2003 than 2004 (95% CL: 7.6, 347.2) and 20.3 times higher in 2003 than 2005 (95% CL: 3.7, 110.3). The odds of predation were 4.6 times higher when visibility was poor (<1600 m) versus good (>1600 m) (95% CL: 1.4, 14.7). Finally, the odds of predation were 6.5 times higher at mid than high tides (95% CL: 1.5, 27.8), 3.4 times higher at low than high tides (95% CL: 0.9, 13.4), and 1.9 times higher at mid than low tides (95% CL: 0.6, 6.3); however, the wide confidence limits that include the value one suggest that odds of predation may actually be similar for low vs. high and mid vs. low tides (Stokes *et al.* 2000). Three other models were competitive with the best model and contained fewer parameters (Table 2). Estimates of relative variable importance confirmed that year and visibility were very important predictors, while tide was moderately important, and period was unsupported (Table 6).

Table 4. Number of predatory Herring (HERG), Great Black-backed (GBBG), and Laughing (LAGU) gulls on Eastern Egg Rock, Maine in 2003-2005. Parentheses indicate number of gulls shot as part of a predator control program in 2004-2005.

Year	HERG	GBBG	LAGU	Total
2003	4 (0)	7 (0)	2 (0)	13 (0)
2004	8 (6)	10 (7)	1 (0)	19 (13)
2005	4 (1)	7 (3)	2 (1)	13 (5)

The best model for probability of Herring Gull predation included only tern breeding period (Tables 2 and 5). The odds of Herring Gull predation were 18.4 times higher during tern hatching/chick-rearing than egg-laying/incubation (95% CL: 3.8, 89.5) and 14.1 times higher during chick-rearing/fledging than egg-laying/incubation (95% CL: 2.8, 71.4). Three other models were within five AIC_c units of the best model (Table 2). Estimates of relative variable importance confirmed that tern breeding period was very important, while tide and visibility were somewhat important, and year was unsupported (Table 6).

DISCUSSION

Tern Census and Productivity

Common, Arctic, and Roseate terns nested on Eastern Egg Rock, Maine in 2003-2005. All species had high hatching success, and clutch sizes were typical for this colony (National Audubon Society Seabird Restoration Program, unpubl. data). With the exception of Roseate Terns, productivity varied widely from year to year, probably reflecting a suite of environmental factors, such as weather conditions, food availability, and predation. In an attempt to separate gull predation from other mortality factors, we used a combination of observational and nest-monitoring data.

Table 5. Parameter estimates ± SE for the best model describing probability of Great Black-backed Gull (left) and Herring Gull (right) predation on Eastern Egg Rock, Maine in 2003-2005.

Great Black-backed Gull		Herring Gull	
Parameter	Estimate ± SE	Parameter	Estimate ± SE
Intercept	0.84 ± 0.34	Intercept	-0.59 ± 0.30
Year ‘2003’	2.32 ± 0.58	Period ‘egg-laying/incubation’	-1.85 ± 0.52
Year ‘2004’	-1.62 ± 0.46	Period ‘hatching/chick-rearing’	1.06 ± 0.35
Tide ‘high’	-1.03 ± 0.44		
Tide ‘low’	0.19 ± 0.36		
Visibility ‘>1600 m’	-0.76 ± 0.30		

Losses to Gulls

Common and Arctic terns experienced heavy nest predation by gulls, while Roseate Tern nests were seldom depredated. Using disappearance of eggs and chicks as a proxy for losses to gulls, we estimate that 23% of Common Tern nests, 32% of Arctic Tern nests, and 6% of Roseate Tern nests were completely depredated during the study period. The latter values are conservative since they do not reflect any older chicks (>15 days old) taken by gulls, nor do they account for partial nest predation.

The lower vulnerability of Roseate Tern nests can likely be attributed to nest-site selection. Unlike Common and Arctic terns that favored bare or sparsely vegetated substrate, Roseate Terns nested in dense vegetation or in rock crevices, both of which may provide a refuge from gull predation. Similar interspecific differences in nest-site selection have been documented elsewhere (Spendelow 1982; Richards and Morris 1984; Ramos and Del Nevo 1995; Hatch 2002), and many studies have shown that nest cover and habitat complexity confer protection from predators (Huffaker *et al.* 1963; Crabtree *et al.* 1989; Burness and Morris 1992; Guyn and Clark 1997; Newton 1998). Gulls were observed capturing occasional Roseate Tern fledglings, suggesting that Roseates become vulnerable upon leaving the protection of the nest.

Table 6. Relative importance of variables included in logistic regression models examining probability of Great Black-backed Gull (left) and Herring Gull (right) predation at Eastern Egg Rock, Maine in 2003-2005.

	Great Black-backed Gull	Herring Gull
Variable	w_+	w_+
Year	1.00	0.00
Period	0.00	1.00
Tide	0.79	0.25
Visibility	0.91	0.26

For Arctic and Common terns, position within the tern colony appeared to be the single most important determinant of nest success. The number of depredated nests differed significantly among plots and subcolonies for Common and Arctic terns, respectively, but not among years for either species. Moreover, the number of gull intrusions per tern nest per block was correlated among years, suggesting that particular sections of the colony were consistently more vulnerable to gull predation than others, despite changes in predator numbers and composition. These differences in predation risk could result from variation in local nest densities and/or distribution patterns. The strong, positive correlation between the number of gull intrusions in a block and the number of tern nests in that block suggests that predatory gulls were attracted to concentrations of prey (Burger and Lesser 1978; Brunton 1997).

We suspect that small-scale differences in topography and in frequency of disturbance by humans were also responsible for at least some of the local variation in tern nest success at Eastern Egg Rock. Patches of substrate lacking vegetation and with flat rock surfaces provided good landing sites for Herring and Great Black-backed gulls entering the tern colony, and nests bordering these areas produced few fledglings (CED, pers. obs.).

Human disturbance (research, camp, and gull control activities) appeared to temporarily disrupt gull predation by frightening predators away from their typical loafing and hunting areas. This idea is further supported by the fact that no nests failed due to predation in the 'Cabin' plot from 2003-2005. This plot was located within 20 m of the cabin, which served as the center of human activities. Nest observers appear to reduce predation at some colonies (Kress and Hall 2002), and terns can habituate to regular disturbances (Nisbet 2000), suggesting that human presence/activities could be used as a means of controlling predation. We suggest that frequent "gull walks" to clear hunting stations and loafing areas, positioning an observer several times daily at a particular hunting station, and/or locating observation blinds in areas suffering chronic gull predation be tried as deterrents to predatory gulls. Human presence, combined with Herring and Great Black-backed gull nest destruction, are probably the two most important factors enhancing tern productivity and ensuring colony persistence at Eastern Egg Rock. Hatch (1970) drew similar conclusions about the potential benefits of human activities at a tern colony at Petit Manan in the northern Gulf of Maine over 30 years ago.

The absence of a year effect in incidence of tern nest predation could be due to a variety of factors. First, predatory gulls were not easily removed, and many known predators continued to feed in the tern colony in 2004-2005. Gulls were seldom shot on the first attempt and were often harassed on many occasions prior to a successful shot. Repeated harassment made gulls wary of humans and changed their loafing and hunting patterns, making identification and tracking progressively more difficult. Moreover, fog and boat traffic around the island limited times that wardens could pursue predators. Second, some predators were removed only to be replaced by new gulls. Guillemette and Brousseau (2001) found that shooting the most successful predatory gull released other gulls from a "despotic system" and led to higher predation rates among the survivors. While we were unable to compare predation rates of the same gulls before and after removal of the top predator, new or surviving predators claimed territories and hunting stations of deceased gulls in at least five instances. Third, absence of a year effect does not mean that predator control was ineffective. Daily watches indicated that Great Black-backed Gull predation was reduced substantially as a result of predator control, and other factors such as weather and food may have made terns especially vulnerable to gulls in 2004 and 2005. Another possibility is that the time-scale of uncontrolled predation (one season) was too short to show impacts on tern breeding success; if predation had continued unchecked for additional seasons, perhaps inter-annual differences would have been more dramatic. Finally, we cannot rule out the possibility that Laughing Gull predation was higher in 2004-2005, making tern nest losses similar in all years. Because terns tolerated Laughing Gulls in tern nesting areas, predation was seldom observed, and the impact of Laughing Gulls could not be determined accurately.

Factors Affecting Gull Predation

Studies of predatory gulls at other seabird colonies have shown that a small number of 'specialist' gulls are typically responsible for most predation losses (Spear 1993; Guillemette and Brousseau 2001). At Eastern Egg Rock, we documented specialization among a subset of Herring and Great Black-backed gulls residing on the island. However, we also found that specialists were sometimes replaced upon removal, undermining the benefit of targeting individual gulls in a predator control program.

Although we detected no year effects in tern nest losses to gulls, observational data indicated that there were annual differences in the probability of Great Black-backed Gull predation. The most important determinants of Great Black-backed Gull predation were year, visibility, and tidal state. Probability of predation was lower for predator control years (2004-2005) than the year without control (2003), presumably because many predatory Great Black-backed Gulls were removed. Predation was also associated with poor visibility, possibly because alternative food sources such as fish offal discarded from lobster boats were less available or because gulls learned that shooting or other human activities were reduced under foggy conditions. It is unclear why predation was associated with low/mid tides. Perhaps this was when gulls were in active feeding mode, consuming not only exposed marine invertebrates but also tern prey. Verbeek (1979) observed that nearly all Great Black-backed Gulls were away from their nesting territories during low tides, so gulls visiting Eastern Egg Rock from nearby colonies may do so primarily at low/mid tides. Weather conditions (Mendenhall and Milne 1985; Gilchrist and Gaston 1997; Gilchrist *et al.* 1998) and the availability of alternative foods (Stenhouse and Montevecchi 1999; Massaro *et al.* 2000) have influenced gull predation rates in other studies.

In contrast, the most important determinant of probability of Herring Gull predation was tern breeding period. Herring Gulls preyed almost exclusively on tern chicks and fledglings, so little predation occurred during the egg-laying/incubation period compared to the hatching/chick-rearing and chick-rearing/fledging periods. Hatch (1970) and Guillemette and Brousseau (2001) also noted that Herring Gull predation coincided with availability of chicks.

Conclusion and Recommendations

Our results highlight the difficulty of removing predatory gulls from a tern colony lacking nesting Herring and Great Black-backed gulls. While observational data suggested that predator removal was effective (at least for Great Black-backed Gulls), disappearance of tern eggs and chicks from monitored nests revealed no annual differences. The obvious question is: should shooting of predatory gulls be continued as a tern management tool? While shooting a few gulls does not necessarily preclude replacements, we believe that limited shooting helps to discourage widespread predation by many gulls (particularly Great Black-backed Gulls). However, given the limitations of capable staff trained in shooting and the time and effort required to remove individual predators, we emphasize the importance of other means for control—especially egg and nest removal combined with human presence throughout the tern nesting season. We suggest that gull management practices intended to increase tern productivity should minimize shooting, while emphasizing nonlethal harassment practices that target all gulls (e.g., egg and nest destruction, conspicuous human observers, gull displacement walks, and pyrotechnics). These combined methods will help to exclude potential predators from tern nesting habitat.

ACKNOWLEDGMENTS

We thank E. E. Peterson, R. V. Borzik, D. J. Wood, and P. Salmansohn for research and logistical support on Eastern Egg Rock. Staff and volunteers of the National Audubon Society's Seabird Restoration Program collected tern census and productivity data. R. Houston mapped available tern nesting habitat. J. A. Correa provided helpful advice on statistical procedures. A. W. Diamond, M. A. Hudson, and an anonymous reviewer made comments that greatly improved earlier drafts of this manuscript. This study was funded, in part, by the Garden Club of America and Cornell Lab of Ornithology (Frances M. Peacock Scholarship for Native Bird Habitat awarded to CED). Additional support was given by the Department of Natural Resource Sciences and the Avian Science and Conservation Centre of McGill University.

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