

Comparison of Common Tern Reproductive Performance at Four Restored Colonies along the Maine Coast, 1991-2002

C. SCOTT HALL¹ AND STEPHEN W. KRESS²

¹National Audubon Society—Seabird Restoration Program, 41 Northport Ave., Belfast, ME 04915, USA
Internet: shall@audubon.org

²National Audubon Society—Seabird Restoration Program, 159 Sapsucker Woods Rd., Ithaca, NY 14850, USA

Abstract.—We compared the reproductive performance of the Common Tern (*Sterna hirundo*) from 1991-2002 at four restored colonies in Maine that differ in location (inshore, nearshore and offshore sites), colony age and size and predation. Specifically, phenology, clutch size, survival, growth, provisioning rates and predation intensity and frequency were compared between sites. Common Terns nesting on the two inshore islands laid larger clutches, hatched chicks earlier that grew faster, reached a greater asymptotic mass, and had a greater chance of fledging than conspecifics on a nearshore and an offshore colony, despite greater predation pressure. Individuals nesting at the offshore site suffered reduced reproductive performance, which may be due to colony location with respect to foraging areas. Clutch size, chick provisioning rates and first hatch dates (earlier) declined as colony size increased. Although inshore nesting terns produced more chicks on average, extensive predation in some years caused high breeding failure, resulting in a “boom or bust” productivity situation for these islands. Differences in predation and performance between inshore, nearshore and offshore islands have important implications for the restoration, conservation and management of terns in this region. Nearshore sites offer the best restoration potential and should be strongly considered when available. Received 23 December 2003, accepted 5 September 2004.

Key words.—Common Tern, *Sterna hirundo*, reproductive performance, predation, restoration, inter-colony variation, Maine.

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Seabird restoration techniques developed in Maine (Kress 1983; Kress and Nettleship 1988; Podolsky and Kress 1989) are widely used to create new colonies at historic nesting islands (Kress and Hall 2003). The success of a restoration program is often determined by the initiation of breeding, rather than using demographic, reproductive and other biological data from the site. Since 1968, several tern restoration programs have been initiated in the northeastern US (USFWS 1998; Kress and Hall 2002; Nisbet 2002). However, although a few studies report either diet, reproductive or growth data for a single colony, no studies have evaluated success of restoration efforts at multiple sites over many years for a single species [in this case, the Common Tern (*Sterna hirundo*)] using a suite of biological parameters to characterize performance. Site differences in performance have important implications for restoration and management of terns in the region.

Colonial nesting seabirds may have to make choices between breeding sites that are favorable for raising offspring, but unfavorable for other reasons (e.g., predation

and crowding; Lack 1968; Bried and Jouvettin 2001). The location of breeding sites relative to foraging areas has important implications for provisioning, growth and survival of offspring. Several studies have documented reduced breeding performance (including clutch size, provisioning rates, and the growth and survival of offspring) as a result of increased foraging effort for individuals nesting at “offshore” sites distant from foraging areas (Hunt 1972; Lemmetyinen 1973; Davoren and Montevecchi 2003). Increased foraging effort can result in decreased nest attendance rates and thus increased chick mortality due to predation (Hunt 1972). However, predation is also relative with respect to predator population sources. Nesting on inshore islands close to mainland predator sources may translate into increased predation risk (Hall 1999).

Variation in reproductive performance between colony sites has been attributed to differences in colony size (Hunt *et al.* 1986) and may also be affected by colony age; new colonies are generally comprised of young breeders (Coulson and White 1956) and

breeding age is known to affect performance (Nisbet *et al.* 1984; Hamer *et al.* 2001). In this study, we examined differences in the reproductive performance of Common Terns at four restored colonies off the coast of Maine that differ in location, colony age and size and predation. Specifically we collected data on predation intensity and frequency, first hatch and peak hatch dates, clutch size and the survival, growth and provisioning rates of Common Tern chicks on each island. We predict that Common Terns nesting at the offshore site will exhibit reduced performance relative to conspecifics nesting at inshore sites. Conclusions made in this study will be used to develop recommendations regarding the selection of tern restoration sites.

STUDY SITES

This study was conducted at four restored tern colonies along the Maine coast from 1991-2002 (Fig. 1). Islands were categorized as inshore (<5 km from mainland), nearshore (5-10 km), or offshore (>10 km) using

distance to the mainland as the criteria for classification. All sites were restored using the same techniques. Nesting Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*L. marinus*) were removed from the islands using the avicide DRC1339 and discouraged from reoccupying sites by establishing resident field camps on the islands (Kress and Hall 2002). Playbacks of tern colony sounds and decoys were used to lure terns to the site (Kress 1983).

The first tern restoration program was initiated at Eastern Egg Rock (EER) in 1978 (43°52'N, 69°22'W; Table 1). EER is a 2.8 ha island located at the mouth of Muscongus Bay, 8.4 km (near-shore island) from New Harbor, Lincoln Co., Maine. The island's location (in the outer reaches of Muscongus Bay) makes the site inaccessible to most mainland-based predators, although a Mink (*Mustela vison*) was removed from the island in 1988. Terns recolonized the site in 1980 after a 66-year absence. Common Tern numbers rapidly increased to 950 pairs in 1983, before declining again in 1984 due to an outbreak of avian cholera and predation by a Black-crowned Night Heron (*Nycticorax nycticorax*). During the study period the Common Tern number fluctuated from 869 to 1,514 pairs, with an average of 1,254 pairs (SD \pm 197). Roseate Terns (*Sterna dougallii*; 160 pairs) and Arctic Terns (*S. paradisaea*; 80 pairs) also nest on EER in distinct sub-colonies.

Seal Island National Wildlife Refuge (SI; 43°53'N, 68°44' W; Table 1) located 38 km SE of Rockland, Knox Co., Maine, is a 26.3 ha offshore island located in outer

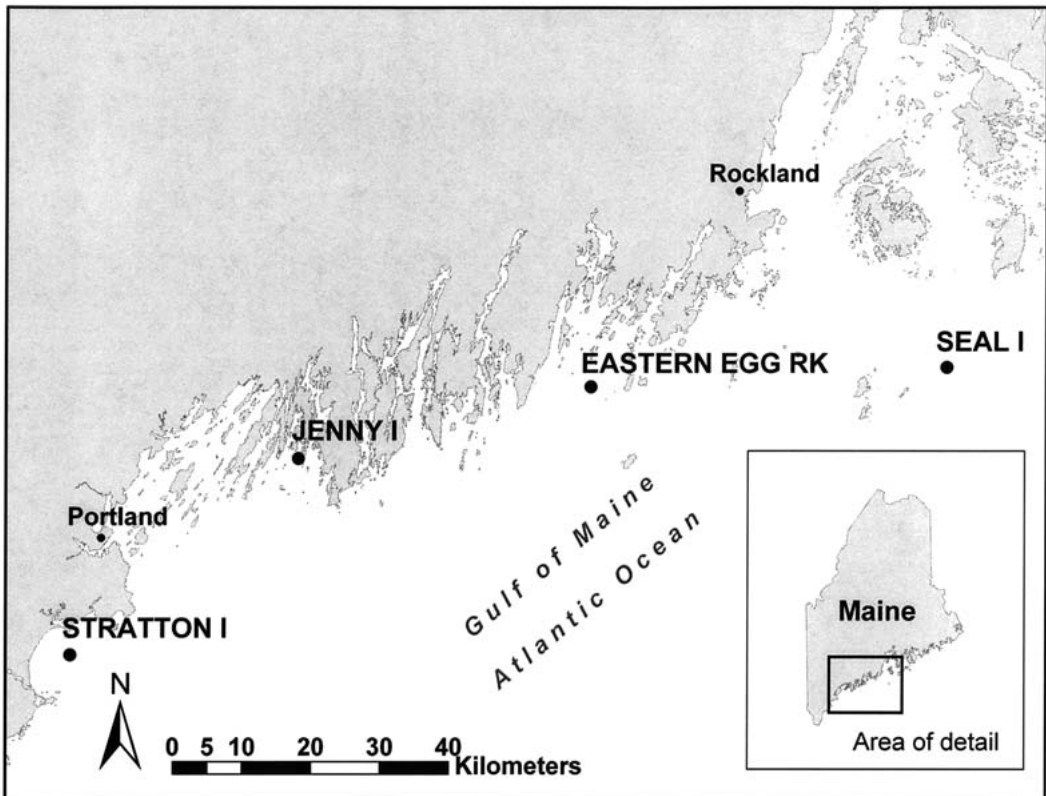


Figure 1. Locations of four restored Common Tern colonies studied in the Gulf of Maine from 1991-2002.

Table 1. Characteristics of four Maine coast Common Tern colonies studies from 1991-2002.

Island name	Distance to mainland (km)	First nesting year	Restoration initiation	Average number of pairs	Minimum number of pairs	Maximum number of pairs
Jenny Island (JI)	0.8	1991	1991	601	57	1,167
Stratton Island (STI)	2.6	1987	1986	751	248	1,881
Eastern Egg Rock (EER)	8.4	1980	1978	1,254	869	1,514
Seal Island NWR (SI)	19.5	1989	1985	825	369	1,568

Penobscot Bay. No mammalian and few avian predators have been recorded at this site. The Peregrine Falcon (*Falco peregrinus*) occasionally takes adult or fledgling terns, and one Snowy Owl (*Nyctea scandiaca*) was present in 1992. Restoration of the SI colony was initiated in 1985. One pair of Common Terns and 16 pairs of Arctic Terns nested in 1989, these were the first terns nesting at the site in 53 years. Between 1991-2002 an average of 825 pairs (SD \pm 390) nested.

Stratton Island (STI; 43°31'N, 70°19' W; Table 1) is a 12.2-ha inshore island located three km off Prout's Neck, York Co., Maine. STI is, historically, one of the most important tern nesting islands in southern Maine. The island was spontaneously recolonized by Common Terns and Roseate Terns during the late 1960s and early 1970s after a 20-year absence, but was abandoned again by 1982. Tern restoration activities were initiated in 1986. Recovery of terns at this site has been hampered in some years by predation—numerous diurnal and nocturnal predators have been documented on the island including Black-crowned Night Heron, Great-horned Owl (*Bubo virginianus*), Snowy Owl and Mink. In addition to Common Terns, Roseate Terns (14-120 pairs) and Arctic Terns (5-12 pairs) nest on the island. An average of 751 pairs of Common Terns nested during the study period.

Jenny Island (JI; 43°46'N, 69°54'W; Table 1), in eastern Casco Bay, located one km south of West Cundy Point, Cumberland Co., is a low-lying 1-ha island. Historically, Casco Bay was an important tern nesting area; terns have used 32 islands since 1885 (Kress and Hall 2002). By 1990, only 124 pairs of Common Terns were nesting on three islands. The restoration of JI was initiated in 1991, but unlike the restoration of the three other study sites, decoys and sounds were not employed, as a small colony existed (~40 pairs in 1990). During the eleven years of tern restoration work on the island, a number of predators have been present, including Great-horned Owl, Black-crowned Night Heron, Skunk (*Mephitis mephitis*) and Mink. An average of 601 pairs nested during the study period with a maximum of 1,167 pairs. Roseate Terns have nested intermittently since 1993, reaching a maximum of 15 pairs in 1994.

METHODS

Nest Counts, Phenology, Breeder Age, Reproductive Data and Chick Growth

Colony sizes are represented by peak nest counts. Tern nesting islands in the Gulf of Maine were counted annually between 5 and 20 June, which corresponds with the hatching period for most colonies. Nest counts were determined using a Lincoln Index mark/recap-

ture sample. First hatch dates were recorded on each island—hatch dates rather than laying dates were used to indicate phenology because field crews were not always present during egg laying. Although banded terns were trapped or re-sighted throughout the study, sample sizes were small; hence statistical tests had low power. Thus we were unable to assess colony differences of the effect of breeder age on performance.

Reproductive parameters were calculated from nests within fenced enclosures and at observed "feeding study" nests (see Appendix I for annual nest sample sizes). Hall (1996) found no difference in productivity between fenced (N = 29) and unfenced nests (N = 31). One to four enclosures were established on JI, EER and SI and were used as "productivity plots". The plots on these islands were the same in all study years. However, on STI, productivity plots were constructed at the beginning of each season because the distribution and density of nests was highly variable, and terns nested on a sand/cobble beach that was disturbed by winter storm tides and waves.

Fenced enclosures were constructed with either 0.5 cm hardware cloth or small mesh wire (Nisbet and Drury 1972) covered with 10 cm of burlap or landscape fabric. Nests were marked and numbered and final clutch sizes were recorded. Plots were checked every 2-3 days. Daily checks were initiated when hatching started.

Chicks were weighed and marked or banded at hatching. The first, second, and third hatched chicks were designated *a*, *b* and *c* respectively. Chick survivorship was obtained through capture and recording of band numbers during nest checks. Chicks within enclosures were weighed every 2-3 days until death, disappearance, or fledging. A few chicks escaped from the enclosures when over 15 days old; hence chicks were considered to have fledged if they reached the age of 15 days and were not found dead later. In addition to nests in the enclosed plots, we calculated reproductive success for nests observed from blinds. Procedures followed those used in the plots with the following exceptions; 1) study nests were not enclosed; 2) chicks were uniquely color marked thus allowing observers to determine the presence or absence of each chick.

Following Nisbet *et al.* (1995), we calculated linear growth rate (LGR) and asymptotic mass (AM) to describe growth of Common Tern chicks. We defined LGR as the slope of a regression line fitted to mass data during the period of linear growth (4-14 days). Asymptotic mass was defined as the average of mass data during the period of near constant mass (chicks older than 17 days). We calculated LGR for chicks reaching 15 days that had at least three data points and AM for chicks with at least two measurements. To characterize growth for each island, data were pooled for all chicks (without regard to hatch order).

Chick Provisioning

Common Tern chick diet (see Hall *et al.* 2000) and provisioning rate data were collected from 1991 to 2002. For each feed, the nest number; the size, type and number of prey items delivered; the recipient; the provider; and the arrival and departure times of the adult were recorded. Prey deliveries were observed from blinds. During a feeding watch, 4-8 nests were simultaneously observed from 5-7 m.

Predation

Predation was ranked on a 0-3 scale (Appendix 1): 0 (no predation at study nests), 1 (1-25% of study nests were predated), 2 (26-50% of study nests were predated) or 3 (>51% of study nests were predated). We also ranked the risk of predation between sites ("yes" for years when predation occurred; "no" for years without predation). In most years, Herring Gulls and Great Black-backed Gulls were observed taking fledging or near fledging chicks from all islands—little effort has been made to quantify this predation and given the difficulty of associating fledged chicks with individual nests, this type of predation was not included in an island's annual "predation score" or in the assessment of whether predation was occurring at a site during a season.

Statistical Analyses

Because we were interested in assessing differences in reproductive parameters at the colony level rather than exploring variation at the nest level, we used one-way analysis of variance (ANOVA) of yearly colony averages with Tukey's HSD tests to examine differences in clutch size, first and peak hatch dates, number of eggs hatched, productivity (number of chicks fledged), growth parameters and provisioning rates between colonies. Averages for colonies across years were compared to look for colony effects above year variation. Analysis of covariance (ANCOVA) was used to further elucidate the relationships between reproductive parameters and colony sites using year, colony size, colony age or hatch dates as covariates. Colony size and colony age (duration) were highly and significantly correlated ($r^2_{45} = 0.59$; $P < 0.001$), and one or the other parameter was used in the covariate models.

We used contingency tables to evaluate colony differences and colony type differences (inshore, nearshore and offshore) in clutch size (1, 2 or 3 egg clutches), hatching rates (nests hatching 0, 1, 2 or 3 eggs) and

fledging rates (the number of nests fledging 0, 1, 2 or 3 chicks). Similar tables were used to compare predation (ordinal data) and the binomial chance of predation between colonies. Regression analysis was used to compare pairs of independent variables. All statistical analyses were performed using JMP 4.0 (JMP 2000).

RESULTS

Clutch size was recorded in 2,355 Common Tern nests. The average clutch size was larger at STI and JI (the two inshore islands) compared to the nearshore (EER) and offshore island (SI), which had the smallest average clutch size (Table 2, Appendix 2). The differences in clutch size remained significant after controlling for year (ANCOVA [Island] $F_{3,42} = 7.9$; $P < 0.001$, [Year] $F_{1,42} = 4.2$; $P < 0.05$) and colony size (ANCOVA [Island] $F_{3,42} = 6.2$; $P < 0.001$, [Colony Size] $F_{1,42} = 5.2$; $P < 0.03$). Colony-specific differences in clutch size (Tukey's test) were unchanged with year as a covariate but, when colony size was included, the difference in clutch size between EER and STI became non-significant. The proportion of clutches containing 3-eggs varied significantly between islands ($\chi^2_3 = 117$; $P < 0.001$). Fewer 3-eggs clutches were observed on EER and SI than expected (only 28% of clutches contained 3 eggs on SI), whereas ~58% contained 3 eggs on JI and STI (Table 3). Clutch size tended to decrease with increasing colony size ($r^2_{45} = 0.17$; $P < 0.005$) but not with colony age.

First hatch and peak hatch dates were latest on SI (20 June; 28 June) and earliest on STI (15 June and 24 June). First hatch dates were significantly earlier on STI than on SI (Table 4), yet there were no signifi-

Table 2. The average clutch size, average number of eggs hatched per nest and average number of chicks fledged per pair (\pm SD) for Common Terns nesting on four islands in Maine from 1991-2002 (N = the number of sample years).

	Jenny Island (N = 12)	Stratton Island (N = 12)	Eastern Egg Rock (N = 12)	Seal Island NWR (N = 11)
Clutch size ¹	2.52 \pm 0.12	2.59 \pm 0.17	2.35 \pm 0.27	2.24 \pm 0.19
Eggs hatched nest ²	2.02 \pm 0.38	1.93 \pm 0.60	2.02 \pm 0.32	2.03 \pm 0.17
Chicks fledged nest ³	1.32 \pm 0.76	1.19 \pm 0.75	1.19 \pm 0.45	1.05 \pm 0.29

¹Average clutch size on SI is significantly less than on STI and JI and average clutch on EER was significantly less than on STI. Pair wise comparisons assessed with Tukey's HSD test (ANOVA $F_{3,43} = 7.69$; $P < 0.001$).

²No significant differences in average number of eggs hatched per nest between islands (ANOVA $F_{3,43} = 0.17$; n.s.).

³No significant differences in average number of chicks fledged per nest between islands (ANOVA $F_{3,43} = 0.37$; n.s.).

Table 3. The proportion of 3-egg nests, nests hatching no chicks and the proportion of nests fledging 0, 1, 2, or 3-chicks at four Maine islands from 1991-2002 (N = the number of nests).

	Jenny Island (N = 671) ¹	Stratton Island (N = 753) ²	Eastern Egg Rock (N = 589) ³	Seal Island NWR (N = 342)
% 1-egg clutches	6.1	5.7	9.3	7.2
% 2-egg clutches	37.4	33.9	46.9	64.2
% 3-egg clutches	56.3	59.9	42.4	28.6
% nests hatching 0-eggs	12.9	16.6	6.6	3.0
% nests hatching 1-eggs	9.7	10.9	15.8	14.3
% nests hatching 2-eggs	36.4	35.2	46.9	61.4
% nests hatching 3-eggs	41.0	37.3	30.2	21.3
% nests fledging 0-chicks	30.1	29.8	24.1	15.4
% nests fledging 1-chick	20.3	28.6	39.2	62.8
% nests fledging 2-chicks	34.2	32.8	34.3	21.5
% nests fledging 3-chicks	15.4	8.8	2.4	0.3

¹1 nest contained 4 eggs on Jenny Island.

²2 nests contained 4 eggs on Stratton Island.

³7 nests contained 4 eggs on Eastern Egg Rock; 1 contained 6 eggs.

cant differences in peak hatch dates between colonies. Colony age (ANCOVA [Island] $F_{3,43} = 4.81$; $P < 0.01$, [Colony Age] $F_{1,43} = 0.14$; n.s.) and year (ANCOVA [Island] $F_{3,43} = 5.47$; $P < 0.01$, [Year] $F_{1,43} = 0.14$; n.s.) had no effect on first hatch dates. However, first ($r_{45}^2 = 0.18$; $P < 0.003$) and peak hatch dates ($r_{45}^2 = 0.32$; $P < 0.001$) became progressively earlier with increasing colony size. Conversely, first hatch dates were significantly later when heavy predation was observed on an island (2-way ANOVA [island] $F_{3,41} = 8.4$; $P < 0.001$ and [predation] $F_{3,41} = 3.9$; $P < 0.02$) due to nest failure and nocturnal abandonment of incubating terns.

Predation was documented on JI (9 of 12 years), STI (5 of 12 years) and EER (2 of 12 years), but not on SI (Appendix 1); the chance of predation ($\chi^2_3 = 20.9$, $P < 0.001$) and predation intensity ($\chi^2_9 = 23.5$, $P <$

0.005) were significantly different between islands. The chance of predation occurring was greatest on JI and least on SI. Hatch and fledge rates declined with increasing levels of predation; when a predation score of 3 was assessed (N = 7; JI 3, STI 4) the average number of chicks hatched was 1.4/pair (SD ± 0.53) and the average number of chicks fledged was 0.26/pair (SD ± 0.43). When no predation was observed (a score of 0) the average number of chicks hatched was 2.1/pair (SD ± 0.21) and the average number of chicks fledged was 1.34/pair (SD ± 0.43).

Despite heavy predation on JI and STI, there was no difference in hatch rates between colonies (Table 2). Yet, more nests hatched 3-eggs on the inshore islands than on either EER or SI (Table 3; $\chi^2_2 = 44.0$; $P < 0.001$). Conversely, the proportion of nests in which no eggs hatched was significantly greater on the inshore islands (~15%) than

Table 4. The average first hatch and peak hatch dates (\pm SD) for Common Terns in Maine from 1991-2002 (N = the number of sample years; peak hatch dates are annual averages).

	Jenny Island	Stratton Island	Eastern Egg Rock	Seal Island NWR
First hatch date ¹	17 June \pm 4.5 d (N = 12)	15 June \pm 2.4 d (N = 12)	16 June \pm 2.2 d (N = 12)	20 June \pm 2.4 d (N = 12)
Peak hatch date ²	26 June \pm 3.3 d (N = 12)	24 June \pm 5.5 d (N = 12)	24 June \pm 3.1 d (N = 12)	28 June \pm 3.1 d (N = 12)

¹The average first hatch date is significantly later on SI than on STI and EER. Pair wise comparisons assessed with Tukey's HSD test (ANOVA $F_{3,44} = 5.58$; $P < 0.003$).

²No difference in peak hatch dates between islands (ANOVA $F_{3,44} = 2.4$; n.s.).

on either EER (7%) or SI (3%; $\chi^2_3 = 61.6$; $P < 0.001$). STI had the highest proportion of clutches hatching no eggs (Table 3).

Overall, the average number of chicks fledged/pair was greatest on JI (1.32) followed by STI (1.19), EER (1.19) and SI (1.05; Table 2, Appendix 2). Only one α -chick fledged from SI (1% of all 3-egg clutches) and 14 (6%) from EER during the study. However, on JI (27%) and STI (15%) a significantly greater proportion of 3-egg nests resulted in three fledged chicks ($\chi^2_3 = 105$; $P < 0.001$). And the proportion of all nests fledging no chicks was significantly greater ($\chi^2_3 = 32.5$; $P < 0.001$) on (JI 30%) and STI (30%) than either EER (24%) or SI (15%). The higher proportion of nests fledging no chicks on JI and STI was the result of higher predation rates.

Chicks on JI grew faster (7.1 g/day) and reached a greater asymptotic weight (113 g) than conspecifics on SI, but were not significantly different than chicks on STI and EER (Table 5). On SI, chicks grew more slowly (5.7 g/day) and had a lower asymptotic mass (98 g) than at other sites. The differences in growth rates remained significant after controlling for year (ANCOVA [Island] $F_{3,18} = 4.9$; $P < 0.01$, [Year] $F_{1,18} = 1.6$; n.s) and colony size (ANCOVA [Island] $F_{3,18} = 5.3$ $P < 0.01$, [Colony Size] $F_{1,18} = 1.5$; n.s). Island specific differ-

ences (Tukey's test) were unchanged with year as a covariate, but when colony size was included the difference in LGR between EER and SI became significant. Including year ($F_{4,18} = 2.8$; n.s) and colony size ($F_{4,18} = 2.9$; n.s) as covariates removed the significant difference in the value of AM between islands.

Nest provisioning rates (Table 5), the average number of food deliveries per hour of observation, were greatest on Jenny Island (2.7 deliveries per nest) and lowest on Eastern Egg Rock (1.7 deliveries per nest). Only three years of provisioning data were collected on SI (1992, 1993 and 1996)—an inter-island comparison using only the 1992-93 and 1996 data indicate provisioning rates were highest on JI (3.0) and lowest on EER (1.4); STI (2.5) and SI (2.4) were intermediate. There was also a significant negative relationship between provisioning rate and the number of breeding pairs ($r^2_{35} = 0.42$; $P < 0.001$).

DISCUSSION

Observations of Common Terns in Maine indicate that clutches were larger, chicks grew faster, reached a greater asymptotic mass and had a greater chance of fledging from inshore colonies (JI and STI) than either the nearshore or offshore colonies, de-

Table 5. Annual averages (\pm SD) of three chick growth parameters (initial mass, linear growth rate [LGR] and asymptotic mass [AM]) and chick provisioning rates (the number of food deliveries per nest/hour) for Common Terns nesting on four Maine Islands from 1991-2002 (N = the number of sample years).

	Jenny Island	Stratton Island	Eastern Egg Rock	Seal Island NWR
Initial mass ¹	15.4 \pm 0.46 (N = 7)	15.7 \pm 1.57 (N = 5)	15.8 \pm 1.86 (N = 5)	15.4 \pm 1.55 (N = 7)
Linear growth rate ²	7.1 \pm 0.28 (N = 7)	6.8 \pm 0.36 (N = 4)	6.8 \pm 0.33 (N = 5)	5.7 \pm 0.28 (N = 7)
Asymptotic mass ³	112 \pm 7.4 (N = 7)	110 \pm 7.1 (N = 4)	107 \pm 11.2 (N = 5)	98 \pm 7.7 (N = 7)
Provisioning rate ⁴	2.70 \pm 0.89 (N = 12)	2.27 \pm 0.59 (N = 11)	1.70 \pm 0.44 (N = 11)	2.27 \pm 0.88 (N = 3)

¹No significant differences in initial mass between islands (ANOVA $F_{3,20} = 0.12$; n.s).

²The average LGR on SI is significantly less than on JI. Pair wise comparisons assessed with Tukey's HSD test (ANOVA $F_{3,19} = 5.04$; $P < 0.01$).

³The average AM on SI is significantly less than on JI. Pair wise comparisons assessed with Tukey's HSD test (ANOVA $F_{3,19} = 3.86$; $P < 0.03$).

⁴The average provisioning rate on EER was significantly less than on JI. Pair wise comparisons assessed with Tukey's HSD test (ANOVA $F_{3,33} = 4.38$; $P < 0.01$).

spite increased predation on the inshore islands. Eastern Egg Rock, the nearshore colony, was intermediate in all parameters, while Common Terns nesting on SI (offshore site) consistently performed poorly relative to conspecifics on either the nearshore or inshore islands.

Why Common Terns do better on inshore islands than offshore islands in Maine is uncertain. However, the results are consistent with previous studies, which compared reproductive and foraging parameters within a species between inshore and offshore sites. Lemmetyinen (1973) reported that Arctic Terns nesting on outer "skerries" (islands) laid smaller clutches than terns on inner "skerries". Differences in clutch were attributed to differences in prey availability preceding clutch initiation. Davoren and Montevecchi (2003) found that Common Murres (*Uria aalge*) breeding at an offshore site had lower provisioning rates, slower chick growth rates and chicks were in poor condition at fledging relative to chicks at an inshore site. It is possible that longer foraging trips and an inability to compensate for the longer trips by decreasing time spent at the nest resulted in decreased performance by Common Murres at the offshore site. Drury and Nisbet (1972) noted that Herring Gulls breeding on inshore islands (close to human food sources) raised more young than on outer islands (natural food sources). While the authors speculate that food supply was probably the primary factor affecting chick survival, they also note that predation and human disturbance reduces breeding success in some inshore colonies. Hunt (1972) found that Herring Gulls feeding on inshore food resources fledged fewer chicks at offshore sites, however growth rates were similar between inshore and offshore sites. Offshore nesting Herring Gulls apparently compensated for increased foraging effort by decreasing nest attendance rates, resulting in higher nest predation and lower success at the offshore site.

Our findings combined with observations about Common Tern foraging (forage principally inshore, 1-20 km from colony—Lemmetyinen 1976; Uttley *et al.* 1989; Beck-

er *et al.* 1993; Nisbet 2002) support the idea that differential foraging effort between colonies is a plausible explanation for differences in performance. Specifically provisioning rates tended to be lower offshore and hatch rates were similar between colonies suggesting that differences in success are a function of chick survival and are not due to failure during incubation. Combined with observations of lower chick growth rates and asymptotic weight at the offshore site, LGR and AM are a function of food delivery rates (Visser 2001), the case for differential foraging effort between colonies becomes stronger. Perhaps Common Terns nesting offshore, unlike Arctic Terns, are unable to switch provisioning strategies (Boeker 1967; Maranto 2002) to compensate for decreased delivery rates (by increasing the number of short foraging trips) because they are unable to forage efficiently offshore or because of energetic restrictions. Weimerskirch (1998) demonstrated that only individual Sooty Shearwaters (*Puffinus griseus*) with larger energy reserves were able to compensate for decreased provisioning rates to the nest by making numerous short foraging trips.

Predation and the effects of predation were more pronounced on JI and STI than either EER or SI in any year of our study. At least ten predators were documented on the inshore islands, while most predation on EER (5 predators) and SI (4) was due to Herring and Great Black-backed Gulls or transient migratory raptors. Mink, Black-crowned Night Heron and Great Horned Owl predation caused breeding failure in seven of 24 nesting years (Appendix 1) at JI and STI. In effect, success on the inshore islands can be described as boom (high productivity—no predation) or bust (low productivity—heavy predation).

Predation is an important selective pressure operating in a seabird colony (Lack 1968). The response to predators by terns varies at the individual and colony level and with different types of predators (Burger and Gochfeld 1991; Nisbet 2002). For example, diurnal predators elicit a different response than nocturnal predators, as do mammalian and avian predators. Site aban-

donment is the most extreme response, yet requires a trade-off between adult survival, increased short term fitness and the costs of acquiring and defending a new territory, courtship, lack of sufficient knowledge about predators and needing to become familiar with local food resources at the new site (Bried and Jouventin 2001).

In this study, despite heavy predation in two or more consecutive years, the JI and STI colonies persisted in all years except 2001, when 95% of the JI colony deserted due to Mink predation. As with other studies of Common Terns, site abandonment in Maine appears related to predator and perceived threat (Austin 1948; see Nisbet 2002). Nocturnal abandonment was the typical response during periods of Mink, Great Horned Owl and Black-crowned Night Heron predation. However, unlike Black-crowned Night Heron and Great Horned Owl, Mink remained in the colony during the day and may pose an additional visual threat. In the northeastern USA, Common Terns abandon sites in response to combinations of the following factors; mammalian predation, avian predation and displacement by gulls and erosion (Austin 1948, 1951; Drury 1973; Nisbet 1973; Kress 1997; USFWS 1998; Blodgett 1999; Ian Nisbet, pers. comm.). Patterns of predation and abandonment in the region suggest that intense inter-annual predation can trigger site abandonment.

While differential foraging effort between colonies may underlie site differences in performance, colony size and age of breeders are also known to affect performance. In this study, colony size had no effect on chick survival or growth rates, however terns nesting in large colonies tended to lay larger clutch's that hatched earlier and adults fed offspring less frequently. Large numbers of breeding pairs were found on inshore, nearshore and offshore sites; hence it is unlikely that the observed cline in performance can be accounted for by colony size differences alone. Colony age or more directly age of breeders can also be an important determinant of performance (Nisbet *et al.* 1984; Hamer *et al.* 2001). Proposed future projects will focus on attendance pat-

terns, foraging trip times, breeder age and climatic conditions between islands (wind and fog) as possible reasons for site based differences in performance.

Future regional tern restoration activities should consider the long-term costs and benefits of restoring inshore, near-shore and offshore sites. While restoration of inshore sites may provide short-term gains to the region via high fledging rates of chicks in good condition, ongoing predator management is usually required. This is labor intensive and may prove impractical (at some sites), especially where nocturnal predators are present (Kress and Hall 2002). Conversely, offshore sites provide the necessary refuge from predators, but fewer chicks are produced and these are generally in poor condition (lower growth) relative to conspecifics on the inshore islands. For these reasons, combined with few predator visits and an average annual productivity exceeding 1 chick/per nesting pair (a minimum required to maintain a stable colony—DiCostanzo 1980) we conclude that nearshore sites (with a history of tern use) offer the best potential for restoration in the northeastern USA.

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Appendix 1. Colony size, predation score (PS) and the number (N) of study nests (productivity) and study chicks (growth) for each restored Common Tern colony along the Maine coast 1991-2002. Predation was ranked using the following scale: 0 (no predation at study nests), 1 (1-25% of study nests were predated), 2 (26-50% of study nests were predated) or 3 (>51% of study nests were predated).

Year	Jenny Island			Stratton Island			Eastern Egg Rock			Seal Island NWR		
	Pairs	PS	N (nest/chicks)	Pairs	PS	N (nest/chicks)	Pairs	PS	N (nest/chicks)	Pairs	PS	N (nest/chicks)
1991	57	0	32/0	248	3	50/0	869	0	33/0	369	0	NA
1992	167	1	39/0	229	3	25/0	1,102	0	38/0	321	0	36/0
1993	363	0	54/0	194	3	27/0	1,168	0	26/0	427	0	32/0
1994	491	1	52/43	201	0	30/0	1,198	0	42/31	481	0	17/15
1995	542	1	43/50	265	0	48/0	1,333	0	44/39	645	0	25/36
1996	730	1	60/41	708	0	57/57	1,374	0	54/21	780	0	42/19
1997	1,068	0	84/86	829	0	70/82	1,441	0	65/81	1,024	0	26/36
1998	1,167	1	88/21	969	0	97/76	1,396	0	66/59	927	0	31/31
1999	1,129	2	83/32	1,109	0	83/0	1,205	0	55/0	955	0	23/0
2000	1,050	3	72/0	1,109	0	89/0	1,443	0	61/0	1,205	0	35/0
2001	59	3	28/14	1,881	1	91/45	1,514	2	52/0	1,197	0	33/37
2002	397	3	36/0	1,279	3	86/0	1,004	1	53/0	1,568	0	42/59

Appendix 2. Summary of clutch size, hatch rate (the number of eggs hatching per nest) and the success rate (number of chicks fledged per/pair) for four restored Common Tern colonies in Maine 1991-2002 (see Appendix 1 for annual nest sample sizes and Table 2 for mean values of clutch, hatch and fledge parameters).

Year	Jenny Island (JI)			Stratton Island (STI)			Eastern Egg Rock (EER)			Seal Island NWR (SI)		
	Clutch size	Hatch rate	Success rate	Clutch size	Hatch rate	Success rate	Clutch size	Hatch rate	Success rate	Clutch size	Hatch rate	Success rate
1991	2.41	1.84	1.69	2.80	1.88	0.04	2.67	2.45	1.79	—	—	—
1992	2.69	2.54	2.03	2.60	1.00	0.04	2.53	2.24	1.55	2.11	1.92	1.5
1993	2.54	2.19	1.94	2.70	2.04	1.22	1.85	1.69	1.42	2.22	2.00	1.53
1994	2.54	1.98	1.71	2.77	2.23	1.87	2.19	1.88	1.29	2.41	2.12	1.16
1995	2.72	2.37	2.12	2.60	2.33	2.21	2.45	2.20	1.55	2.36	2.12	1.00
1996	2.52	2.27	1.23	2.70	2.40	1.51	2.19	2.02	0.46	2.26	2.14	0.57
1997	2.57	2.31	1.83	2.54	2.31	2.07	2.49	2.31	1.66	2.23	2.04	1.08
1998	2.42	2.15	1.49	2.63	2.20	1.37	2.64	2.23	1.18	2.00	1.81	0.87
1999	2.51	2.19	1.37	2.65	2.36	1.47	2.55	2.18	1.07	2.70	2.43	0.96
2000	2.28	1.36	0.01	2.33	1.89	1.09	2.25	1.84	1.04	2.20	1.94	0.77
2001	2.50	1.54	0.07	2.54	2.04	1.22	1.92	1.31	0.41	2.06	1.94	0.97
2002	2.53	1.53	0.30	2.22	0.47	0.16	2.42	1.87	0.85	2.10	1.88	1.17