

TEMPORAL PATTERNS IN REPRODUCTIVE SUCCESS IN THE ENDANGERED ROSEATE TERN (*STERNA DOUGALLII*) NESTING ON LONG ISLAND, NEW YORK, AND BIRD ISLAND, MASSACHUSETTS

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ABSTRACT.—Roseate Terns (*Sterna dougallii*) nest in few colonies in the northeastern United States, and the population is listed as endangered. We compare reproductive success from 1987 through 1990 at Cedar Beach, Long Island, and in 1980 and 1987 through 1990 at Bird Island, Massachusetts, to examine yearly and seasonal differences. Productivity was highest for terns breeding in the first six days of the egg-laying period and decreased thereafter. Clutch size, hatching success, and productivity declined significantly during the season, with some variations in pattern among years and between colony sites. Pairs initiating nests after 22 June fledged almost no young. Patterns of reproductive success were more irregular at the smaller colony (Cedar Beach) than the larger colony. Reproductive success was related to age of adults; young birds (two to three years old) had lower clutch sizes, had lower reproductive success, and laid later than older birds. The effective reproductive population of the colony included primarily birds that bred in the early and peak periods; thus, monitoring reproductive success only from early or peak nests overestimates overall reproductive success. Selection against even earlier breeding in this species may be due to lower food resources early in the season and higher predation rates on early nests. Received 20 April 1994, accepted 2 July 1994.

SEASONAL DECLINES in reproductive success have been reported in many bird species. Among seabird species, such declines have been reported in albatrosses and petrels (Harris 1969, Fisher 1971, Ollason and Dunnet 1978), pelicans (Knopf 1979), gulls (Weidmann 1956, Brown 1967, Viksne and Janus 1980, Boersma and Ryder 1983, Coulson and Porter 1985), and alcids (Nettleship 1972, Harris 1980, Birkhead and Nettleship 1982). Among terns, seasonal declines have been reported in the Common Tern (*Sterna hirundo*; Morris et al. 1976, Maxwell and Smith 1983, Nisbet and Welton 1984, Becker and Frank 1985), Arctic Tern (*S. paradisaea*; Lemmetyinen 1973), Roseate Tern (*S. dougallii*; Langham 1974, Spendelow 1982), Sandwich Tern (*S. sandvicensis*; Veen 1977), Least Tern (*S. antillarum*; Massey and Atwood 1981), and Black Noddy (*Anous minutus*; Ashmole 1962).

Many of the published papers, however, report only changes in overall productivity (fledged chicks per pair). Although some papers

report declines in clutch size, hatching success, or fledging success, it is not clear how consistent these changes are among colony sites or years, nor how strongly each may contribute to the observed declines in productivity. Most papers report differences between late-nesting birds and peak-nesting birds, rather than changes within the entire nesting period. In some studies the earliest nesting birds were most productive (Spendelow 1982); in others the earliest nesting birds produced fewer young than peak or late-peak nesters (Nisbet 1975, Nisbet and Welton 1984). Moreover, the contribution of parental age to seasonal declines in productivity has rarely been examined (see Coulson and Porter 1985).

This paper compares breeding performance of Roseate Terns in two colonies in the northeastern United States differing in size, substrate, and predation pressure. We measured clutch size, hatching success, fledging success, and productivity as functions of laying date

TABLE 1. Models explaining variations in nesting phenology, clutch size, and reproductive success in Roseate Terns.

	No. nests	Clutch size	Hatching success	Productivity
Model^a				
F	2.00	11.3	10.2	11.9
R ²	0.80	0.15	0.19	0.24
df	4 and 36	18 and 1,150	15 and 675	11 and 408
P	0.05	0.001	0.001	0.001
Factors entering^b				
Site	6.6 (0.01)	ns	24.7 (0.001)	14.1 (0.002)
Season ^c	4.6 (0.004)	26.6 (0.001)	13.8 (0.001)	17.1 (0.001)
Year	ns	2.5 (0.05)	10.0 (0.001)	ns
Site × season	ns	ns	4.4 (0.001)	4.6 (0.003)
Site × year	ns	12.4 (0.001)	ns	ns

^a GLM model (SAS Institute 1985) treating site and season as categorical variables, and season as ordinal variable.

^b F-value and probability.

^c Period within year.

during five years in one colony and four years in the other. Parental ages were known for a subsample of the birds studied at one colony.

STUDY SITES AND METHODS

We studied Roseate Terns at Bird Island, Massachusetts (41°40'N, 70°43'W) in 1980 and 1987–1990, and at Cedar Beach, New York (40°37'N, 73°21'W) in 1987–1990. The Bird Island colony contained about 1,600 pairs, which is about one-half of the regional population (U.S. Fish and Wildlife Service 1989). Common Terns nesting at this site increased from about 900 pairs in 1980 to 1,500–1,800 pairs in 1987–1990. Roseate Terns at Bird Island nest mainly among dense herbaceous vegetation, among tide wrack, or on cobbles; nest density averages about 0.5 nests/m² and locally reaches 2 to 3 nests/m². Further description of the habitat can be found in Nisbet et al. (1990).

The Cedar Beach colony included about 100 pairs of Roseate Terns, 3% of the regional population (U.S. Fish and Wildlife Service 1989). The colony site is located on an interdune area of a barrier beach. Roseate Terns nest in discrete subgroups of 5 to 40 pairs interspersed among much larger numbers of Common Terns. Roseate Terns usually nest under dense vegetation, whereas Common Terns usually nest in more open sites. Further description of the habitat can be found in Gochfeld (1976) and Burger and Gochfeld (1988, 1991).

Because of the differences in numbers, dispersion, and substrate, we used slightly different methods at the two sites. At Cedar Beach, most of the nests (52 to 105) were studied in each year. At Bird Island, all the nests in one or two central quadrats and two or three peripheral quadrats (50–100 m²) were studied; different quadrats were sampled in successive years. The study areas were selected to include all parts of the colony and all types of substrate.

From mid-May until mid-June we searched the nesting area or sample plots daily; thereafter, nest searches were conducted during the monitoring of existing nests or during searches for chicks. The small numbers of nests initiated after 3 July (Bird Island) or mid-July (Cedar Beach) were not monitored because we would have been unable to follow chicks to fledging. Each new nest was marked, and eggs were marked in order of laying. Nests were checked periodically until hatching or abandonment; clutches that failed altogether were usually incubated for 35 to 45 days before the parents abandoned them. Usually, it was possible to determine the fate of each egg.

Nests were checked daily or on alternate days around the time of hatching and chicks were banded when first encountered. In cases where nests were not checked daily, the date of hatching was assigned based on initial mass and/or date of hatching of the sibling. The first and second chicks in each brood are referred to as A- and B-chicks, respectively.

Methods for determining chick survival and productivity have been described in detail by Nisbet et al. (1990). At Cedar Beach, almost all nests were enclosed with low wire fences (Nisbet and Drury 1972) or with automobile tires. This did not affect predation rates, as all enclosures were large enough to include several bushes where chicks could hide; the enclosures were larger than individual territories. Chicks were checked and weighed daily until they died, disappeared, or reached the age of fledging (25+ days). Several aerial predators were active in the colony (Burger and Gochfeld 1991), and most chick disappearances were attributed to predation. However, some chicks escaped from the enclosures and a few of these were encountered in good condition outside. At Cedar Beach we define productivity as the number of chicks per nest known to have survived to 15 days (after Nisbet et al. 1990).

At Bird Island, chicks could not be fenced in because Roseate Terns at this site often move their chicks,

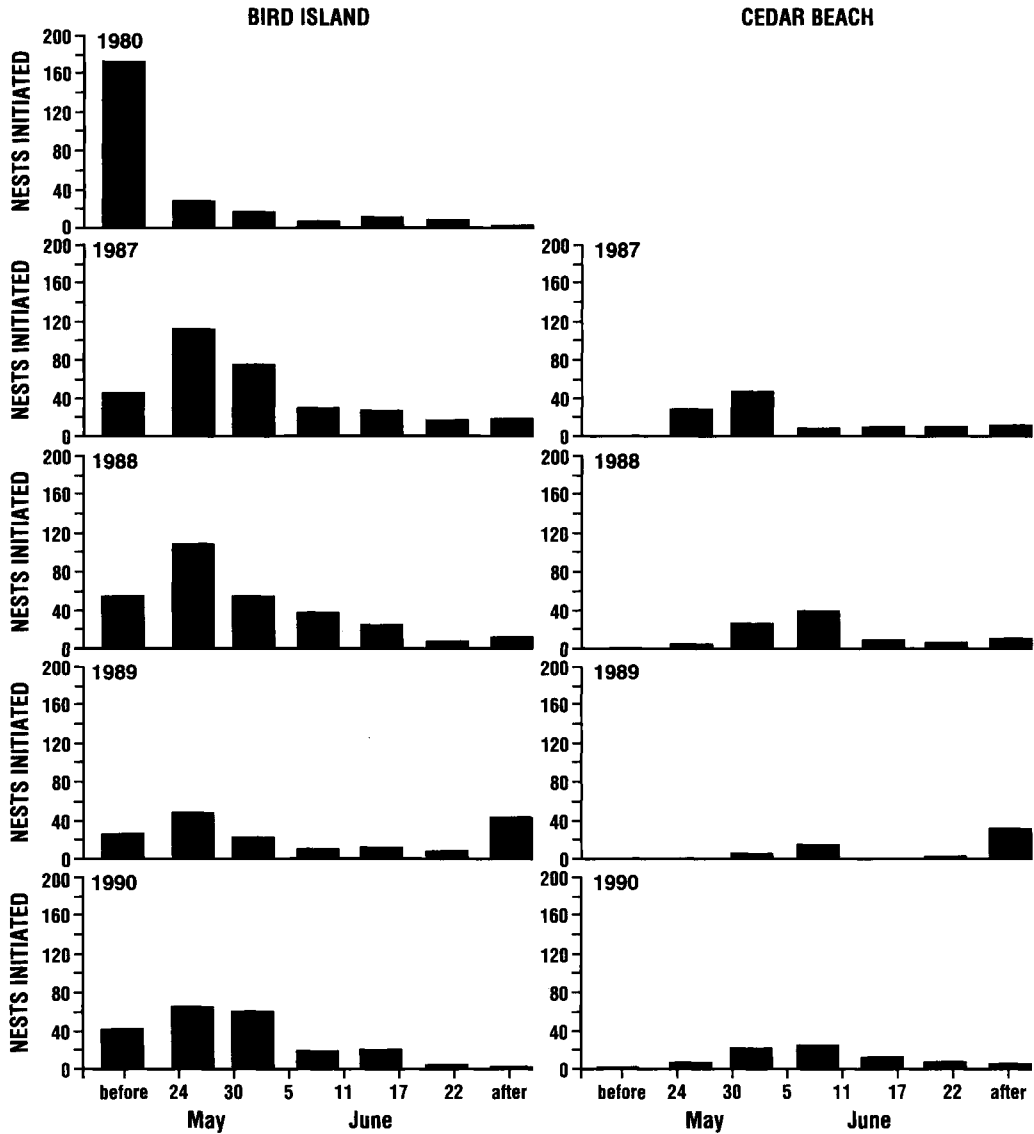


Fig. 1. Comparison of egg-laying phenology at Cedar Beach (1987-1990) and Bird Island (1980, 1987-1990). Shown are number of nests initiated per six-day period.

and fences sometimes cause disruption (Nisbet et al. 1990). Chicks were searched for daily for the first few days after hatching and on alternate days thereafter; all chicks were weighed when found. No chicks were taken by predators, but many chicks moved out of the areas that were searched and only about one-half of these were found later. We estimate productivity at Bird Island as the number of chicks that are known to have reached five days of age and were in good condition when last encountered, divided by the total number of nests followed (after Nisbet et al. 1990). Chicks that were in marginal condition at last encounter were counted as 0.5 fledglings.

Although the estimates of chick survival were obtained by different methods at the two colonies, each is believed to be the most reasonable, unbiased estimate for that colony (Nisbet et al. 1990). The values should be comparable within the colonies to about ± 0.03 chicks per nest, and between the colonies to about ± 0.1 chicks per nest.

For the analysis of seasonal patterns, we divided the egg-laying season into six periods of six days, from 18 May through 22 June, based on the date of laying of the first egg in each nest. All nests started after 22 June were included in a seventh category.

At Bird Island, we trapped 83 birds that had been

TABLE 2. Statistical comparisons for seasonal differences in reproductive measures for Roseate Terns by year and site. Given are Kruskal-Wallis chi-square values, degrees of freedom, and *P*-values.

	Cedar Beach			Bird Island		
	df ^a	X ²	<i>P</i>	df ^a	X ²	<i>P</i>
Clutch size						
1980	—	—	—	6	13.7	0.03
1987	5	31.2	0.001	6	29.3	0.001
1988	5	21.4	0.001	6	19.6	0.003
1989	5	13.9	0.03	6	79.6	0.001
1990	5	20.7	0.002	6	31.2	0.02
All years	5	89.4	0.001	6	16.12	0.001
Hatching success						
1980	—	—	—	5	10.4	—
1987	5	61.1	0.001	6	30.2	0.003
1988	5	41.1	0.001	6	26.0	0.01
1989	5	19.1	0.001	6	7.7	0.0001
1990	5	32.8	0.001	6	18.0	0.001
All years	5	88.8	0.001	6	107.8	0.001
Productivity						
1980	—	—	—	4	22.5	0.001
1987	4	21.1	0.001	4	14.3	0.01
1988	4	9.9	0.05	4	71.1	0.001
1989	4	11.5	0.009	4	80.2	0.001
1990	4	9.8	0.005	4	18.6	0.01
All years	4	12.5	0.005	6	80.6	0.001

^a Comparisons are among six-day periods (18 May–22 June) at Cedar Beach and seven six-day periods (12 May–22 June) at Bird Island. For productivity, comparisons are among five periods (18 May–16 June) at each site.

banded as chicks and, hence, were of known age. Only one bird of known age was trapped at each nest, but ages of mates are known to be correlated, both in Roseate Terns (Nisbet unpubl. data from 1991–1992) and in other species (Reid 1988).

We used regression models (PROC GLM; SAS Institute 1985) to analyze variations in measures of outcome. Site and year were treated as categorical variables and season was treated as an ordered variable. We used Kruskal-Wallis and contingency chi-square tests to determine differences among nest-initiation time intervals, A- and B-chicks, and sites. Kendall tau correlation coefficients were used to test for correlations among different variables for the known-aged terns.

RESULTS

We used regression models to explain the differences in number of nests initiated, clutch size, hatching success and productivity (Table 1). Season was the only variable that entered all models as a significant contributor.

The number of nests initiated per six-day period showed strong seasonal variation and significant differences between sites (Tables 1 and 2, Fig. 1). At Bird Island ($n = >150$ nests/year), the laying pattern showed a marked peak in the

second six-day period in each year, and a slow decrease in subsequent periods. At Cedar Beach ($n = >50$ nests/year), the peak was consistently later than that at Bird Island and was in the third six-day period in only one of the four years. The peak occurred in the fourth period in 1988 and 1990, and in the last period in 1989.

Clutch size (mean number of eggs/completed clutch) declined significantly with season in each year at each site (Table 2), and the overall pattern is shown in Figure 2. There was no significant difference between sites in the overall analysis, but there was a strong site \times year interaction (Table 1). This was due to yearly variation at Cedar Beach, with low average clutch sizes in 1987 and 1989, but high averages in 1988 and 1990. Averaging over all years, Bird Island showed a significant decline in the last three periods, whereas Cedar Beach showed a significant decline only in the last period (Fig. 2).

Hatching success (percent of eggs in completed clutches that hatched) varied strongly with season, site, and year (Tables 1 and 2). At both colonies, the most consistent pattern was a low average in the last one or two periods of the season (Fig. 2). At Bird Island, hatching suc-

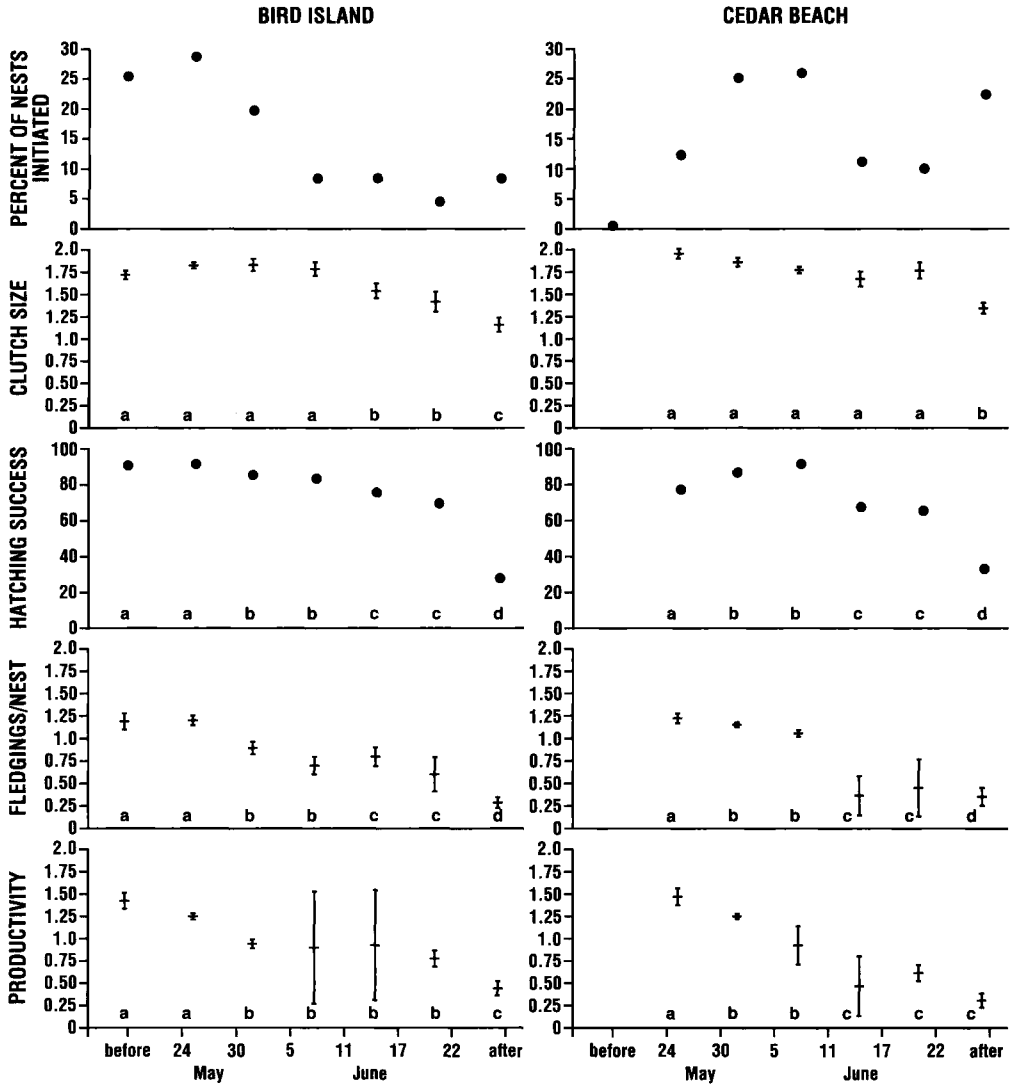


Fig. 2. Summary of overall egg-laying patterns and reproductive-success measures (1987-1990) for Cedar Beach and Bird Island. Dates indicate period of initiation of egg laying. Periods sharing the same letter (a-d) did not differ significantly.

cess was consistently high earlier in the season (although varying significantly among years). At Cedar Beach, hatching success was higher in the first three periods compared to the last three.

Overall fledging success decreased seasonally (Fig. 3). Fledging success of A-chicks varied with site and with year at Cedar Beach (Fig. 3, Table 3). At Bird Island, fledging success of A-chicks was uniformly high (averaging 96%), except for a decline in the last period in two years; at Cedar Beach, fledging success of A-chicks was signif-

icantly lower (averaging 65%), with more variable patterns (Table 3, Fig. 3). Fledging success of B-chicks varied strongly with season (Table 3, Fig. 3). The differences between A- and B-chicks were large and consistent at Bird Island (Table 3). In each year, fledging success of A-chicks was significantly higher at Bird Island, but there were no significant differences between colonies for B-chicks.

Productivity is the product of three other outcome variables (clutch size × hatching success

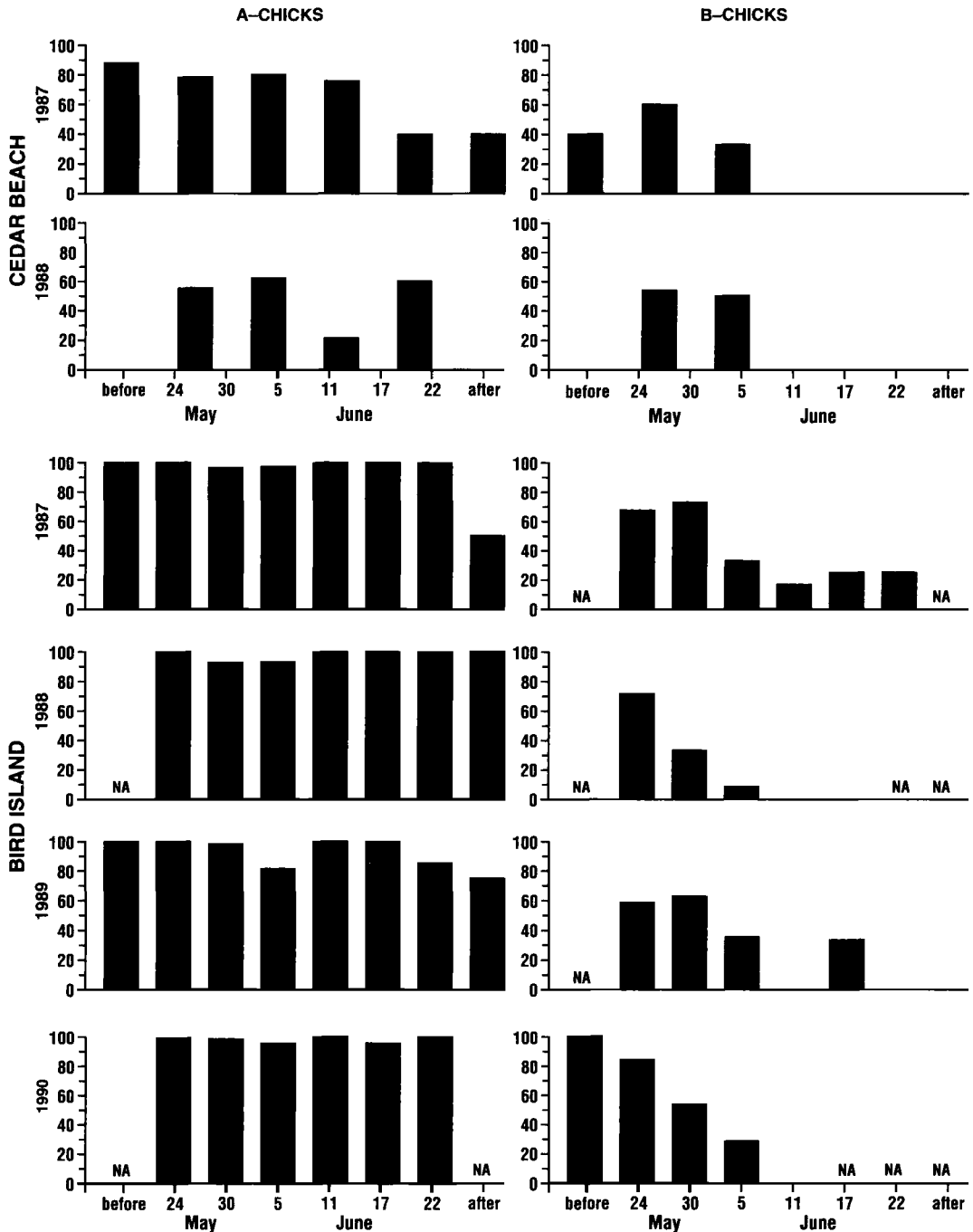


Fig. 3. Survival of A- and B-chicks at Bird Island and Cedar Beach (NA, not available). Dates indicate period of initiation of egg laying.

× fledging success). Productivity varied strongly with season and site, but did not vary significantly among years in the overall analysis (Tables 1 and 2). At Bird Island, productivity

declined significantly with season in each of the five years (Tables 2 and 4). At Cedar Beach, seasonal patterns of productivity were variable among years (Table 4), but the pattern averaged

TABLE 3. Survival of A- and B-chicks. Given are percent surviving (number of chicks in parentheses) and contingency chi-square test ($df = 1$), with probability level in parentheses (ns, $P > 0.05$).

	1987	1988	1989	1990	Comparison among years ^a
Cedar Beach					
A-chick	77 (75)	43 (61)	65 (60)	69 (63)	13.1 (0.01)
B-chick	43 (30)	38 (47)	40 (45)	46 (48)	ns
$X^2 (P)$	16.2 (0.001)	ns	6.5 (0.05)	3.9 (0.05)	—
Bird Island					
A-chick	98 (143)	96 (144)	92 (123)	98 (166)	ns
B-chick	57 (77)	31 (77)	49 (74)	47 (90)	7.6 (0.06)
$X^2 (P)$	71.0 (0.001)	105 (0.001)	46 (0.001)	99 (0.001)	—
Comparison between sites^b					
A-chick	20.3 (0.001)	70.5 (0.001)	16.5 (0.001)	41.9 (0.001)	—
B-chick	ns	ns	ns	ns	—

^a Contingency chi-square test, $df = 30$.

^b Contingency chi-square test, $df = 10$.

TABLE 4. Temporal patterns of productivity estimates (no. young fledged/nest) at Cedar Beach and Bird Island (see Methods for explanation).

Time period	1980	1987		1988		1989		1990	
	Bird Island	Cedar Beach	Bird Island	Cedar Beach	Bird Island	Cedar Beach	Bird Island	Cedar Beach	Bird Island
Before 18 May	1.58	—	1.00	—	—	—	2.00	—	—
18–23 May	1.44	—	1.33	—	1.30	—	1.57	1.00	1.33
24–29 May	1.41	1.30	1.26	0.33	1.11	—	1.38	2.00	1.22
30 May–4 June	1.22	0.89	0.97	0.81	0.88	0.00	0.87	1.23	1.02
5–10 June	1.50	0.62	0.86	0.57	0.94	1.00	0.78	1.00	0.81
11–16 June	1.33	0.33	0.81	0.28	0.92	—	1.00	0.25	0.75
17–22 June	1.00	0.20	0.82	0.40	0.67	2.00	0.86	0.00	0.50
After 23 June	—	0.18	0.25	0.0	0.33	0.34	0.68	0.00	0.00
Overall	1.43	0.87	1.07	0.64	1.09	0.83	1.09	1.10	1.12

TABLE 5. Correlations among reproductive success measures at Bird Island (above diagonal) and Cedar Beach (below diagonal) for 1987–1990. Given are Kendall tau correlation coefficients (all $P < 0.001$, except one marked ns [$P > 0.05$]). Correlations are among six-day periods ($n = 24$).

	Laying date	Clutch size	Hatching success	Fledging success	Productivity
Laying date	—	−0.19	−0.27	−0.17	−0.40
Clutch size	−0.30	—	0.68	ns	0.34
Hatching success	−0.35	0.66	—	0.62	0.67
Fledging success	−0.29	0.23	0.79	—	0.33
Productivity	−0.38	0.38	0.56	0.47	—

TABLE 6. Reproductive parameters ($\bar{x} \pm SD$, with sample size in parentheses) of known-aged Roseate Terns at Bird Island.

	Age (years)			F (P)
	2-3	4-5	6-16	
Laying date ^a	22 June \pm 2.6 (28) A ^b	3 June \pm 1.5 (22) B	28 May \pm 1.6 (30) C	45.5 (0.001)
Clutch size	1.31 \pm 0.09 (26) A	1.91 \pm 0.15 (22) B	1.77 \pm 0.08 (26) B	8.70 (0.001)
No. eggs hatched/nest	0.86 \pm 0.14 (7) A	1.47 \pm 0.17 (15) B	1.72 \pm 0.10 (18) B	6.84 (0.003)
Productivity	0.33 \pm 0.21 (6) A	1.14 \pm 0.14 (14) B	1.53 \pm 0.11 (17) B	12.41 (0.001)

^a SD for laying date in days.

^b Entries on same line with different letters are significantly different ($P < 0.05$; Duncan's multiple-range test).

over the four years was similar to that at Bird Island (Fig. 2). At both colonies, average productivity was high in the first period of the season (pre-peak) and declined to below 0.5 in the last period (Fig. 2). In the overall analysis (Table 4), the mean difference between the sites was 0.23 fledglings per nest, but much of this difference is attributable to later nesting at Cedar Beach, based on the regression coefficients in the linear models.

All four outcome variables were significantly positively correlated with each of the other three at each site. All four outcome variables were significantly negatively correlated with laying date at each site (Table 5).

Reproductive outcomes were acquired for 83 birds of known age at Bird Island (Table 6). Because of small sample size, the birds are grouped into three age categories: 2-3 years, 4-5 years, and 6-16 years. The youngest group (2-3 years) laid later than the older birds, laid smaller clutches, and had lower hatching success and productivity than older birds. None of the reproductive success variables differed significantly between birds aged 4-5 years and birds aged 6-16 years (Duncan's multiple-range test, $P > 0.05$), although all three groups differed with respect to mean laying date (Table 6). Within the oldest group (6-16 years), there were no discernible trends with age per se.

With the available data, there were no differences as a function of year of data collection (Table 7). Reproductive success measures increased with age and decreased with laying date (Table 8); both trends were significant (Table 7). Of the three outcome variables, only clutch size is more strongly associated with date than with age per se (Table 7).

DISCUSSION

Seasonal patterns in productivity.—Our data show highly consistent seasonal declines in productivity, statistically significant in each of five years at Bird Island and each of four years at Cedar Beach. Despite the differences between sites in some years, the average patterns were similar at the two sites. There also were significant declines in each of the components of productivity (clutch size, hatching success, fledging success) at each site. These declines were more consistent at Bird Island than at Cedar Beach, but were similar at both sites when averaged over all years. At Bird Island, there also

TABLE 7. Models explaining variations in clutch size and reproductive success of known-aged Roseate Terns.

	Clutch size	No. eggs hatched/nest	Productivity
Model			
F	4.34	3.41	9.67
R ²	0.35	0.47	0.73
df	8 and 73	8 and 39	8 and 36
P	0.001	0.006	0.001
Factors entering			
Age (years)	7.12 (0.001)	8.72 (0.006)	29.94 (0.001)
Date ^a	11.62 (0.001)	6.32 (0.01)	24.72 (0.006)
Year ^b	ns	ns	ns

^a Date is ordinal.^b Year when data collected.

were strong seasonal declines in survival of B-chicks.

At Cedar Beach, productivity was significantly higher among the earliest-nesting birds (before 30 May) than among peak-nesting birds (30 May–10 June). Fledging success was also significantly higher among the earliest-nesting birds than among the peak-nesting birds, although clutch size was not significantly higher and hatching success was significantly lower. At Bird Island, there were no significant differences in clutch size or hatching success between the earliest-nesting birds and the peak-nesting birds. However, both fledging success of the B-chicks and overall productivity were significantly higher in the period before 24 May than in the period 24–29 May. Overall, productivity was consistently higher among the earliest-nesting birds than among peak-nesting birds, although the components of this difference varied between sites.

Importance of predation and age.—Our results provide information about the potential importance of predation and age. Predation was responsible for much of the difference between Cedar Beach and Bird Island in survival of A-chicks and for part of the differences in overall productivity. However, we found no evidence

that predation contributed to the seasonal decline in productivity. That is, a similar proportion of chicks was taken by predators in all periods at Cedar Beach. Moreover, we found a seasonal decline in productivity at Bird Island, despite the lack of predation there.

The seasonal decline in productivity at Bird Island was accompanied by a seasonal decline in the age of breeders. However, age explains only part of the seasonal decline in breeding performance. After the effect of age is controlled for in the models, date still entered the models as a significant variable. Therefore, age alone does not account for the temporal patterns.

Why do Roseate Terns not breed earlier?—Seasonal declines in productivity have been recorded in many species of birds (see Introduction). Our data extend those of most other studies by showing that the earliest nesting birds have even higher productivity than birds laying at the peak a few days later. This suggests strong selection for earlier breeding. Why then do Roseate Terns not nest even earlier than they do? Breeding dates in our area have remained essentially unchanged for at least 70 years (Forbush 1925, Nisbet unpubl. data).

In some species of birds, breeding date is her-

TABLE 8. Kendall tau correlation coefficients (above diagonal) and statistical significance (below diagonal) of reproductive-success variables for known-aged Roseate Terns. Correlations are among individual birds ($n = 83$).

	Age	Laying date	Clutch size	Hatching success	Productivity
Age	—	−0.58	0.32	0.36	0.51
Laying date	0.001	—	−0.45	−0.53	−0.68
Clutch size	0.002	0.001	—	0.72	0.45
Hatching success	0.008	0.001	0.001	—	0.70
Productivity	0.001	0.001	0.003	0.001	—

itable (Perrins and Jones 1974, van Noordwijk et al. 1980, 1981, Findlay and Cooke 1982, Gustafsson 1986). For such species, one would expect breeding dates to become progressively earlier, unless strong selection for earlier breeding is offset by selection against the very earliest birds. Three general hypotheses have been suggested for this counter-selection:

(1) Differential costs of early breeding. Hypothetically, early-breeding birds might incur higher costs of reproduction, which might reduce their future survival (Clutton-Brock 1988). This might function if food were in low supply early in the season, exacting a high survival cost on females that produce early clutches. We have no information on survival of Roseate Terns as a function of breeding date.

(2) Predation. Hypothetically, predation might act differentially on birds breeding earlier (and later) than the peak period, thereby selecting for synchrony (Patterson 1965, Parsons 1975). Cases have been reported in which predation fell differentially on the earliest-nesting birds (Nisbet 1975, Nisbet and Welton 1984), but such cases appear to be infrequent. Roseate Terns usually have effective antipredator adaptations and rarely suffer substantial predation on eggs or chicks in most colonies. However, Nisbet (1992) described two recent incidents in which numbers of adult Roseate Terns settling at Bird Island at the beginning of the season were killed by falcons (*Falco* spp.). It is possible that sporadic predation of this kind might act as a selecting factor against early breeding, but our data are insufficient to evaluate this hypothesis.

(3) Food availability. Hypothetically, low availability of food early in the spring might act as a constraint on early breeding (Perrins 1970). Under this hypothesis, the timing of the breeding season is adapted to a seasonal maximum in food availability, but most birds are unable to breed at the optimum time because food is not available for forming eggs early enough in the spring. Most birds then lay while food supply is increasing and raise young while food supply is decreasing (Perrins 1970). Each bird would then lay as early as it can, resulting in laying dates being determined by individual quality (e.g. age and experience), which would enable some birds to exploit the spring food supply more rapidly than others. Our results are consistent with this hypothesis in that one variable that declines rapidly with season is the

survival of the *B*-chicks. This suggests that productivity is limited by the parents' ability to bring food for two chicks, with the "best" birds laying earliest. Moreover, average clutch size varies from year to year at Cedar Beach. In some years the modal clutch is two, whereas in others it is one. In the latter case the inter-egg interval of pairs laying two eggs is longer than usual, indicating food stress. Sometimes, food availability appears very limiting early in the season, as happened in 1989 and 1993, when some pairs defended territories and made scrapes, but did not lay eggs. Overall, our results support the hypothesis that food availability prevents earlier breeding by Roseate Terns at Bird Island and Cedar Beach, although our results do not exclude either of the other two hypotheses.

Our results also have implications for demographic models. Calculations of annual production of young need to take into account the fact that early and peak-nesting birds are much more productive than later-nesting individuals. Annual censuses of colonies within this population have not been fully consistent: some counts are limited to peak nests, while others include all nests initiated during the season (U.S. Fish and Wildlife Service 1989). If total nests are reported, this figure should be multiplied by the average productivity for the year, including the reduced productivity of the late nesters. If only peak nests are reported, this should be multiplied by the productivity of the peak birds, which is more often measured and reported (Nisbet et al. 1990). The latter procedure may be more biologically meaningful, because our data suggest that the peak nesters produce most of the young.

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