An Analysis of Temporal Variation in, and the Effects of Habitat Modification on, the Reproductive Success of Roseate Terns

JEFFREY A. SPENDELOW

Department of Biology, Yale University, P. O. Box 6666, New Haven, Connecticut 06511 USA

Abstract.—The Roseate Terns (Sterna dougallii) that nested on Falkner Island, Connecticut in 1981 began laying eggs in mid May and continued to lay through mid July. Most of the egg loss that occurred was attributed to nest desertion, infertility, rabbit activity, and storms. Predation by red ants accounted for one-third of the known chick mortality. Nests initiated after 10 June were not as successful as those begun earlier. Much of the temporal variation in reproductive success probably was due to the youth and relative inexperience of many of the pairs whose first eggs were laid more than 10 days after the initial peak of nesting.

Because of ant predation and nest abandonment due to vegetative growth, Roseate Terns that nested in vegetated sites on the slopes and top of the island were not as successful as those that nested on the beach. Some of the nesting habitat was modified by placing boards to create and maintain access to nest sites in vegetated areas, and by using boards, driftwood, and old tires to create additional sheltered nest sites on the beach. The Roseate Terns that used these sites had greater reproductive success than those that nested in natural, unmodified sites.

Key words: Roseate Tern; Sterna dougallii; reproductive success; temporal variation; habitat modification; Falkner Island, Connecticut.

In 1978 a long-term study of the population biology and reproductive ecology of the Common (Sterna hirundo) and Roseate (S. dougallii) Terns that nest on Falkner Island was begun. During the first 3 years of this study several small-scale experiments were conducted to determine if the reproductive success of either species could be increased by modifying the nesting habitat. Some results of this earlier work have been discussed in Nisbet’s unpublished 2-volume report (1980, 1981a) on the status, trends, and biological characteristics of Roseate Terns, but in response to the growing concern over the declining North Atlantic populations of this species (Duffy 1977; Thomas 1978; Buckley & Buckley 1980, 1981) and the need for data on current productivity and the factors affecting reproductive success (Nisbet 1980, 1981a), I undertook a more comprehensive study to measure temporal variation and compare the success of pairs nesting in natural and modified nest sites.

STUDY AREA AND METHODS

Falkner Island is located in Long Island Sound about 5 km south of Guilford, New Haven Co., Connecticut. The island is about 2 ha in area and consists of a densely vegetated interior plateau surrounded by a relatively narrow strip of rocky beach where most nesting takes place. The average distance from the base of the 5- to 10-m high bluffs out to the mean high tide line is about 5 m. The southern half of the island is lower in elevation than is the northern half, and the western slopes, especially along the southwestern corner, are more vegetated and not as steep or eroded as are the eastern ones.

Relative to the southern shore, the beach of the northern shore is made up of smaller rocks, and the extreme northern tip of the island is a narrow gravel-covered spit that becomes exposed at low tide to a distance about 0.5 km from the mean high tide line. Each spring the surface of the upper part of this spit is littered with old logs, boards, and other debris left behind by the waves that wash over this area during severe winter storms.

Fig. 1 shows that the highest concentrations of nesting Roseate Terns occur at the northern and southern ends of the island. At the southern end Roseate Terns nest next to or under thick vegetation on the top and slopes, and, on the beach among
large rocks that create hidden and protected nest sites. Many that nest on the beach of the northern end, however, must do so in open, exposed areas, and therefore must compete with the more aggressive Common Terns (Cooper et al. 1970, Langham 1974) for available nest sites. A few pairs nest in the vegetation on the slopes of the plots just south of the northern tip, and many pairs nest in the vegetation along the edge of the plateau on this end of the island. Terns nesting in vegetated habitats must compete for the use of sheltered sites with the feral rabbits that overrun the interior of the island, and abandoned rabbit burrows are often used by Roseate Terns as nest sites.

Each nest was marked with a numbered stick, and location within a gridded coordinate system, the type of habitat it was in, whether or not the site had been modified, and its subsequent history were all recorded. The dates of laying, clutch size, fate of all eggs, and the probable causes of egg loss and chick mortality were noted on censuses of the entire colony made every 2 or 3 days, or during trapping work done on the alternate days in different sections of the colony. The first census was made before the first eggs were laid.

Using treadle traps, we caught adult terns on their nests usually either a few days before or just after the eggs were due to hatch. Nisbet (1981b) has found that trapping much earlier than this increases the risk of desertion, and he recommends against trapping when eggs are pipping or chicks are only a few days old. We did some trapping during this latter stage of the breeding cycle and often trapped both adults the same day. Our trapping, therefore, may have affected the pattern of chick mortality as discussed below.

Chicks were banded when first found, usually within a day or two of having hatched. We continued to search in the immediate vicinity of the nest for dead chicks or older survivors during the next two censuses, but because many adults move their chicks into cover 2-7 days after hatching (Langham 1974, Nisbet 1981a), we made no attempt to search systematically for all chicks 7 or more days old. We found it difficult to find any 4-day or older chicks, alive or dead, in the grasses on the top of the island, but in several cases chicks from well-protected sites in tires, under large rocks, or in abandoned rabbit burrows remained in these hiding places for more than 2 weeks after hatching. During several intensive searches of the beach that were made late in the season we discovered a few dead chicks that probably had died several days, or even weeks, earlier.

In several other studies of Roseate Terns, most chick mortality usually occurred within the first week after hatching (Langham 1974, Nisbet & Cohen 1975), and the mean age at death for chicks in Massachusetts was 3.3 days in 1971 and 4.4 days in 1972 (Nisbet 1978). In this study most of the known mortality occurred within the first two nest censuses after hatching, i.e., before the chicks were 4-5 days old. In calculating breeding success,
therefore, I have assumed that chicks that could not be found during the census following banding had died, whereas those found during that census, but not on the next one, were assumed to have survived unless they were found dead at a later date. As it is doubtful that we were able to find every chick that died, these assumptions probably lead to an overestimation of fledging success and productivity for this colony in comparison to other studies where fledging success was calculated in a more traditional manner. However, because most mortality occurred at a very early age and many fledged immatures (50 or more at a time) were seen roosting on the dike or on the spit during early July, I feel that the upward bias is small, and the figures presented here are good approximations of the true productivity of the colony. Also, any such bias probably would not affect the within-colony comparisons of temporal variation. As a result, a nest was considered to have been successful if at least 1 chick was known to have survived 3-5 days without being found dead later.

Three locations for habitat modification experiments were chosen in 1981.  
1) Vegetated sites on the top of the island: On 13 May, before any Roseate Terns laid eggs, 25 boards or other flat objects were placed in the vegetation along the edge of the plateau on the northern end of the island to provide landing areas for the terns. A few planks about 20 cm in width and more than 2 m in length were used, but most boards were roughly square in shape and less than 1 m in either length or width. Some of the vegetation (mostly grasses and Poison Ivy, Rhus radicans) next to each board was then scuffed and trampled to provide an opening for a nest site. In addition, several boards from previous years were left in place along the edge of the top of the southern end of the island, but the vegetation growing over and around them was not altered.

2) Rocky sites on the shore: Throughout mid and late May boards, logs, pieces of styrofoam, and other objects that had washed ashore were collected and put in likely-looking spots to provide sheltered nest sites (Fig. 2). Although most of these

Fig. 2. A Roseate Tern nest under a board in plot 50.
objects were over 30 cm in width, a few were as narrow as 15 cm. Sometimes large rocks were moved to provide a more stable support for the boards, and in many cases gravel was added underneath to make the substrate smoother and more level. Most of these modifications were made on the northern end of the island because I thought that the terns nesting there would be more likely to make use of modified sites in what I judged, relative to the southern shore, to be otherwise less suitable habitat.

3) Gravel sites on the spit: On 16 May, just 1 day before the first Roseate Tern eggs were found elsewhere on the island, 22 tires were laid on the surface of the gravel spit. (Some of the tires had washed ashore; others had been brought to the island for an experiment done in 1980.) Eight days later 20 of the 22 tires were half-buried on a 30-45° angle to the surface on the upper end of the spit; the other 2 tires were not moved so as to avoid disturbing eggs laid on the gravel in the center of each. By 31 May, after the peak of nest-initiation, 13 more tires had been set in place, 10 further out on the spit in the same plot, and 3 along the southeastern corner of the gravel area in a neighboring plot. The tire openings were oriented to the east to provide protection against the prevailing westerly winds and storms. Again, boards were propped up on logs and some of the larger stones to create other potential nest sites, and a plastic bucket that had washed ashore was half-buried in the middle of the spit as shown in Fig. 3. The tires were removed from the beach at the end of the 1981 breeding season, stored over the winter on the top of the island, and used again in 1982.

Loftin & Thompson (1979) made artificial nest structures for Least Terns (Sterna antillarum) by burying tires underneath existing nest sites. They did this to raise the nests a few inches higher than the surrounding beach, and thereby reduce losses to high tides. On Falkner Island we half-buried tires so as to create new potential nest sites in the sheltered areas between the sides of each tires.

The data were analyzed using several

Fig. 3. The gravel spit at the northern end of the island in July 1981 following extensive habitat modification.
ROSEATE TERN REPRODUCTIVE SUCCESS

procedures available in the SAS statistical package maintained by the Yale Computer Center.

RESULTS

Timing of nest-initiation, renesting, and population size

Fig. 4 shows the number of new nests found on each census date and the mean number of nest starts per day between censuses. In the early part of the breeding season nest-initiation was highly synchronized with the peak of nesting occurring within a week after the first eggs were discovered on 17 May. A much smaller second wave of nest-initiation occurred between 3 and 10 June. This wave included several 7-year-old birds, presumably already renesting soon after their first clutches had been abandoned, collected, or destroyed. The last new nest was started on 20 July. Although the beginning and peak of egg-laying on Falkner Island in 1981 occurred

![Graph showing number of new nests per day and total number of new nests found on each census date.](image)

Fig. 4. The mean number of new nests per day (height of bars) between censuses, and the total number of new nests (number over bars) found on each census date. Figure 4 is drawn such that the area under each segment of the bar graph (= number of days between census x mean number of new nests per day) represents the total number of new nests found at the end of the census.
about 2 weeks earlier, the pattern of nest-initiation was similar to that seen in 1965 on Coquet Island, England (Langham 1974).

Our trapping results showed that a pair whose first nest on the top of the island failed when their chick was killed by ants on 24 June laid a new egg in a tire on 4 July, 10 days later. Based on the maximum number of active nests at any one time, and using 10 days as the minimum length of time it takes a pair to renest once an attempt fails (DiCostanzo 1980), the minimum breeding population was estimated to be 185-190 pairs.

Egg loss, chick mortality, and overall reproductive success

Table 1 shows the mean clutch size, mean number of eggs that hatched, mean number of presumably surviving chicks, and the number of successful nests. Roseate Terns laid 391 eggs in the 215 nests that were discovered and 280 (71.6%) of these eggs hatched. Roughly two-thirds of the egg loss (71/111) was attributed to a combination of possible infertility or disruption of normal development (28), nest desertion (25), and rabbit activity (18). Storms destroyed 15 eggs, either by washing them away or by burying them, and also may have been responsible for producing some of the rotten and over-aged eggs in which normal development had been disrupted. Tom Custer collected 10 eggs on 18 May for pesticide analysis. Other human disturbance, both our own and that of uninvited visitors, was believed to have been responsible for the loss of another 15 eggs and two chicks.

About two-thirds of the deserted eggs (17/25) were from 1-egg clutches. Nisbet (1981a) noted that some 1-egg clutches are abandoned without ever having been incubated. We did not note in the field which of the single-egg clutches we found may have fallen into this category, and so they are all included in the calculations of clutch size and hatching success presented here. I would agree, however, with Nisbet that in future studies unincubated clutches should be eliminated from such calculations.

Thirty-nine (13.9%) of the chicks that hatched were found dead or were presumed to have died (six individuals) because they disappeared before they were 2-3 days old. All other chicks were known to have survived for at least 3-4 days after having been banded, and were presumed to have survived to fledging. A similar definition and figures for fledging success are given in Nisbet’s Table V.6 (1981a) for Roseate Terns nesting at Coquet Island, England.

With one possible exception, all 13

<table>
<thead>
<tr>
<th>Date of nest-initiation</th>
<th>No. of nests</th>
<th>Mean clutch size</th>
<th>Mean number of chicks hatched</th>
<th>Mean number of presumed survivors</th>
<th>No. nests successful</th>
<th>% nests successful</th>
</tr>
</thead>
<tbody>
<tr>
<td>5/14 - 5/20</td>
<td>78</td>
<td>1.94 ± .05ab</td>
<td>1.47 ± .09a</td>
<td>1.26 ± .10a</td>
<td>58</td>
<td>74.4</td>
</tr>
<tr>
<td>5/21 - 5/27</td>
<td>69</td>
<td>1.87 ± .05ab</td>
<td>1.46 ± .09a</td>
<td>1.26 ± .10a</td>
<td>54</td>
<td>78.3</td>
</tr>
<tr>
<td>5/28 - 6/08</td>
<td>21</td>
<td>1.62 ± .11abc</td>
<td>1.00 ± .17bc</td>
<td>0.91 ± .17bc</td>
<td>14</td>
<td>66.7</td>
</tr>
<tr>
<td>6/04 - 6/10</td>
<td>18</td>
<td>1.89 ± .11abc</td>
<td>1.39 ± .22bc</td>
<td>1.22 ± .22a</td>
<td>14</td>
<td>77.8</td>
</tr>
<tr>
<td>6/11 - 6/24</td>
<td>18</td>
<td>1.89 ± .12cde</td>
<td>0.72 ± .21cde</td>
<td>0.56 ± .17bc</td>
<td>4</td>
<td>44.4</td>
</tr>
<tr>
<td>6/25 - 7/08</td>
<td>6</td>
<td>1.33 ± .21e</td>
<td>0.85 ± .31bcd</td>
<td>0.83 ± .31abc</td>
<td>4</td>
<td>66.7</td>
</tr>
<tr>
<td>7/09 - 7/22</td>
<td>5</td>
<td>1.20 ± .20bc</td>
<td>0.0d</td>
<td>0.0d</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>Total</td>
<td>215</td>
<td>1.82 ± .03</td>
<td>1.30 ± .06</td>
<td>1.12 ± .06</td>
<td>152</td>
<td>70.7</td>
</tr>
</tbody>
</table>

1Means are given as the mean ± the standard error of the mean. Four clutches initiated in the first period and one in the fourth were 3-egg clutches. A 4-egg clutch initiated in the second period probably was laid by two different females.

2Superscript letters indicate the statistical significance of differences between means in the same column as determined by Duncan’s Multiple Range Tests. Means sharing the same letter are not significantly different (p < 0.05).
chicks that died as a result of predation by an unidentified species of small red ant were killed during hatching or within a day of having hatched. The first chick to hatch from nest TOP-15 was not found 3 days later during the next nest-check. At that time the second egg in the nest had hatched and the younger chick had been killed by ants. A new nest was discovered 3 weeks later at this site. It was assumed, therefore, that the missing older chick had been attacked by ants and, in its efforts to escape, had fallen over the edge of the top of the island into the dense grasses on the slopes below. On at least two other occasions Roseate Tern chicks from nests on the top of the island that had been attacked by ants had been found dead later on the earthen slopes below their nests.

Relative to the day on which they were first found, the other 21 dead chicks were found on days 1 (4), 2 (1), 3 (4), 4 (4), 5 (2), and 9 or more (6). It is probable that two or three of the six chicks found dead nine or more days after having been banded had actually died much earlier. Some volunteers did not spend as much time looking for dead chicks as did others, and the approximate stages of development, as given by Nisbet & Drury (1972), of dead chicks were not recorded by inexperienced volunteers in several cases. Nevertheless, at least 82% (27/33) of all chicks found dead were believed to have been no more than 5 days old when they died.

**Temporal variation in reproductive success**

The egg-laying stage of the breeding season (Figure 4) was divided into 7 periods, the first four were 1-week in length and the last three were 2-weeks in length. The amount of egg loss and chick mortality from the nests initiated during each period is listed in Table 1, and the percentage losses are illustrated in Fig. 5. There was a seasonal decline in productivity. The pairs that started their nests in the period from 28 May to 3 June and in the last three 2-week periods averaged less than one surviving chick per nest attempt. An examination of the ratio of successful to unsuccessful nests (Table 1) shows that the nests started after the second wave of egg-laying were not so successful (12/29) as were those initiated during the first four periods (140/186) ($\chi^2 = 15.9$, df = 1, $p < 0.001$).

Many of the nests started in July were deserted. Nisbet (1981a—Table V.9) noted a similar seasonal drop in the productivity of Roseate Terns nesting in Massachusetts.

**Productivity of nests in different habitats**

The nest sites used by Roseate Terns were divided into different habitat categories as follows: seven were in holes or abandoned rabbit burrows; 39 were in vegetated, usually grassy sites; 85 were next to, or under, rocks; 65 were next to logs or under boards; and 19 were inside tires. Ninety-one (42.3%) of the nests were in sites that we had modified in some way. Besides the 19 nests inside tires on the spit, 22 nests were next to landing boards placed on top of the island, one was under a rock shelter, and 49 were under boards or other objects propped up against rocks or logs on the beach.

Table 2 shows the mean clutch size, mean number of eggs that hatched, mean number of presumably surviving chicks, and the number of successful nests for each habitat category and for the natural and modified-site nests. The percentage egg loss and chick mortality for the nests in each habitat category are illustrated in Figure 6. Overall, nests in modified sites had a higher success rate (71/91) than did nests in natural sites (81/124) ($\chi^2 = 4.09$, df = 1, $p < 0.05$).

While there was no significant variation in clutch size means (Table 2) among the nests from different habitats, there were significant differences in the mean number of eggs hatched and the mean number of presumably surviving young. Most of the variation was due to differences in the number of eggs that hatched. While the total chick mortality from nests in different habitats did not vary significantly, 11 of 43 chicks hatched in vegetated-site nests were lost to ant predation, and only two other Roseate Tern chicks were killed by ants.

A contingency table analysis of the number of successful and unsuccessful nests in each habitat category shows that the nests in vegetated sites had a relatively poor success rate (19/39). Even though nest
Fig. 5. Relative percentage egg loss and chick mortality as a function of the date of nest-initiation.

Desertion due to vegetative growth was reduced in some cases by providing landing boards (see further discussion below), nests in these sites were still subject to rabbit disturbance and ant predation. Nests in rock sites and those inside tires had average success rates (59/85 and 13/19, respectively), and the relatively well-protected nests under boards, by logs, or in burrows had the highest success rate (61/72) ($\chi^2 = 16.05$, df = 3, $p < 0.005$).

**Landing boards on the top of the island**

One of the boards left on the top of the southern end of the island was used successfully by the only pair of Roseate Terns that nested there in 1981. Of the 25 boards placed along the edge of the top of the northern end of the island, 16 were used by Roseate Terns to provide access to 21 nest sites and a 17th board was used by a pair of Common Terns. One board was used simultaneously by three pairs of Roseate Terns, and three other boards were used by two pairs each. Of the 22 nests in sites next to landing boards, 15 were successful, two were abandoned, three were lost to ants, and two were lost to other causes. Eleven other Roseate Tern nests on the top of the northern end of the island were not located near landing boards: two were in abandoned rabbit burrows and nine were in vegetated sites. Only one of the latter was successful: five nests were deserted before the eggs hatched and in three other nests all the chicks were killed by ants soon after hatching. Both burrow nests were successful. Despite the small sample sizes, the difference in the success of the landing-board nests (15/22) and the natural-site nests (3/11) is significant ($\chi^2 = 4.95$, df = 1, $p < 0.05$), and comparing the success of all modified-site nests (15/22) and natural-
TABLE 2. Reproductive success of Roseate Terns in 1981 on Falkner Island, Connecticut as a function of the habitat in which the nest was placed.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>No. of nests</th>
<th>Mean(^1) clutch size</th>
<th>Mean number of chicks hatched</th>
<th>Mean number of presumed survivors</th>
<th>No. nests successful</th>
<th>% nests successful</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Part A</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nest in burrow</td>
<td>7</td>
<td>2.00(^{±,02})</td>
<td>1.57 ± 0.03(^{,02})</td>
<td>1.13 ± 0.30(^{,06})</td>
<td>6</td>
<td>85.7</td>
</tr>
<tr>
<td>Nest under board</td>
<td>49</td>
<td>1.94 ± 0.05(^a)</td>
<td>1.61 ± 0.10(^b)</td>
<td>1.43 ± 0.11(^a)</td>
<td>42</td>
<td>85.7</td>
</tr>
<tr>
<td>Nest by log</td>
<td>16</td>
<td>1.88 ± 0.13(^a)</td>
<td>1.50 ± 0.18(^b)</td>
<td>1.25 ± 0.19(^b)</td>
<td>13</td>
<td>81.3</td>
</tr>
<tr>
<td>Nest inside tire</td>
<td>19</td>
<td>1.63 ± 0.11(^a)</td>
<td>1.16 ± 0.21(^b)</td>
<td>1.05 ± 0.20(^a)</td>
<td>13</td>
<td>68.4</td>
</tr>
<tr>
<td>Nest by rocks</td>
<td>85</td>
<td>1.78 ± 0.05(^a)</td>
<td>1.19 ± 0.09(^b)</td>
<td>1.08 ± 0.09(^a)</td>
<td>59</td>
<td>69.4</td>
</tr>
<tr>
<td>Vegetated-site, nest with board</td>
<td>22</td>
<td>1.86 ± 0.10(^a)</td>
<td>1.36 ± 0.17(^ab)</td>
<td>1.06 ± 0.18(^a)</td>
<td>15</td>
<td>68.2</td>
</tr>
<tr>
<td>Vegetated-site, no landing board</td>
<td>17</td>
<td>1.71 ± 0.14(^a)</td>
<td>0.76 ± 0.22(^b)</td>
<td>0.35 ± 0.17(^b)</td>
<td>4</td>
<td>23.5</td>
</tr>
<tr>
<td><strong>Part B</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Modified sites</td>
<td>91</td>
<td>1.86 ± 0.05(^a)</td>
<td>1.45 ± 0.08(^a)</td>
<td>1.25 ± 0.09(^a)</td>
<td>71</td>
<td>78.0</td>
</tr>
<tr>
<td>Unmodified sites</td>
<td>124</td>
<td>1.79 ± 0.05(^a)</td>
<td>1.19 ± 0.08(^b)</td>
<td>1.02 ± 0.08(^b)</td>
<td>81</td>
<td>65.3</td>
</tr>
</tbody>
</table>

\(^1\)Means are given as the mean ± the standard error of the mean.

Within each separate part of the table (Part A or Part B, but not A and B together), superscript letters indicate the statistical significance of differences between means in the same column as determined by Duncan's Multiple Range Tests. Means sharing the same letter are not significantly different (p < 0.05).

site nests (4/17) in vegetated habitats results in a significant difference at the 1% level (\(χ^2 = 7.65, df = 1\)). The 22 modified-site nests on the top of the island produced 1.09 chicks per nest, as compared to the average of 0.46 chicks produced by the 11 other nests on the top of the island, and the 0.35 chicks per nest produced by all 17 of the unmodified vegetated-site nests on the top and slopes.

**Modified-site and natural-site nests on the gravel spit**

After they had been put on the surface of the spit, but before they were buried, three tires were used as nest sites (the eggs were laid in the open on the gravel in the center of each of these tires, but in the later nests the eggs were laid under the rim of the half-buried tires) by the first three pairs of Roseate Terns that nested in this area. Two of these nests, however, were deserted soon after the tires were moved, and thereafter the majority of tire-site nests were not initiated until well after the first peak of nesting. By 3 June, 10 days after we had buried the first set of tires, only four more tire-site nests had been found, but six more were started during the following week. This, together with the relatively low mean clutch size for these nests (Table 2) suggests that most of the pairs that made use of the tires may have been young birds making their first nesting attempt or, as the only pair to be trapped on two different nests in 1981 demonstrated, older birds re-nesting late in the season. Four nests on the spit were under boards. The bucket was not used as a nest site although similar
buckets and half-buried baskets have been used in the past both here and elsewhere (Duffy 1977).

The three nests on the spit that did not make use of modified sites were all unsuccessful, but the Roseate Terns that nested inside tires did as well as those that nested in rock-site nests, both in terms of the number of chicks produced per nest and the ratio of successful to unsuccessful nests (Table 2, Fig. 6). Despite the fact that most tires were not used until after the peak of nesting and other nests initiated during the latter part of the season had relatively poor success (Table 1), 13 of the 19 tires used as nest sites presumably produced surviving young. In addition, six other tires were used as hiding places by 1- to 3-week old chicks, some from other tire-site nests, and some from wood- and rock-site nests in neighboring plots. Our own research activity probably caused the loss of four of the six tire-site nests that failed.

**DISCUSSION**

Temporal variation in clutch size, hatching success, and fledging success

Previously reported mean clutch sizes for Roseate Terns nesting in Long Island Sound (Cooper et al. 1970, Hays 1970, Nisbet 1981a) are lower than those reported in this study. The reasons for the apparent difference are unknown, but may reflect the age-structure and maturity of the populations, as well as differences resulting from variation in food supply, the timing of nest-initiation, and reactions to human disturbance. The overall mean and pattern of temporal variation in mean clutch sizes reported in this study are similar to those found for Roseate Terns nesting in Massachusetts (Nisbet 1981a).

The mean clutch size of the nests initiated in the third period (28 May-3 June) was somewhat, but not significantly, less than those of the nests initiated in periods

<table>
<thead>
<tr>
<th>HABITAT</th>
<th>20</th>
<th>40</th>
<th>60</th>
<th>80</th>
<th>100</th>
</tr>
</thead>
<tbody>
<tr>
<td>NEST IN BURROW</td>
<td>N=14</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NEST UNDER BOARD</td>
<td>N=95</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NEST BY LOG</td>
<td>N=30</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NEST INSIDE TIRE</td>
<td>N=31</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NEST BY ROCKS</td>
<td>N=51</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NEST IN VEGETATION (WITH LANDING BOARD)</td>
<td>N=41</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NEST IN VEGETATION (WITHOUT LANDING BOARD)</td>
<td>N=2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 6. Relative percentage egg loss and chick mortality as a function of the habitat is which the nest was placed.
1, 2, and 4, and the nests started in these three other periods were slightly more successful than were the third period nests. A similar slight mid-season drop in productivity was recorded for the birds nesting on Coquet Island, England in 1965 (Langham 1974).

After 10 June mean clutch size decreased significantly as did hatching success and productivity. Nisbet (1981a) found a marked seasonal decline in productivity at Bird Island, Massachusetts and attributed this primarily to a decline in the average clutch size. On Falkner Island temporal variation in hatching success was also important, in contrast to Nisbet's results, and the higher overall productivity in Massachusetts reflects both the higher hatching success and the lack of ant predation.

A more detailed analysis of the timing and breeding success of known-age Roseate Terns will be the topic of a future paper, but at this time it is known that (a) several of the Roseate Terns that began laying eggs in the third period were banded as chicks in 1977, and (b) most of known-age birds that began laying in period 2, and several of those that initiated nests in period 4 during the second wave of nest-initiation (and more than 10 days after some of the period 1 nests had failed) were birds banded as chicks in 1972-1975. Hays (1978) found that 7- and 6-year-old Common Terns began nesting earlier, had larger average clutch sizes, and had greater productivity than did younger birds. She suggested that her results reflected the relative inexperience of the younger birds. It seems probable, then, that the temporal variation in productivity of Roseate Terns found in the present study is at least in part the result of similar differences in the age and experience of the birds that initiated nesting in the different periods; most of the birds that began nests in period 3 were young birds and most of the renesting done by older birds probably took place in period 4.

*The timing of chick mortality*

Before we were aware of Nisbet's (1981b) studies of the behavior of Roseate Terns after trapping, we often trapped adults on pipping eggs and recently-hatched chicks, and also often trapped both adults on the same day. Nisbet has suggested that such a pattern of trapping can lead to the neglect of the eggs or chicks at a critical time. The younger the chick, the more likely it would be to suffer as a result of such neglect. It is possible, therefore, that our trapping may have influenced the pattern of chick mortality by causing more chicks to die at an earlier age than they otherwise might have died, and thereby resulting in fewer deaths of older chicks.

*Productivity of vegetated-site nests*

Buckley & Buckley (1981) reported that Roseate Terns that nested in vegetated sites on Long Island salt marshes were unsuccessful due to rat predation and tidal flooding. Gochfeld (1976) reported that Roseate Terns nesting beneath Seaside Goldenrod (*Solidago sempervirens*) either abandoned clutches or led their chicks to other areas when several patches of these plants were defoliated by larvae of the chrysomelid beetle *Trirhabda canadensis*. Roseate Terns that nest in vegetated sites on Falkner Island have low reproductive success for different reasons. Some of the eggs are abandoned as the breeding season progresses and the vegetation grows and increases in density, thereby preventing access to the nest by the incubating adults. A similar loss in nesting habitat due to vegetational growth has occurred on other islands (Duffy 1977, Nisbet 1981a, H. Hays, pers. comm.). A few eggs are kicked out of the nests and broken by rabbits seeking shady resting areas on Falkner Island, and in other nests, particularly those in grassy areas, ants swarm over the pipping eggs and recently hatched chicks.

Placing boards and removing some vegetation to provide open areas in vegetated habitats appears to be a quick and successful method of giving the terns access to sites that are not used as much by the rabbits and are less likely to be deserted because of vegetative growth than are unmodified sites. Chick losses due to ant predation remain a problem. The ants seem to prefer certain types of vegetation, so it may be possible to reduce predation losses by carefully choosing the sites where the boards are placed. It is also possible that trampling and packing the ground next to
the landing board may make it less suitable as a site for an ant colony. Further studies along these lines are needed.

**Productivity of beach-site nests**

Roseate Terns that nest on the open, exposed areas of the beach on Falkner Island must compete with the more aggressive Common Terns for available nest sites. Because Common Terns prefer relatively open areas while Roseate Terns prefer sheltered areas (Langham 1974) where there is limited access to nest sites, the placing of boards, logs, tires, and other objects in appropriate places can increase the latter species' chances of finding a suitable nest site and may result in increased productivity on a per nest basis.

Generally speaking, the most sheltered sites are the first ones to become occupied, may be defended more vigorously than exposed sites, and are used by the most productive pairs. It seems probable that these sites are being used by the older and more experienced birds in the colony, but further work needs to be done before this hypothesis can be tested.

Although the reproductive success of the Roseate Terns that nested inside tires was similar to that of those that nested in natural rocky habitat along the shore, we had expected the former to be more successful. The lack of greater success probably was due to the fact that the preparations for the tire experiment were not completed until after the birds had started laying. Burying the tires when we did may have disrupted those pairs that were attempting to make use of the spit during the peak of nesting, thereby causing them to nest elsewhere. As a result, most of the birds that eventually used the tires as nest sites may have been young, inexperienced birds, or older birds renesting late in the season.

Whereas most Roseate Tern chicks from nests in open sites or under small boards left the immediate vicinity of the nest site before they were a week old, chicks from tire-site nests tended to continue to use their own nest tire or a neighboring one, if it were vacant, as a hiding place for as long as 3 weeks after hatching. It seems likely that this continued use of a sheltered site might result in a reduction of chick mortality due to predation or aggression by neighboring adults. Chick shelters have been used to reduce avian predation in Least Tern colonies in Massachusetts (Jensk-Jay 1982).

**ACKNOWLEDGMENTS**

This work could not have been accomplished without the help and support of many people. I would like to thank the U.S. Coast Guard for giving us permission to work on the island; D. O. Logan for loaning us his Boston Whaler; K. M. Waage, M. C. Brinigar, J. Sweeting, J. E. Rodman, and C. G. Sibley of Yale University's Peabody Museum of Natural History for allowing us to use museum equipment and arranging for boat transportation; M. W. Reed for piloting the Yale boat and providing assistance in numerous other ways; F. M. and S. W. Richards for providing additional boat transportation; L. Schlesinger, G. Letis, and M. Letis for their efforts in obtaining support by the New Haven Bird Club; F. Gallo and S. Hopkins for their dedicated service as Warden/Biologists for the tern colony; and the more than 50 volunteers, many of them NHBC members, who helped gather the census and trapping data in 1981. For financial support I would like to thank everyone who contributed to the Bird-a-thon that raised money for the project, and Dr. Karl M. Waage, Director of the Peabody Museum Field Station, for providing services to the project.

Helen Hays, Director of the Great Gull Island Project, provided the initial impetus that resulted in the organization of the Falkner Island Tern Project and has continued to support and encourage our work in many ways. Fred Sibley served as Co-Director of the project for 3 years and provided much of the inspiration for this year's work. Pat Lynch prepared the figures, and the manuscript has benefited from comments and suggestions made by Paul Buckley and Ian Nisbet. For additional assistance I am grateful to Steve & Teri Bennett, Frank Gallo, Scott Hopkins, Pat Lynch, Linda & Matt Reed, Sally Richards, Linda, Ruth, & Howard R. Spendelow, Jr., and Janet Sweeting.
LITERATURE CITED


