SEASONAL VARIATIONS IN BREEDING SUCCESS OF COMMON TERNS: CONSEQUENCES OF PREDATION

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ABSTRACT.—We studied the breeding of 125 pairs of Common Terns (Sterna hirundo) in a large colony at Monomoy, Massaschusetts, in 1979. The colony was subjected to predation by one or more Great Horned Owls (Bubo virginianus). The adult terns deserted the colony for 6.5–8 hours each night throughout the season. Although the owl(s) took no adults and only about 20 chicks from our study plots, the terns suffered unusually heavy losses from other causes, including breakage and disappearance of eggs, hatching failures, attacks by ants (Lasius neoniger), chilling of newly-hatched chicks, and predation by Black-crowned Night-Herons (Nycticorax nycticorax). In a 10-year study, most of these causes of egg and chick loss have been associated with nocturnal desertion and predation by Great Horned Owls. Although nocturnal desertion is effective in minimizing owl predation on adults, it leaves the eggs and chicks vulnerable to chilling and predation. In 1979, both direct and indirect effects of predation fell more heavily on terns that laid in May than on terns that laid in June. Differential predation on early nesters tends to offset other factors that presumably favor early nesting.

Predation is one of the most important selective forces influencing breeding behavior in ground-nesting colonial birds, such as gulls and terns (Lack 1968). When a nocturnal predator gains access to a colony, larids usually have no effective defenses (Austin 1948, Ashmole 1963, Southern et al. 1982). However, avian predators and diurnal mammals often take only limited numbers of colonial larids (Hatch 1970. Nisbet 1975, Southern et al. 1982). Consequently, the study of differential mortality in a larid colony can throw light on the role of predation in influencing timing, synchrony, and spacing behavior (Ashmole 1963, Kruuk 1964, Patterson 1965, Tinbergen 1967, Parsons 1971, Nisbet 1975).

Nisbet (1975) reported that Great Horned Owls (*Bubo virginianus*) preying on nesting Common Terns (*Sterna hirundo*) took a much higher proportion of chicks hatched earlier in the season than of chicks hatched later. We describe here a study of another Common Tern colony subjected to predation by one or more Great Horned Owls. In the case described here, direct predation by the owl(s) was less important than other causes of egg and chick losses. However, we present evidence that at least some of these other losses were indirect consequences of the owl's activity. This paper analyzes seasonal variations in both direct and indirect effects of owl predation.

STUDY AREA AND METHODS

We studied 125 pairs of Common Terns within a colony of about 3,300 pairs at Monomoy

National Wildlife Refuge, Massachusetts (41°38'N, 69°58'W) in May-August 1979. This was part of a long-term study of this colony, whose results are summarized in Table 1. In 1979, we selected two study plots about 75 m apart, comprising a total area of about 570 m². Each plot was on the edge of a large open sandy area surrounded by dense beach grass (Am*mophila breviligulata*). Common Terns nested earliest and most densely in a partially vegetated border strip containing scattered clumps of live and dead beach grass, seaside goldenrod (Solidago sempervirens) and beach pea (Lathvrus japonica). Although both study plots included areas of dense grass and open sand, Common Terns occupied these habitats later and less densely than the border strips. The plots were selected to be representative of the whole colony, and the density and patterns of occupation appeared similar in other parts of the colony.

We visited the study plots on most days from 22 May to 9 July, on 20, 21 and 28 July, and on 7 August 1979. P. Trull visited the colony on five other days between 10 and 25 July. Nests and eggs were marked when first seen, and eggs were weighed. When eggs were not found on the day of laying, this date was estimated from laying and hatching patterns and by flotation (Hays and LeCroy 1971); weights of fresh eggs were estimated from data on the rate of weight loss (Rahn et al. 1976). Nine banded adults, including two nesting outside the plots, were trapped to determine their ages. Chicks were banded at hatching and checked

TABLE 1. Predation, nocturnal desertion, and success of Common Terns at Monomov National Wildlife Refuge. Massachusetts, 1972-1981.^a

| Year | Estimated no. of pairs | Predation by Great Horned Owls ^b | Predation by Black-crowned Night-Herons ^e | Egg and chick mortality from ants ^d | Nocturnal desertion ^e | Mean incubation period (days) ^r | Productivity: fledged chicks/pair ^s |
|------|---------------------------|--|--|--|----------------------------------|---|--|
| 1972 | 1,600 | Some | Not seen | Heavy | No data | ca. 28 | 0.65 (s) |
| 1973 | 2,100 | July only | None | Light (1/72) | None | 22.6 | 1.2 (s) |
| 1974 | 2,200 | Intermittent | None | Light (1/40) | Partial | 25.7 | 1.6 (s) |
| 1975 | 2,250 | None | None | None | None | 22.1 | 2.15 (s, cr) |
| 1976 | 2,350 | None | None | None | None | 22.1 | 1.7 (s, cr) |
| 1977 | 2,100 | July only | July only (heavy) | Light (3/55) | None (May-June) | 22.5 | 2.2 (s) 1.5 (cr) |
| 1978 | 2,700 | Intermittent | Heavy [†] | Moderate | Throughout | ca. 27 | 0.8 (cr) |
| 1979 | 3,300 | May–July | Heavyt | Heavy (20/94) | Throughout | 28.7 | 0.9 (s, cr) |
| 1980 | 3,400 | May-July | Heavyt | Heavy | Throughout | ca. 28 | 0.25 (cr) |
| 1981 | 1,900 | May–July | Heavy [†] | Heavy | Throughout | ca. 29 | 0.001 (cr) |

From Nisbet 1972, 1973, 1978, 1983; Nisbet and Cohen 1975; Nisbet et al. 1978, and unpublished data.

From Nisbet 1972, 1973, 1978, 1983; Nisbet and Cohen 1975; Nisbet et al. 1978, and unpublished data.
⁶ Based on shed feathers, decapitized and dismembered prey, and pellets.
⁶ Based on sightings, footprints, broken eggs and stabbed chicks. One or two herons were shot in each of the years marked (†).
⁹ Mainly Lasius neoniger (see text); figures in parentheses are the number of nests affected in intensively studied plots.
⁶ Based on direct observations during five or more all-night watches.
⁷ For A-eggs only; ca. indicates an estimate based on the interval between the peak of laying and the peak of hatching, rather than a precise sample mean.
⁸ s: precise measurement in sample plot; cr: estimate for whole colony based on capture-recapture analysis of banded chicks; the two estimates differed in 1977 because predation affected only part of the colony.

at two- to three-day intervals until they disappeared, died, or fledged. A blind overlooking the larger plot was used to study behavior and to monitor brood sizes in 64 broods, including a representative number from each laying period. Hatching success was recorded precisely for almost all nests started prior to 1 July. Except for six broods that moved into dense cover and could not be monitored reliably, chick survival was recorded in all of the 92 broods hatched before 30 July. Seventyfour chicks were monitored until they could fly, and eight or nine more were last seen in good condition at ages 7-21 days. These are treated in the analysis as having fledged, since only one other chick was found dead after age seven days. The plots were searched almost daily for broken eggs, carcasses, feathers, footprints and other traces of predation. All-night watches were maintained on 14 nights, at intervals between 27 May and 18 July.

As a result of long-term study, the colony was habituated to human disturbance, and we observed no egg or chick losses attributable to our activities.

The three main periods of laying, in May, June, and July, are designated I, II, and III, respectively. Because about three times as many nests were started in period I as in II or III, we subdivided I into three subperiods, Ia, Ib, and Ic, in which approximately equal numbers of nests were started (see Table 2). The first, second and third eggs in each clutch are designated A, B, and C respectively. Eggs and chicks are assigned to subperiods according to the date of laying of the A-egg in the clutch.

For statistical comparisons between periods and subperiods, we used the Fisher exact probability test or chi-square test for dichotomous variables (clutch size, hatching and fledging success) and analysis of variance for other variables (egg-weight, incubation period, and productivity). To determine levels of statistical significance in the presence of multiple comparisons, the Bonferroni inequality was used for statistical tests on dichotomous variables, and Duncan's multiple range test for other variables (Miller 1966). Generally, we used the nest as the statistical unit, since predators often take more than one egg or chick from a nest.

TABLE 2. Breeding performance of Common Terns according to dates of laying.

| Period | Dates of laying of A-eggs | Ages of banded birds | No. of nests | Mean clutch size ^d | Mean weight of A-egg (g) | Mean incubation period (days) ^e | Hatching success ¹ | Fledging success ¹ | Mean no. chicks fledged/pair ⁽ |
|--------|------------------------------|----------------------------|--------------------|-------------------------------------|-----------------------------|---|----------------------------------|----------------------------------|--|
| Ia | 18-22 May | 8 | 23 | 2.96ª | 21.56 ± .25* | 28.50 ± .36 ^{ab} | 81%ª | 40% ^{ab} | 0.95 ± 0.24^{b} |
| Ib | 23-24 May | 6,4 | 29 | 2.93ª | $21.49 \pm .21^{a}$ | 27.68 ± .45 ^b | 67%ª | 35% ^ь | 0.68 ± 0.22^{b} |
| Ic | 25-29 May | 4 | 25 | 2.76ª | $21.42 \pm .35^{ab}$ | $28.88 \pm .38^{ab}$ | 88%ª | 25% ^{ab} | 0.61 ± 0.16^{b} |
| 11 | 1–25 June | 4, 3 | 24 | 2.71ª | $20.74 \pm .27^{bc}$ | $29.43 \pm .39^{a}$ | 89%ª | 70%ª | 1.73 ± 0.26^{a} |
| III | 1–31 July | 3, 2, 2 | 23 | 2.04 ^b | $20.12 \pm .26^{\circ}$ | no data | (36%) ^g | (25%) ^s | (0.15) ^g |

*** Figures in the same column without a letter in common are significantly different from each other (see Methods for details of statistical tests used). ^a All clutches had either two or three eggs, except for one c/1 in period III. ^c For A-egg only. Incubation periods for B- and C-eggs were shorter by about 0.5 and 1.5 days, respectively (cf. Nisbet and Cohen 1975). ^c For sample sizes see Tables 3 and 4. ^{*} Rough estimates only.

However, in analyzing the effect of weather on chick survival, we used the chick as the statistical unit, since there is little reason (other than similarity of ages) to expect weather-related deaths to be correlated within broods.

RESULTS

Laying took place in three discrete "waves" (Table 2). The main, synchronized wave of laving throughout the colony occurred in period I (18-29 May). A gap of several days then ensued before the second wave of laying in period II (peak 5-15 June). A third wave of laving in July (period III) included three relayings by pairs that had lost broods in June, and three or four unusual second clutches laid by successful pairs. Otherwise, most of the birds laying in July had white or speckled foreheads and appeared to be two or three years old. The mean egg weight and the mean clutch size decreased progressively during the season, paralleling a decrease in the ages of nesting birds (Table 2).

About 20 adult terns and about 40 large chicks were found killed in various parts of the colony between 27 May and 7 August. We did not witness any of the killings, but we suspect that the predator responsible for most of them was a Great Horned Owl (or owls). Fresh Great Horned Owl feathers were found at intervals in different parts of the colony, and most of the prey had been decapitated and dismembered in the manner characteristic of this species (Nisbet 1975). We found no evidence of surplus killing by Great Horned Owls (cf. Southern et al. 1982). In addition to the killing of adults and large chicks, we believe that the owl(s) preved fairly extensively on small chicks, since about 20 small chicks disappeared from our study plots without trace (cf. Nisbet 1975). The only other nocturnal predators seen in the colony were Black-crowned Night-Herons (Nycticorax nycticorax), which hunted on foot and left conspicuous footprints (see below). Short-eared Owls (Asio flammeus) hunted regularly around the colony at dawn and dusk, but their pellets analyzed by us in 1979 contained only mammalian remains. Although adult Common Terns were killed in other parts of the colony, the only adult tern killed in our study plots was a Roseate Tern (Sterna dougallii).

During each of our all-night watches, the adult terns deserted the colony throughout each night, for periods of 6.5 to 8 h. The normal pattern of behavior was for the birds to become restless about 20 min after sunset. As it became dark, groups of 200-400 birds would fly up and sweep silently around the colony, flying within 1–2 m of the ground. Just as it became

too dark to see clearly (typically about 20:45-21:00), all the birds in the colony would rise en masse and disappear silently. Even on the first night we watched (27/28 May), we are confident that the birds became restless and abandoned the colony before the arrival of a Great Horned Owl. Short-eared Owls and Black-crowned Night-Herons approached the colony on some evenings, but were mobbed vigorously and did not appear to be the primary cause of the terns' restlessness and departure. On most nights the colony remained deserted until dawn, but on some nights small numbers of terns remained or returned and could be seen incubating near our blind. On one night when a thin layer of clouds was illuminated by the moon, P. Trull saw groups of terns flying very high over the colony. The terns returned en masse at first light (typically between 03:45 and 04:15) and settled noisily on their nests. At this time there was often much confusion and fighting, as many birds landed in the wrong territories in the dim light and some even sat briefly on the wrong nests.

Presumably as a consequence of the nocturnal desertion, incubation periods were increased from the usual 21–23 days to 27–31 days (cf. Nisbet 1975, Nisbet and Cohen 1975). The mean incubation period was slightly longer for eggs laid in period II (29.43 \pm 0.39 days) than in period I (28.40 \pm 0.23 days; t = 2.28, P < 0.02), but we obtained no direct evidence to associate this change with different patterns of desertion.

Between 4 and 14 June we found footprints and evidence of egg predation by an adult Black-crowned Night-Heron in various parts of the colony. During three all-night watches at this period, we saw and heard the heron in the colony only for brief periods (up to about 20 min) between 21:45 (after the terns had left) and 02:00. Egg losses in the study plots were attributed to the heron when its footprints were found near nests in which there were broken or missing eggs, or fragments of eggshell. The heron was shot on 14 June, and we found no further evidence of predation until 5 July, although herons could occasionally be seen and heard outside the colony and they fed in the nearby salt-marshes. After 5 July, one or more herons were active in the colony and took a number of eggs and chicks from various areas, including the plots.

Productivity (chicks fledged per pair) was highest from nests started in period II (Table 2). Productivity was significantly lower in subperiods Ib and Ic (P < 0.01) and in subperiod Ia (P < 0.05, Duncan's multiple range test). The difference was primarily due to low chick survival in period I (30/71 successful broods

| TABLE 3. | Causes of | egg | losses. |
|----------|-----------|-----|---------|
|----------|-----------|-----|---------|

| | Laying period | | | | |
|----------------------------------|-----------------------|-------------|-------------|-------------|--|
| | Ia | Ib | Ic | II | |
| No. of nests/eggs checked: | 23/68 | 29/85 | 25/69 | 17/47 | |
| Crushed, broken or pecked | 2/5 (7%) ^a | 4/6 (7%) | 0 | 0 | |
| Disappeared | 2/2 (3%) | 6/11 (13%) | 1/1 (1%) | 0 | |
| Deserted | 0 | 4/6 (7%) | 0 | 0 | |
| Incubated fully, failed to hatch | 4/4 (6%) | 4/5 (6%) | 2/2 (3%) | 4/5 (11%) | |
| Died after pipping | 2/2 (3%) | Ò | 5/5 (7%) | 0 | |
| Hatched | 21/55 (81%) | 21/57 (67%) | 25/61 (88%) | 16/42 (89%) | |

* The figures given for each category are the number of clutches/number of eggs, with the percentage of eggs in parentheses. For statistical analysis, see Table 2 and the text. Data for period III were incomplete.

vs. 12/15 in period II, $\chi^2_1 = 5.63$, P < 0.02). Hatching success was also lower in period I, but not significantly so when compared on a nest-by-nest basis. Hatching and fledging success in period III were not measured precisely, but both were very low: only four or five unfledged chicks (6–10 days old) were seen on the last visit on 7 August, and their subsequent survival is conjectural.

We classified observed hatching failures into five categories (Table 3). Eleven eggs were found crushed, broken, or pecked, and 14 disappeared. These categories are not clearly separated, because Common Terns usually remove broken eggs from the nest within a few hours. Three other eggs were deserted after two eggs in each clutch had been broken or taken. Another clutch of three eggs was deserted, probably after the embryos had died. Including these 3 eggs, 19 eggs (7%) were incubated to term but failed to hatch. This is outside the range (1-5%) of hatching failures at this colony in years without nocturnal desertion, but is surprisingly low in view of the nocturnal desertion and cold nights in late May and late June. Seven embryos died after pipping; in at least five cases they were killed by ants (Lasius *neoniger*) that entered the egg through the piphole.

The only significant seasonal pattern in egg losses was that broken and disappeared eggs were more frequent in period I than in period II (14/77 vs. 0/17 nests with losses in one or both of these categories; P = 0.048, Fisher exact test). Such losses were significantly more frequent in subperiod Ib than in period II (9/29 vs. 0/17, P = 0.027), but the other differences between subperiods were not significant. Almost all these losses occurred between 27 May and 14 June. About 11 eggs were taken or broken by the Black-crowned Night-Heron. Of the remainder, two entire clutches (five eggs) were found crushed in the nest, and three single eggs were found with peck holes on both sides that fitted a Common Tern's bill.

Losses to ants were recorded only for eggs laid in period I, conforming to the pattern of ant predation on chicks (see Table 4). There was no significant seasonal pattern in hatching failures.

Of five categories of chick losses (Table 4), the most important cause of loss was a series of cold nights between 23 and 29 June, when the temperature frequently fell to 5–11°C and many unbrooded chicks apparently died of exposure. This mortality fell most heavily on chicks from subperiods Ib and Ic, which were hatching at this time; most chicks from subperiod Ia were then three or more days old, and chicks from period II had not yet hatched. The incidences of death from exposure in subperiods Ib and Ic did not differ significantly

| | Laying period | | | | |
|-------------------------------------|-------------------------|-------------|-------------|-------------|--|
| | Ia | Ib | Ic | Ш | |
| No. of broods/chicks followed: | 20/47 | 28/54 | 23/55 | 15/37 | |
| Killed by ants | 8/16 (35%) ^a | 2/3 (6%) | 3/6 (11%) | 1/3 (8%) | |
| Died on cold nights, 23–29 June | 3/4 (8%) | 7/13 (24%) | 15/23 (42%) | 0 | |
| Died on other dates | 1/1 (2%) | 4/4 (7%) | 3/4 (7%) | 1/1 (3%) | |
| Missing (mostly taken by predators) | 2/4 (8%) | 6/12 (22%) | 5/7 (13%) | 2/3 (8%) | |
| Not determined | 2/3 (6%) | 3/3 (6%) | 1/1 (2%) | 4/4 (11%) | |
| Fledged | 9/19 (40%) | 11/19 (35%) | 10/14 (25%) | 12/26 (70%) | |

TABLE 4. Causes of chick losses.

* The figures given for each category are the number of broods/number of chicks, with the percentage of chicks in parentheses. For statistical analysis, see Table 2 and the text. Data for period III were incomplete.

 $(\chi^{2}_{1} = 3.12, P > 0.05)$, but each was significantly greater than that for period II (P < 0.01 and P < 0.00001, respectively, Fisher exact tests with Bonferroni correction); the incidence in subperiod Ia was significantly smaller than that for subperiod Ic ($\chi^{2}_{1} = 12.78, P < 0.01$), but not significantly different from those for subperiod Ib or period II (P > 0.1).

The other major cause of death was ants, which either killed newly hatched chicks or blinded them so that they were unable to take food. This mortality fell significantly more heavily on broods from subperiod Ia than from subperiod II (P < 0.05, Fisher exact test with Bonferroni correction), but the other differences between periods and subperiods were not significant (P > 0.1).

The chicks classified as "missing" were probably taken by predators, since searches were thorough enough for most carcasses to have been found. The three "missing" chicks from period II disappeared in early July from territories in which fresh Black-crowned Night-Heron tracks were found. Eighteen of the 23 chicks "missing" from period I disappeared in twos and threes from their nests when they were zero to three days old-ages at which dead chicks can usually be found near the nest. This pattern of disappearance is characteristic of predation by Great Horned Owls (Nisbet 1975). The frequency of this type of disappearance was greatest in subperiod Ib, but the differences were not statistically significant.

The other two categories in Table 4 showed no seasonal pattern. Only 10 chicks were found dead outside the cold period 23–29 June. "Not determined" refers to chicks that disappeared singly after the age of three days, or from peripheral broods that were not checked intensively. Some of these chicks may have died in cover, while others may have been taken by predators, and a few may have survived and escaped our searches.

Although many broods suffered unusually heavy early losses from predation, ants, and exposure, survival after the first few days was exceptionally good. Among 15 pairs that hatched three chicks and raised them to age three days, 9 pairs raised all three to fledging. These included three of nine such pairs from period II, including one pair in which the male was known to have been only four years old. In other years, usually only early-nesting pairs raise three chicks, and four-year-old birds usually raise only one, or at most two. Thus, 1979 appears to have been an exceptionally favorable year for raising chicks, at least as good as the exceptional season of 1975 (Nisbet et al. 1978).

DISCUSSION

The principal causes of egg and chick losses (Tables 3 and 4) were the following:

1. Exposure during cold nights (40 newly hatched chicks).

2. Attack by ants (5 pipped eggs, 28 newly hatched chicks).

3. Predation by Great Horned Owl(s) (about 20 newly hatched chicks).

4. Hatching failure (19 eggs, about 11 more than the average rate in years without predation).

5. Breakage (about 13 eggs, plus 3 consequently deserted).

6. Predation by Black-crowned Night-Herons (about 12 eggs, 3 chicks).

7. Unknown (10 chicks).

Although direct predation by the Great Horned Owl accounted for only about 13% of these losses, we believe that each of the other five types of loss was caused by or enhanced by the owl's activity. First, the nocturnal desertion appears to have been a response to predation by the owl. At Monomov, nocturnal desertion and lengthened incubation periods have occurred only in association with other evidence of predation by Great Horned Owls (Table 1). The same association has been found at other colonies (Nisbet and Cohen 1975). In the absence of predation, even the earliest-laying Common Terns have incubation periods of about 21-22 days (Nisbet and Cohen 1975 and unpubl. data), indicating that they incubate at night from the start. At Monomov in 1979, the birds were already deserting by 27 May, after the first Great Horned Owl kills had been found, but before we found evidence of predation by herons. Short-eared Owls were seen hunting around the colony in 1975–1977, when there was no evidence of nocturnal desertion (Table 1).

In the absence of nocturnal desertion, few chicks die during their first two days of life: even the youngest chicks in the brood usually survive to days two to five (Nisbet 1978). The heavy mortality of chicks at ages zero to two days during cold nights in 1979 therefore can be attributed to nocturnal desertion. The unusually high rate of hatching failure is also probably attributable to nocturnal desertion: a similar high rate (12%) was noted at Yarmouth in similar circumstances in 1973 (Nisbet 1975).

Mortality of tern chicks resulting from attacks by ants has been reported by several authors (Mackay 1895; Floyd 1925, 1930; O. L. Austin, unpubl.; Austin, Jr., 1929, 1932; Nisbet 1972; Gochfeld 1976; Sibley and Spendelow 1978; Spendelow 1982). Most reported cases coincided with predation by Great Horned Owls (Floyd 1925, 1930; O. L. Austin, unpubl.; Austin, Jr., 1932; Nisbet 1972) or Short-eared Owls (Mackay 1897, Gochfeld 1976). At Monomoy, a few chicks are killed by ants in most years, but substantial losses have occurred only in years with owl predation and extensive nocturnal desertion (Table 1). Mortality caused by ants is also frequent in three other colonies in Massachusetts that are subject to predation by owls (Nisbet 1972, unpubl. observ.). We suspect, therefore, that brooding adults are generally able to keep ants out of their pipping eggs, but that nocturnal desertion allows the ants access to the eggs for long enough to kill or blind the chicks.

Lasius neoniger is an ant species commonly inhabiting sand dune habitats, where it forages primarily at night (Talbot 1946, Wilson 1955). These ants are most active during May and June when they need the most food for rearing broods. This coincides with the hatching of tern chicks from period Ia, which suffered the most ant-induced mortality. Although L. neoniger forages on open sand, its colonies are always associated with vegetation (Talbot 1946) and thus tend to occur in the areas chosen by early-nesting terns. At Monomoy in 1979, chicks from subperiods Ib and Ic probably escaped heavier attacks because they hatched in a spell of cold nights when the ants would have been less active; chicks from subperiods Ic and II probably suffered less because they were situated on open sand, where there were fewer ant colonies.

The rate of egg breakage at Monomoy was much higher in 1979 than in years without predation, when it never exceeded 1%. Although we did not observe how eggs were broken, we suspect that most were broken by the terns themselves. Some eggs had peck-holes that fitted a tern's bill, while others were crushed in nests where there were no heron footprints or other signs of predation. A similar pattern of egg breakage has been noted at other Massachusetts tern colonies in association with predation by Great Horned Owls (P. Trull, pers. comm.). Eggs are most likely to be broken when the terns leave the colony abruptly in the late evenings, and during their confused return in the early mornings. Breakage was not a consequence of direct alarm responses to predators, since the birds left the colony before the predators arrived, and returned after they left. Palmer (1941) described Common Terns breaking eggs during abrupt departures and in fights, but we have rarely seen eggs broken during normal daytime activity.

Black-crowned Night-Herons have been reported as predators of tern eggs and chicks by several authors (Palmer 1941, Collins 1970, Hays 1970, LeCroy and Collins 1972, Nisbet and Drury 1972, Hunter and Morris 1976, Duffy 1977). At Monomoy, conspicuous losses have occurred only in coincidence with owl predation (Table 1). Black-crowned Night-Herons apparently can take some chicks without assistance from owls, but they are attacked vigorously when they do so. Nocturnal desertion allows easy access to the colony and seems to encourage the herons to continue killing chicks after they are satiated. In July 1979, about 15 large chicks (15-25 days old) were found wounded or killed and left uneaten by the herons.

Five of the six identified causes of egg and chick loss listed above were more frequent early in the season (Table 3 and 4):

1. Deaths from exposure during cold nights were limited to the period 23–29 June, and hence affected newly hatched chicks primarily from subperiods Ib and Ic.

2. Attacks by ants primarily affected eggs and chicks from subperiod Ia. As stated above, we believe that chicks hatched later suffered less mortality either because they were on open sand, or because they hatched during a cold spell.

3. Predation by the Great Horned Owl apparently fell mainly on newly hatched chicks, and was heavier (although not significantly so) early in the season. The same pattern was observed in 1973 and probably reflected the fact that the chicks were both few and small early in the season, so that a large fraction of the available prey was needed to satisfy the owl's demands. Later in the season the chicks were more numerous and larger, so that the owl's food demands were "saturated" (Nisbet 1975).

4. Hatching failures followed no significant seasonal pattern.

5. Breakage and disappearance of eggs were almost limited to subperiods Ia and Ib. Although it is not clear why this should be, a possible explanation is that the terns became habituated to the pattern of nocturnal desertion and early morning return.

6. Predation by the Black-crowned Night-Herons fell primarily on eggs from subperiods Ia and Ib, because the first heron was shot on 14 June. But for this, heron predation would probably have continued through the season, as occurred in 1978 and 1980. In those years, heron predation also fell heavily on late nesters, because two or three herons were active in July.

In summary, nocturnal desertion appears to be a behavioral response to predation by Great Horned Owls. Although effective in minimizing predation on adults, it leaves the eggs and chicks vulnerable to other causes of loss. In 1979, both direct and indirect effects of owl predation at Monomoy fell more heavily on terns that laid in May than on those that laid in June. The same temporal pattern was noted for direct predation at Yarmouth in 1973 (Nisbet 1975). However, in 1973 the most successful terns were those laying around the median date for the colony, whereas in 1979 the most successful terns laid after the median date. The difference was due primarily to the late spell of cold weather in 1979.

The early part of the season appears to be the preferred period for nesting by Common Terns. Older birds lay consistently earlier than younger birds (Nisbet 1983). The earliest nesters lay the largest clutches (Table 2) and the largest eggs (Nisbet and Cohen 1975, Nisbet 1978), and in the absence of predation they are consistently the most successful (Nisbet et al. 1978). Thus, some factors must act strongly to favor early nesting, offsetting the periodic losses caused by predation and bad weather. The timing and synchrony of nesting are presumably set by balancing these factors against those such as experience that permit older birds to lay early (Perrins 1970). Because predation and bad weather strike irregularly (Table 1), long-term studies are needed to elucidate these interactions.

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LITERATURE CITED

- ASHMOLE, N. P. 1963. The biology of the Wideawake or Sooty Tern Sterna fuscata. Ibis 103b:297-364.
- AUSTIN, O. L. Unpublished notebooks, 1927–1957. Massachusetts Audubon Society, Lincoln, MA.
- AUSTIN, O. L. 1948. Predation by the Common Rat (*Rattus norvegicus*) in the Cape Cod colonies of nesting terns. Bird-Banding 19:60–65.
- AUSTIN, O. L., JR. 1929. Contributions to the knowledge of the Cape Cod Sterninae. Bull. N.E. Bird-Banding Assoc. 5:123-140.
- AUSTIN, O. L., JR. 1932. Further contributions to the knowledge of the Cape Cod Sterninae. Bird-Banding 3:123-139.
- Collins, C. T. 1970. The Black-crowned Night Heron as a predator of tern chicks. Auk 88:584–586.
- DUFFY, D. C. 1977. Breeding populations of terns and skimmers on Long Island Sound and eastern Long Island: 1972–1975. Proc. Linn. Soc. N.Y. 73:1–48.
- FLOYD, C. B. 1925. Six days in a Massachusetts tern colony. Bull. N.E. Bird-Banding Assoc. 1:58-60.
- FLOYD, C. B. 1930. Further banding notes from Tern Island, Massachusetts. Bird-Banding 1:181-184.
- GOCHFELD, M. 1976. Waterbird colonies of Long Island,

New York. 3. Cedar Beach ternery. Kingbird 26:62-80.

- HATCH, J. J. 1970. Predation and piracy by gulls at a ternery in Maine. Auk 87:244-254.
- HAYS, H. 1970. Great Gull Island report on nesting species 1967–68. Proc. Linn. Soc. N.Y. 71:105–118.
- HAYS, H., AND M. LECROY. 1971. Field criteria for determining incubation stage in eggs of the Common Tern. Wilson Bull. 83:425-429.
- HUNTER, R. A., AND R. D. MORRIS. 1976. Nocturnal predation by a Black-crowned Night Heron at a Common Tern colony. Auk 93:629–633.
- KRUUK, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus* L.). Behaviour Suppl. 11:1–130.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- LECROY, M., AND C. T. COLLINS. 1972. Growth and survival of Roseate and Common tern chicks. Auk 89:595–611.
- MACKAY, G. H. 1895. The terns of Muskeget Island, Massachusetts. Auk 12:32-48, 178.
- MACKAY, G. H. 1897. The terns of Muskeget Island, Massachusetts. Part III. Auk 14:383-390.
- MILLER, R. G., JR. 1966. Simultaneous statistical inference. McGraw-Hill, New York.
- NISBET, I. C. T. 1972. Disaster year for terns. Man and nature, Massachusetts Audubon Society Bulletin, Dec. 1972:16-21.
- NISBET, I. C. T. 1973. Terns in Massachusetts: present numbers and historical changes. Bird-Banding 44:27– 55.
- NISBET, I. C.T. 1975. Selective effects of predation in a tern colony. Condor 77:221-226.
- NISBET, I. C. T. 1978. Dependence of fledging success on egg-size, egg composition and parental performance in Common and Roseate terns, *Sterna hirundo* and *S. dougallii*. Ibis 120:207–215.
- NISBET, I. C. T. 1983. Paralytic shellfish poisoning: effects on breeding terns. Condor 85:338-345.
- NISBET, I. C. T., AND M. E. COHEN. 1975. Asynchronous hatching in Common and Roseate terns, *Sterna hirundo* and *S. dougallii*. Ibis 117:374–379.
- NISBET, I. C. T., AND W. H. DRURY. 1972. Measuring breeding success in Common and Roseate terns. Bird-Banding 43:97–106.
- NISBET, I. C. T., K. J. WILSON, AND W. A. BROAD. 1978. Common Terns raise young after death of their mates. Condor 80:106–109.
- PALMER, R. S. 1941. A behavior study of the Common Tern (*Sterna hirundo* L.). Proc. Boston Soc. Nat. Hist. 42:1-119.
- PARSONS, J. 1971. Cannibalism in Herring Gulls. Br. Birds 64:528-537.
- PATTERSON, I. J. 1965. Timing and spacing of broods in the Black-headed Gull Larus ridibundus. Ibis 107: 433-459.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. Ibis 112:242–255.
- RAHN, H., C. V. PAGANELLI, I. C. T. NISBET, AND G. C. WHITTOW. 1976. Regulation of incubation waterloss in seven species of terns. Physiol. Zool. 49:245– 259.
- SIBLEY, F. C., AND J. A. SPENDELOW. 1978. Falkner's Island tern project—1978. Unpubl. rep., Peabody Museum, Yale Univ., New Haven, CT.
- SOUTHERN, L. K., S. R. PATTON, AND W. E. SOUTHERN. 1982. Nocturnal predation on *Larus* gulls. Colonial Waterbirds 5:169–172.
- SPENDELOW, J. A. 1982. An analysis of temporal variation and the effects of habitat modification on reproductive success of Roseate Terns. Colonial Waterbirds 5:19-31.

- TALBOT, M. 1946. Daily fluctuations in above ground activity of three species of ants. Ecology 27:65-70.
- TINBERGEN, N. 1967. Adaptive features of the Blackheaded Gull Larus ridibundus L. Proc. XIV Int. Ornithol. Congr. (1966):43–59.
- WILSON, E. O. 1955. A monographic revision of the ant genus Lasius. Bull. Mus. Comp. Zool. 113:1–199.

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RECENT PUBLICATIONS

Ontario Birds .- This new journal, published by the Ontario Field Ornithologists, is intended to provide an outlet for the documentation of the birds of Ontario. The contents of the first issue (April 1983) exemplify the kinds of material desired: "full length articles or short notes on the status of bird species in Ontario, significant provincial or county distributional records, tips on bird identification, behavioral observations of birds in Ontario, location guides to significant birdwatching areas in Ontario, book reviews and similar material of interest on Ontario birds. We do not accept submissions dealing with 'listing' and we discourage Seasonal Reports of bird sightings." Items for publication should be sent to the Editors, % O.F.O., Box 1204, Station B, Burlington, Ont. L7P 3S9. Annual membership in the O.F.O. costs \$10.00 and should be sent to the same address.

Birding in Ohio.—Tom Thomson. 1983. Indiana University Press, Bloomington. 256 p. \$15.00. This book provides a guide to good birding places in Ohio and an annotated list of the State's birds. Over 200 sites are described with directions and maps for finding them. They are grouped according to region: the northern counties, the west-central counties, and the unglaciated southern and eastern counties. These descriptions tell the best season(s) for visiting, and the birds to be expected. The check-list follows the latest AOU list and is the first statewide review of Ohio's birds in many years. The entries briefly give seasonal and geographic status, a few notable records, and—in a vague and somewhat confusing manner—the average periods of migration or residence. The book will certainly be useful to Ohio birders, yet if a revised edition

is planned, one hopes that it will include an overview of the State's topography, climate, vegetation, and habitats, as well as more details and documentation in the species accounts. List of local nature clubs and birding hotlines; references; index.

Birds of the Netherlands Antilles.-K. H. Voous. 1983. De Walburg Pers [Zutphen, Netherlands]. 327 p. Source: De Walburg Pers, Postbus 222, 7200 AE Zutphen, Netherlands. The territory of the Netherlands Antilles consists of two groups of islands: one (Aruba, Curaçao, and Bonaire) off the coast of Venezuela, and the other (St. Martin, Saba, and St. Eustatius) some 900 km to the northeast, and 250 km east of Puerto Rico. Their birdlife (a total of 252 known species) is described in this admirable little handbook, based on the author's 1955 Dutch edition. In view of the marked faunistic differences between the two groups of islands (predominantly South American vs. West Indian), the book is divided into two parts. Each opens with a brief account of the island habitats and general features of their birdlife. The species accounts which follow treat the appearance, occurrence, habits, food, breeding, voice, and distribution, often in considerable detail. For species that occur in the northern as well as the southern islands, the northern accounts are confined to a summary of local records and breeding data, if any. Color plates by H. J. Slijper show more than half of the species, depicting the plumage or race seen in the islands. The book is not merely a field guide to the birds of its region, but also a good source of information about the natural history of species that breed there. References, indexes, and endpaper maps.