COMPARATIVE BREEDING BIOLOGY OF THE SANDWICH TERN

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PREVIOUS studies on the biology of the Sandwich Tern (*Thalasseus sandvicensis*) include those of Dircksen (1932), a brief comparative account by Cullen (1960a), and a general account by Marples and Marples (1934). Some aspects of its breeding behavior have been described by Desselberger (1929), Steinbacher (1931), Assem (1954a, 1954b), and Cullen (1960b). None of these accounts records breeding success or gives details of factors influencing it in this species. In the present study, the Sandwich Tern's breeding biology was examined in conjunction with simultaneous studies on the Roseate Tern (*Sterna dougallii*), Common Tern (*S. hirundo*), and Arctic Tern (*S. paradisaea*).

THE STUDY AREA

The study area was on Coquet Island, Northumberland, England, 55° 38′ N, 1° 37′ W, about 32 km south-southeast of the Farne Islands, the next nearest breeding station for the four species of terns mentioned above.

Coquet Island is a low island about 1.6 ha in area, rising only some 10 m above sea level and mostly covered with vegetation. It is composed of sandstone and has been eroded so that extensive shelves of rock are exposed at low tide. The island itself has steep edges with an almost flat top. The lighthouse grounds occupy 1,000 m^2, and tracts of stinging nettles (*Urtica dioica*) not occupied by terns comprise a further 2,500 m^2. This leaves about 12,750 m^2 available to the terns.

Historical records around 1830 (Marples and Marples 1934) refer to the occurrence of all four species of tern on Coquet Island. The construction of the lighthouse buildings in 1834, with cultivation of the island, and the introduction of domestic animals, evidently disturbed the terns breeding there and led to their disappearance about 1882 (Marples and Marples 1934). Although the Eider (*Somateria mollissima*) probably continued to nest, it was not until 1958 that two pairs of Common Terns began to breed again (Coulson, pers. comm.). Subsequently other tern species returned and the nesting pairs on the island during the study period are recorded in Table 1. Several other species nest on the island, of which the Black-headed Gull (*Larus ridibundus*) has increased rapidly and is associated with the Sandwich Tern. In 1967 a pair of Herring Gulls (*Larus argentatus*) and two pairs of Lesser Black-backed Gulls (*L. fuscus*) nested on the island.

NEST SITES

Sandwich Terns either nested among other tern species or in close proximity to Black-headed Gulls, choosing level ground where high nesting densities were possible. Usually the nesting birds were two "beak

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TABLE 1

NUMBERS OF PAIRS OF TERNS AND GULLS BREEDING ON COQUET ISLAND

Species	1965	1966	1967
Sandwich Tern	313	797	ca. 1,750
Roseate Tern	85	179	102
Common Tern	ca. 1,200	ca. 1,000	1,212
Arctic Tern	ca. 500	ca. 500	560
Black-headed Gull	10	57	68

stretches" apart (Steinbacher 1931). The density of nests within a subcolony of 19 pairs of Sandwich Terns was 2.1/m^2.

In contrast the Roseate Tern usually preferred to nest under cover as noted by Bent (1921) and Marples and Marples (1934). In the Bahamas and West Indies however, this species seems "to nest in open situations with Cabot's [Sandwich] and Sooty Terns [*S. fuscata*], laying their eggs in hollows in the sand, on bare ground, or on rocks without any attempt at concealment" (Bent 1921). On Coquet Island in 1965, 33 Roseates nested in burrows, 22 under sheep's sorrel (*Rumex acetosa*), 15 in hollows, 14 among rocks, and 1 under stinging nettles. In 1966 a higher proportion nested under rocks on the shore, where none nested in 1967, probably because of an increase in the number of Black-headed Gulls nesting there. Roseate Terns nested in loose groups, the density of nests in one group of 20 pairs being 0.4/m^2.

Boecker (1967) discussed the height and density of vegetation in which Arctic and Common Terns nested on Wangerooge, Germany. I found a similar situation on Coquet Island where the Common Tern was restricted almost entirely to areas dominated by sheep's sorrel, apart from a few nests in Yorkshire fog grass (*Holcus lanatus*). The distribution of these two plants determined the distribution of the Common Tern nests. Both plants grew rapidly from the start of nesting and reached a height of 50–80 cm, providing adequate cover for the chicks from predators and inclement weather. In contrast the Arctic Tern nested either among the rocks and shingle on the east shore or in areas of sheep's fescue (*Festuca ovina*) grazed to a few centimeters by the large rabbit population. A study area containing 175 nests had an average density of 0.02/m^2, but densities were locally much higher where the ground was littered with debris. The average density of Common Tern nests in the study area ranged from 0.06 to 0.13/m^2 in different years. The density of nests is inversely correlated with the pugnacity of the four species. The Arctic, Common, Roseate, and Sandwich Terns represent a series with decreasing aggressive behavior, and this in turn is correlated with a decrease in reliance on camouflage for protection of the nest's contents (Cullen 1960a).

TABLE 2
DATES OF FIRST ARRIVAL AND FIRST LAYING ON COQUET ISLAND IN 1965 AND 1966

	1965			1966			
Species	Arrival	Laying	Diff. (days)	Arrival	Laying	Diff. (days)	Av. difference
Sandwich Tern	9 May	11 May	2	9 May	13 May	4	3
Roseate Tern	13 May	(29 May)	ca. 16	13 May	9 June	27	ca. 21
Common Tern	8 May	22 May	14	9 May	27 May	18	16
Arctic Tern	8 May	24 May	16	19 May	29 May	10	13

OCCUPATION AND SPECIES ASSOCIATION

Table 2 shows the dates of first arrival of each species of tern on the island and the dates of first laying for 1965 and 1966. The Black-headed Gulls set up their territories on the island in early April and began laying at the end of the month. The numbers of this gull increased rapidly over the period of this study and appeared to influence the nesting distribution of the Sandwich Tern, the first tern to lay. Association between these two species is very common, although where Black-headed Gulls are absent the Sandwich Tern nests successfully among other tern species.

The dense nesting habit of the Sandwich Tern is associated with a reduction in aggression, but by nesting close to Black-headed Gull nests, it can benefit from the gull's pugnacity against aerial predators such as Carrion Crows (*Corvus corone*) (Assem 1954a, Cullen 1960a, Lind 1963, Croze 1970). Sandwich Terns nesting among Common or Arctic Terns also benefit from the greater aggressiveness of these two species towards predators. Although Sandwich Terns are reported to suffer fewer depredations when nesting among Black-headed Gulls than when associated with other tern species, some disadvantages result from their association with the gulls, such as egg and chick predation and food parasitism (Assem 1954b, Roth 1958, Lind 1963). These disadvantages are usually slight, and only when a large number of gulls are associated with a small colony of Sandwich Terns can food parasitism become serious. This situation apparently caused the failure of the Sandwich Tern colony on Havergate Island, Suffolk (Olney, pers. comm.). Predation was never important on Coquet Island, and food parasitism was obvious only in 1967.

The first Common and Arctic Terns arrived on the island about the same time as the Sandwich Terns, which made the aggressiveness of the Black-headed Gulls superfluous. Had ground predators been present, the Black-headed Gulls may have been of greater survival value to the terns. Neither the Common or Arctic Tern was influenced by the loca-

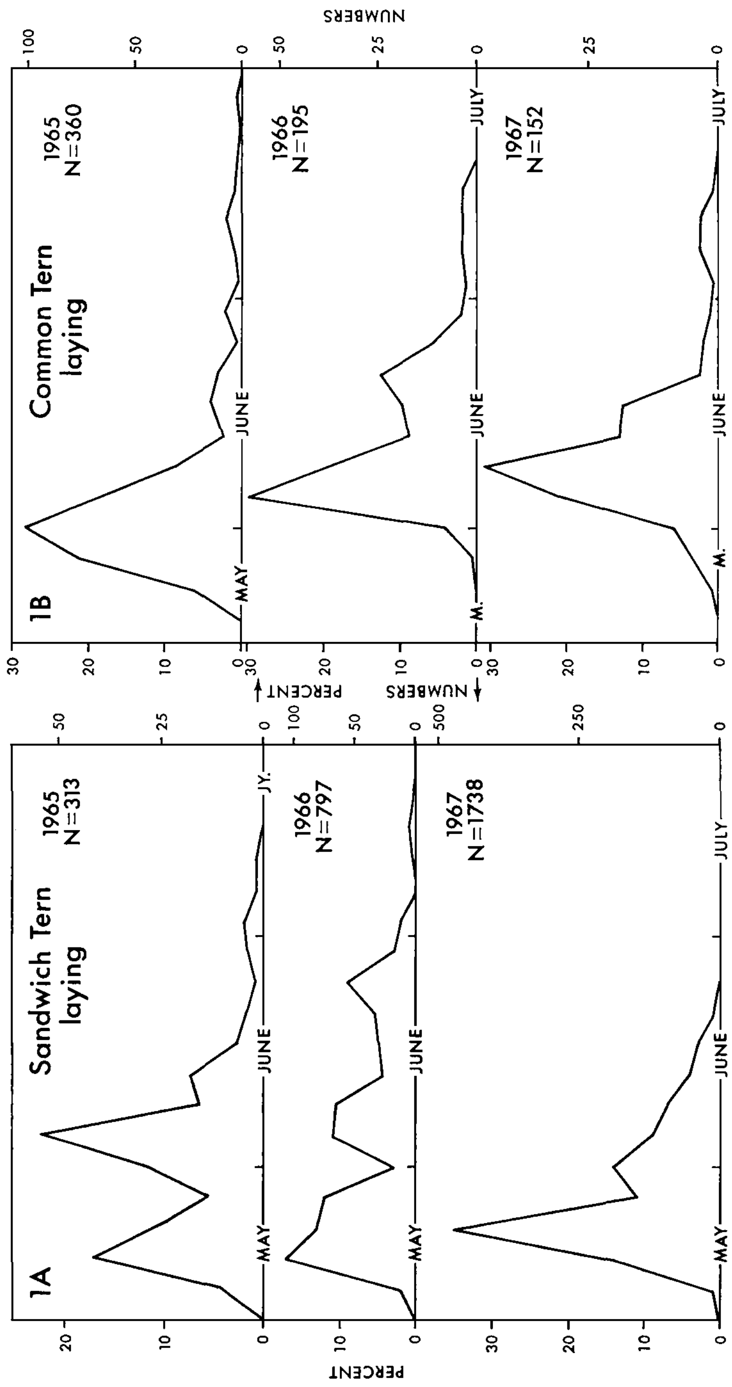

Figure 1. Laying of first eggs in 1965, 1966, and 1967. A, Sandwich Tern; B, Common Tern; C, Arctic Tern; and D, Roseate Tern.

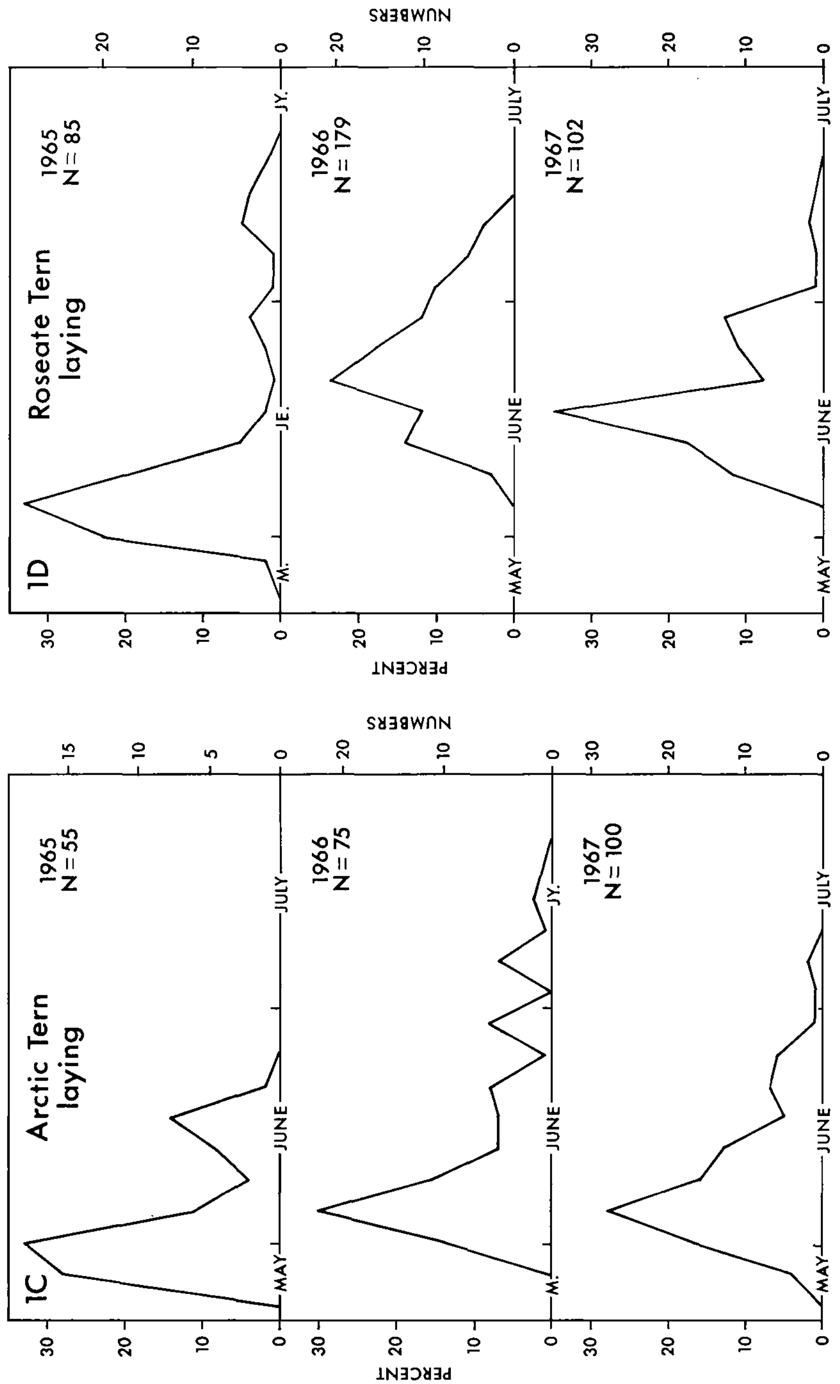
1C
Arctic Tern
laying
1965
N = 55
1966
N = 75
1967
N = 100
1D
Roseate Tern
laying
1965
N = 85
1966
N = 179
1967
N = 102
PERCENT
NUMBERS
MAY
JUNE
JULY
M.
JE.
JY.

TABLE 3
DURATION OF LAYING BETWEEN 5–95% IN FOUR TERNS OVER 3 YEARS

Species, year	5% started	Diff. (days)	50% started	Diff. (days)	95% started	Duration (days)	Average duration (days)
Sandwich Tern							
1965	16 May	15	31 May	27	27 June	42	
1966	17 May	15	1 June	27	28 June	42	36.7
1967	17 May	6	23 May	20	12 June	26	
Roseate Tern							
1965	29 May	6	4 June	34	8 July	40	
1966	10 June	16	26 June	10	6 July	26	29.0
1967	7 June	8	15 June	13	28 June	21	
Common Tern							
1965	23 May	8	31 May	30	30 June	38	
1966	1 June	6	7 June	29	6 July	35	36.3
1967	30 May	8	7 June	28	5 July	36	
Arctic Tern							
1965	25 May	5	30 May	17	16 June	22	
1966	29 May	8	6 June	31	7 July	39	28.3
1967	29 May	7	5 June	17	22 June	24	

tion of Black-headed Gulls or Sandwich Terns, but they set up territories in their respective vegetation types described above.

The Roseate Terns appeared on the island on 13 May in both years soon after the first Common Terns, but did not start to lay until much later. Many of the Roseate Terns nested close to Sandwich Terns or among Common and Arctic Terns, but often these associations were unavoidable in such a restricted area.

LAYING

In 1965 and 1966 the Sandwich Terns began laying on 11 and 13 May respectively, but the first few eggs laid were deserted almost immediately. During this period, mounting and copulation took place on the tidal rocks, and circling upflights were accompanied by a characteristic noisy "chatter" as the birds resettled on the island. In 1965 it was not until 16 May that two definite centers of laying (subcolonies) were established near Black-headed Gulls nests and the eggs consistently incubated. Prior to this incubating birds appeared to leave the island at night and return to their eggs in the morning, as recorded for the Caspian Tern (*Hydroprogne caspia*) (Bergman 1953). The seasonal pattern of laying was very different in the 3 years (Figure 1A).

The Common Tern showed a similar pattern of laying in all 3 years (Figure 1B), except for a suggestion of a second peak in 1966 caused by relaying after a large scale desertion of early clutches. This deser-

TABLE 4
AVERAGE TOTAL DURATION OF LAYING IN SUBCOLONIES AND TOTAL COLONY FOR THE SANDWICH TERN

	1965		1966		1967	
	Sub-colony	Colony	Sub-colony	Colony	Sub-colony	Colony
Number of days duration	18.0	57	18.3	67	21.2	42
Average number of nests	29.4	294	56.9	797	94.8	1,706

tion may have been caused by the shortage of fish at that time as shown by fecal analysis and general observations of the colony. The laying curves of the Arctic Tern were variable, but all had a single marked peak with a second peak only in 1965 (Figure 1C). The laying season was much shorter than in the Common Tern except in 1966. The Roseate Tern showed a single peak in all 3 years (Figure 1D). In all species except the Sandwich Tern, laying began earlier in 1965 and latest in 1966.

The Sandwich Tern showed least variation in the date of laying in successive years and the Roseate Tern most variation. The annual variation in the spread or duration of laying was similar in the Sandwich, Roseate, and Arctic Terns (16, 19, and 17 days respectively (Table 3); but was only 3 days in the Common Tern.

SYNCHRONIZED LAYING

The Sandwich Tern nested in subcolonies, i.e. dense groups of nests spatially separated from one another, as did the Roseate Tern to a lesser extent where the density of nest sites permitted. Large subcolonies of the Sandwich Tern could be subdivided further according to laying dates, which form geographical units within the subcolony. Rather than join an existing subcolony, some birds starting to nest formed a new subcolony. The reason for this is not clear, but probably a difference in the reproductive cycle of the two groups was partly responsible.

The Sandwich Terns are paired before they enter the colony and pairs began laying within 2 or 3 days once a nest site was selected. Copulation occurred on the tidal rocks or at the perimeter of the colony, but rarely among the incubating birds in the dense subcolonies. The length of the laying period for the whole colony may vary by as much as 25 days from year to year. The average duration of laying within a subcolony varies relatively little irrespective of size, suggesting there is a limit to the growth of a subcolony determined by the difference in breeding cycle (Table 4). Although some large sub-

TABLE 5
TOTAL TIME (DAYS) SPENT WITHIN THE NEST VICINITY

Species	Prelaying	Laying	Incubation	Post-hatching	Total
Sandwich Tern	4	18	25	5	52
Roseate Tern	20	24	22	5	71
Common Tern	15	39	22	20	96
Arctic Tern	10	35	22	20	87

colonies had long laying periods, no correlation occurred between subcolony size and duration of laying. The subcolonies of the Roseate Tern were much smaller with an average of 16 nests and, although the duration of laying was smaller compared with the whole colony, this difference was not significant. Subdivisions of the Common and Arctic Tern study areas showed slight reductions in the duration of laying compared with the whole areas, but again these reductions were not significant. This synchronization of laying together with short prelaying and post-hatching periods in the Sandwich Tern subcolonies means that as little time as possible is spent within the nesting area (see Table 5). This is important in a "white-washed" nesting place that is obvious to predators (Cullen 1960a, Croze 1970).

CLUTCH SIZE

Table 6 shows the average clutch sizes for the four species. The average clutch size did not vary much over the 3 years within a species, but the lowest occurred in 1966 and the highest in 1965, strongly suggesting that some common environmental factor was involved. In 1966 all species except the Roseate Tern had extended laying seasons. As there is a seasonal decline in clutch size, it follows that all species would have the lowest annual clutch size in 1966.

In the Roseate, Common, and Arctic Terns the average clutch size rose rapidly and then declined slowly, or declined progressively through the season, with minor fluctuations (Figures 2B, 2C, 2D). These declines in average clutch size were statistically significant in the Common and Arctic Terns in 1965, and in the Roseate Tern in 1965 and 1967. The only exception was in the Common Tern in 1966 when the maximum clutch size occurred much later in June and was about 0.3 of an egg more than the average clutch size in the corresponding period in 1965 and 1967. Possibly the adverse conditions, followed by desertion, and the subsequent relaying meant that older and more experienced individuals were laying later than in the other years.

The average clutch size variation in the Sandwich Tern with season was found to be notably different from the other species (Figure 2A).

TABLE 6
CLUTCH SIZES OF THE COQUET ISLAND TERNS OVER 3 YEARS

Species	1965	N[1]	1966	N	1967	N	Un-weighted mean
Common Tern	2.54	265	2.31	118	2.38	115	2.41
Arctic Tern	1.86	55	1.80	45	1.81	82	1.82
Roseate Tern	1.59	85	1.38	117	1.54	74	1.50
Sandwich Tern	1.41	164	1.15	454	1.24	1,664	1.27

[1] N = number of clutches.

Although in 1965 the average clutch size tended to decline with season, in 1966 there was a rise and then a decline, and in 1967 the reverse occurred. The two peaks in laying frequency in 1966 corresponded with the two peaks in average clutch size, and there was a similar correlation with a single peak in 1965, but in 1967 the situation was more complex.

CLUTCH SIZE VARIATION IN SANDWICH TERN SUBCOLONIES

In order to examine the clutch size within the Sandwich Tern subcolonies, the average clutch size for each of the 4-day periods of the duration of the subcolony was considered for the 3 years (Langham 1968). In 1965 the six main subcolonies were considered and of the five smaller ones (12–23 nests each), all tended to show an initial maximum of 1.5 to 2.0 eggs per clutch, which declined to one egg in later clutches. In the single large subcolony of 179 nests, the clutch size rose to a peak at the maximum laying frequency and then declined. In the five smaller subcolonies, the initial maximum clutch size tended to coincide with the peak in laying frequency.

In 1966, 11 subcolonies were examined. In five subcolonies the maximum clutch size coincided with the initial peak of laying frequency, which lasted about a week. However, in the later subcolonies, the clutch size remained low with very few clutches of two eggs. These phenomena resulted in the increase and decrease observed in clutch size with season in the colony as a whole.

In 1967 the maximum clutch sizes within a subcolony coincided with the initial peak of laying in about half of the 18 subcolonies examined. If the clutch sizes for the first 4 days of laying in all the subcolonies are combined and averaged, and so on, little variation in mean clutch size is found over the duration of laying in the subcolonies when considered as a group starting on the same date, e.g. 1.22 (251), 1.24 (451), 1.22 (456), 1.20 (265), 1.33 (101), periods 6–9 inclusive, 1.22 (107), where the figure in parentheses represents the sample size. Therefore the mean clutch size variation observed in 1967 for the

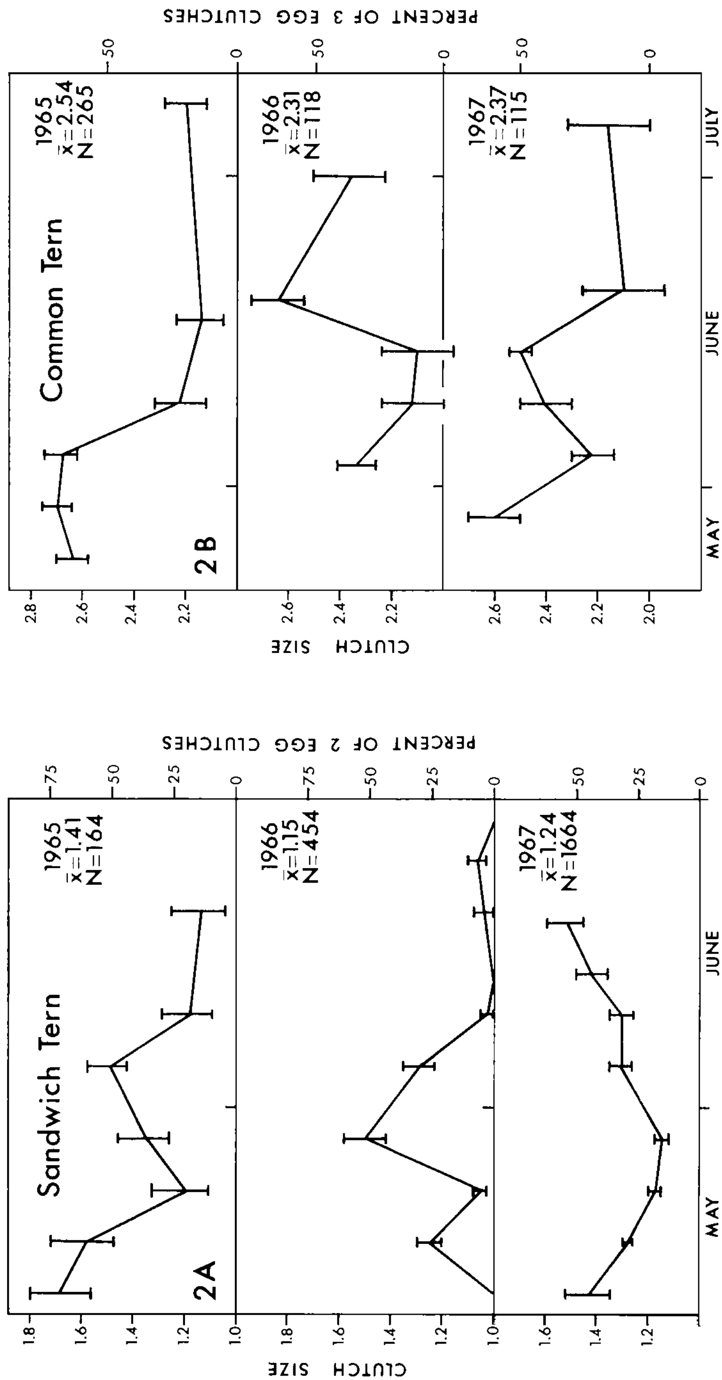

Figure 2. Seasonal variation in average clutch size in 1965, 1966, and 1967, showing two SE either side of the mean. A, Sandwich Tern; B, Common Tern; C, Arctic Tern; and D, Roseate Tern.

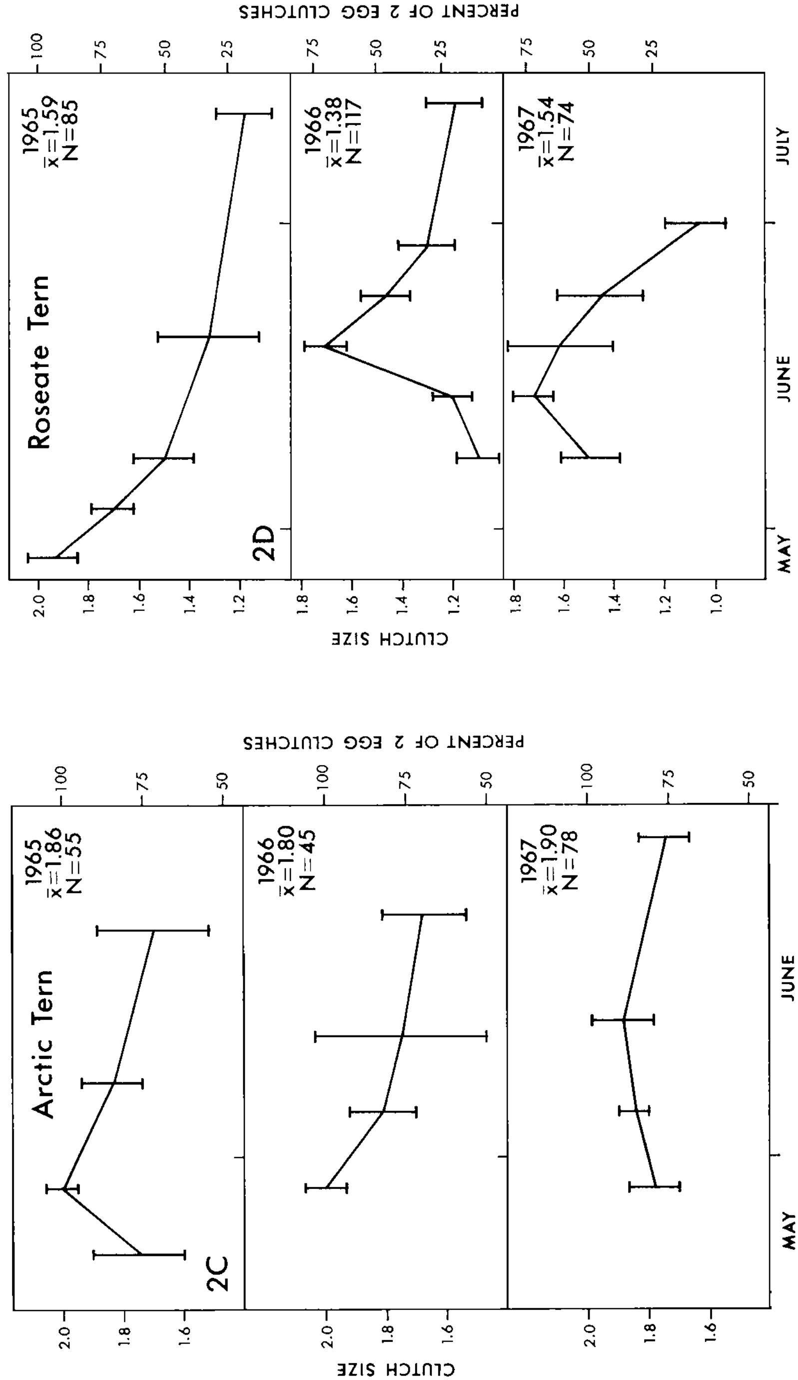
Roseate Tern
2D
1965
$\bar{x}$=1.59
N=85
1966
$\bar{x}$=1.38
N=117
1967
$\bar{x}$=1.54
N=74
PERCENT OF 2 EGG CLUTCHES
CLUTCH SIZE
MAY
JUNE
JULY
Arctic Tern
2C
1965
$\bar{x}$=1.86
N=55
1966
$\bar{x}$=1.80
N=45
1967
$\bar{x}$=1.90
N=78
PERCENT OF 2 EGG CLUTCHES
CLUTCH SIZE
MAY
JUNE

TABLE 7
TERN HATCHING SUCCESS WITH RESPECT TO CLUTCH SIZE

Species	Clutch size	1965 and 1966		1967	
		Success	N[1]	Success	N
Common Tern	1	41.5	41	—	—
	2	64.4	368	—	—
	3	81.6	593	—	—
TOTAL		73.7	1,002	81.2	303
Arctic Tern	1	44.4	45	—	—
	2	74.4	160	—	—
	3	91.7	12	—	—
TOTAL		69.1	217	87.7	163
Roseate Tern	1	87.4	127	—	—
	2	92.4	158	—	—
TOTAL		90.2	285	95.2	99
Sandwich Tern	1	64.9	941	—	—
	2	69.6	161	—	—
TOTAL		65.6	1,102	95.7	1,982

[1] N = number of eggs.

colony when considered as one unit (see Figure 2A) cannot be accounted for by a similar decline and rise within each subcolony.

In 1965 only one subcolony was large enough for the clutch size of the perimeter nests (i.e. those on the edge of a subcolony) to be compared with those in the center. The clutch size was higher in nests in the center (1.28) than those on the perimeter (1.11), but the difference was not statistically significant, and may reflect early and late nests, respectively.

Where the season was prolonged, as in 1966, most later clutches tended to consist of one egg. It might be argued that the correlation observed between maximum clutch size and laying was a result of favorable conditions, but this does not stand critical examination, as these periods are not consistent between subcolonies in a particular year.

I found that different subcolonies often differed in the breeding stage of their members; usually this was only a few weeks, but up to 57 days difference was recorded. A similar, but less marked, synchronization occurred within the subcolonies of the Roseate Tern where the numbers and density of nests was much lower.

ASYNCHRONOUS HATCHING

The approximate incubation period for the Sandwich Tern of 25 days was longer than in the three other species, where it was about 22 days. Incubation began soon after the first egg was laid and, as the eggs

TABLE 8
SANDWICH TERN SUBCOLONY SIZE AND HATCHING SUCCESS

1965 subcolonies		1966 subcolonies		1967 subcolonies	
Size	% hatching success	Size	% hatching success	Size	% hatching success
5	28.6	6	80.0	12	82.4
6	57.1	7	28.5	14	93.8
9	84.6	8	77.8	25	93.3
9	18.2	17	47.4	37	95.0
12	53.3	51	76.5	40	80.4
15	33.3	53	63.9	50	91.1
15	0	56	78.3	51	88.5
21	75.9	58	66.7	61	98.4
23	58.1	79	72.4	67	92.2
179	67.4	87	67.4	70	94.9
		99	65.2	77	100.0
		114	70.1	88	100.0
				89	99.0
				99	96.4
				107	95.4
				209	97.0
				296	98.2
				346	95.0
294	53.9	780	72.3	1738	95.7

were laid at varying intervals, the chicks hatched asynchronously. The importance of this in chick survival for the Common Tern was examined elsewhere (Langham 1972), and it also appeared to operate in the other species.

In the Sandwich Tern the laying interval varied as much as 5 days, and not uncommonly the parent bird left the nest with the first chick before the second emerged. This seemed more prevalent in colonies subject to disturbance where chicks were led away from the conspicuous nesting area. In undisturbed colonies chicks remain in the nest vicinity until they fledge, and hatching success is usually higher (Chestney, pers. comm.).

HATCHING SUCCESS

The estimate of hatching success (i.e. the percentage of eggs that hatch of those laid) was based on the Common and Arctic Tern clutches within their respective study areas, whereas almost all the Roseate and Sandwich Tern clutches were considered. These estimations in 1965 and 1966 were related to clutch size, but in 1967 the visits to the colony were so brief that only overall hatching success was recorded (Table 7).

In the Sandwich Tern hatching success increased with the increase in colony size on Coquet Island over the 3 years (53.9%, 72.2%, and 95.7%). In the large subcolony of 1965, the success was significantly higher in the center (76%) than on the perimeter (62%); and in

1966 a dispersed colony had a lower success (65%) than a compact one (72%), but the differences were not statistically significant. The hatching success was high in all large colonies, but was very variable in small ones (Table 8). In 1965 the hatching success varied considerably; most of the subcolonies were small, and the overall colony small. In 1966 there were more large subcolonies and overall success was higher, although some small subcolonies also had high success rates. In 1967 most of the subcolonies were large and hatching success was consistently high, even in the two very small subcolonies. Comparing subcolonies of less than 20 nests with those of more than 20 nests, the hatching success in 1965 (55% and 65%) and 1966 (54% and 74%) was significantly higher in the latter subcolonies in both years. However, it seemed that synchronization was more important than size in determining success. Large subcolonies were usually composed of smaller units that laid their eggs almost simultaneously, and it was these units that had high success. Sometimes small detached units (i.e. small subcolonies) would lay almost simultaneously, and on these occasions had a high hatching success (see Table 8). Nevertheless there were too many exceptions to the above to explain the variations in hatching success solely in these terms and other factors were also involved.

Fledging Success

Estimates of fledging success (i.e. the percentage of chicks hatched that survive to fly) were obtained from the same pairs used in the estimates of hatching success, so that they could be directly related to clutch size and hatching success. In order to reduce the error in estimating fledging success, the island was searched thoroughly and regularly for dead chicks. The methods used to obtain an accurate determination of fledging success is described elsewhere (Langham 1972).

There was little evidence of any decline in fledging success as the season progressed, except at the end of the more prolonged season of the Common Tern.

The asynchronous pattern of hatching resulted in a differential mortality with order of hatching that was similar in all four species. In broods of two, the second chick invariably had less chance of survival than the first chick, although this was less discernible in 1967, when overall survival was much higher. This differential fledging success occurred in the Sandwich Tern (Table 9) though in some cases the second chick was a "runt," smaller than the first chick on hatching, often with thinner tarsi, but further work involving exchanging these "runts" with chipping first eggs is necessary to test their survival.

This differential mortality was even more marked in the broods of

TABLE 9
SANDWICH TERN FLEDGING SUCCESS ACCORDING TO BROOD SIZE AND HATCHING SEQUENCE

Brood size	Hatching sequence	1965 Fledging success	1965 N[1]	1966 Fledging success	1966 N	1967 Fledging success	1967 N
B1	1	92.5	169	88.0	550	—	—
B2	1	100.0	33	82.8	29	—	—
		} 88.3		} 65.5			
	2	66.7	33	48.3	29	—	—
Overall fledging success		88.1	235	85.9	608	95.2	1,897

[1] N = number of chicks.

three occurring in the Common Tern, where the third chick to hatch had about one-third the survival chance of a first chick (Langham 1972). As the success of the first Arctic Tern chick to hatch in a brood of two was comparable with that of single chicks in all 3 years, the second chick bore the brunt of any environmental changes making conditions unsuitable for rearing two chicks. On Machias Seal Island, Canada, Hawksley (1957) found nests with one chick had a fledging success of 71% compared with 35% where there were two young, making the two brood sizes of this species equally productive. Yet on Coquet Island, broods of two were always more productive. The differential success of broods of two was similar in the Roseate Tern, although it was less marked.

In all four species the main chick mortality occurred within the first week after hatching, so that relatively little food was wasted on unsuccessful chicks, which could endanger the whole brood. This mortality was usually the result of starvation, especially in the third chicks in Common Tern broods of three. Apparently the begging of the last chick was insufficient to overcome the brooding drive, as Carrick (in Dunnet 1955) suggested for the Starling (*Sturnus vulgaris*). The maintenance and growth requirements of Common Tern broods and observations indicating the above mechanism of mortality in third chicks are recorded elsewhere (Langham 1972).

BREEDING SUCCESS

Breeding success represents the combination of hatching success and fledging success (i.e. the number of fledged chicks expressed as a percentage of the number of eggs laid). Unfortunately most seabirds also have a high postfledging mortality, which, as in this instance, is usually unknown. However breeding success does give some relative measure of productivity. Table 10 gives the breeding success in 1965 and 1966.

TABLE 10
FLEDGING PRODUCTION WITH RESPECT TO CLUTCH SIZE IN 2 YEARS

		1965		1966	
Species	Clutch size	Breeding success	Fledged/pair	Breeding success	Fledged/pair
Common Tern	1	43.8	0.44	21.1	0.21
	2	59.3	1.19	39.7	0.79
	3	48.1	1.44	41.9	1.26
TOTAL		48.6	$\bar{x} = 1.22$	39.9	$\bar{x} = 0.88$
Arctic Tern	1	64.3	0.64	34.4	0.34
	2	52.1	1.04	66.3	1.33
	3	77.8	2.33	66.7	2.00[1]
TOTAL		52.9	$\bar{x} = 0.96$	57.4	$\bar{x} = 0.91$
Roseate Tern	1	87.2	0.87	90.1	0.90
	2	77.1	1.54	81.7	1.63
TOTAL		79.8	$\bar{x} = 1.36$	86.6	$\bar{x} = 1.15$
Sandwich Tern	1	46.3	0.46	63.5	0.64
	2	57.7	1.15	58.1	1.16
TOTAL		47.0	$\bar{x} = 0.55$	62.5	$\bar{x} = 0.66$

[1] Based on only four clutches.

The overall breeding success for the four species in 1967 was: Common Tern 71.3%, Arctic Tern 79.4%, Roseate Tern 92.0%, and Sandwich Tern 91.1%.

Breeding success was highest in 1967 and lowest in 1965, except in the Common Tern where breeding success was lowest in 1966. This poor success in 1966 was due to the large scale desertion of eggs in this species probably caused by shortage of suitable fish, but the breeding cycle was only delayed in the Roseate Tern. The Arctic Tern probably found sufficient food offshore, as this species fed mainly out to sea, whereas the Common Tern preferred fishing along the coastline (Langham 1968). The success of the Sandwich Tern increased with the colony size. This was due to improved synchronization in the subcolonies, resulting in fewer desertions of second eggs or second chicks in clutches of two.

The number of chicks fledged per pair for each species for 1965 and 1966 with reference to clutch size was calculated (Table 10). In all instances and in both years the larger clutch sizes produced more young per pair. In 1967, with the increase in overall breeding success, this trend was further emphasized.

The overall chick production per pair varied relatively little in the 2 years examined, although the production by each species was distinctive. The number of chicks fledged per pair would be expected to decrease in the same sequence their average clutch size decreased:

TABLE 11
CHICKS FLEDGED PER PAIR WITH TIME IN 1965

Start of 5-day period	Common Tern		Arctic Tern		Roseate Tern		Sandwich Tern	
	Chicks	No. of pairs	Chicks	No. of pairs	Chicks	No. of pairs	Chicks	No. of pairs
13 May							0.81	32
18 May	1.40	10					0.47	60
23 May	1.43	47	1.13	16	1.38	13	0.64	33
28 May	1.37	73	1.00	24			0.68	38
2 June	1.30	47	0.63	16	1.21	24	0.84	79
7 June					0.90	21	0.70	27
12 June	1.31	36	1.00	16	1.14	7	0.61	23
17 June								
22 June								
27 June					1.00	10	0.38	21
2 July								
7 July	1.41	17						
12 July					0.86	14		
AVERAGE	1.36	230	0.94	72	1.08	89	0.66	313

Common, Arctic, Roseate, and Sandwich Tern, but the Arctic and Roseate Tern are reversed, as the Arctic produces fewer young on the average. This result is all the more surprising because high wind speeds were found to have a detrimental effect on the fishing ability of the Roseate but not of the Arctic Tern (Langham 1968). The reason for the greater breeding success in the Roseate Tern would appear to be due to their less exposed nest sites. Roseate Tern chicks had a slower growth rate than the other species, but still had the same fledging period, which means that they fledge below the adult weight and as a result might suffer a greater postfledging mortality.

The average number of chicks fledged per pair with time in 1965 (Table 11) and 1966 showed a definite decrease in the Sandwich Tern, which was also apparent in the Roseate Tern. There was only a slight decrease in the Arctic Tern in 1965, but this was much more marked in the prolonged 1966 season where chick production for the last 17 pairs fell to 0.12 chick per pair. The Common Tern showed the least decrease in chick production with time both in 1965 and 1966, which accounted for its more prolonged breeding season.

DISCUSSION

Comparison of the nest sites of the four species of terns nesting on Coquet Island in close proximity to one another showed distinct preferences in at least three species. The nest sites did not appear to be limiting the number of terns, as their numbers were still increasing on the island. In particular the Sandwich Tern showed a large increase over the years of this study. However nest sites may soon become limiting for the Common and Arctic Terns, which occupied most of the island at their normal densities of about $0.1/m^2$ and $0.02/m^2$ respectively. This is especially likely for the Arctic Tern, as sheep's sorrel is increasing at the expense of the short rabbit-cropped fescue grass.

The correlation between pugnacity, density, and the relative importance of camouflage in the four tern species has already been mentioned (Cullen 1960a). Although the eggs and young of the Sandwich and Roseate Terns are hard to discern in their guano-spattered subcolonies, the area itself is much more conspicuous than those of the Common and Arctic Terns. To compensate for this, the Sandwich and the Roseate Terns not only have more synchronized breeding behavior, but also lead their young away from the nesting area to better cover within a few days after hatching. Furthermore these two species, and especially the Sandwich Tern, nest in association with more aggressive tern species or Black-headed Gulls that help to deter predators.

In general the Sandwich Tern showed least variation in the onset of breeding in successive years, whereas the Roseate Tern exhibited most. In some instances, such as median laying dates and duration of laying, the Common Tern showed least variation, but the variation shown by the Roseate Tern indicated that it was most influenced by environmental conditions.

The importance of synchronized breeding in the Sandwich Tern has been emphasized in shortening the time this species spends within a relatively vunerable nesting area. The Sandwich Tern achieves this by arriving at the colony already paired, copulating outside the breeding groups, then reducing the spread of laying to an average of about 20 days by nesting in subcolonies. Incubation is slightly longer, but as the chicks are led out of the subcolony after about 5 days, the adults and potential young are only in the subcolony for about 50 days. The Common and Arctic Terns spend about twice this time in the colony. Although the Roseate Tern spends about 3 weeks on the island prior to laying, its young also leave the nest area within 5 days, so that the time spent there is intermediate between those of the Sandwich Tern and the other species.

High nesting density made the Sandwich Tern breeding area conspicuous, and the subdivision into subcolonies not only favors synchronization, but also reduces the chance of discovery by ground predators, where the subcolony is among other more aggressive species. If the Sandwich Tern nested in one group, ground predators might wipe out the entire colony. The subcolonial habit is still maintained where ground predators are absent, such as on Coquet Island, for the tendency of this species to change its breeding ground may place it within reach of ground predators. The tendency of Sandwich Terns to move from their breeding site if disturbed by ground predators in the nesting season affords further protection. In safe sites where a colony has been long established, the subcolonial habit becomes superfluous and the groups tend to merge into one another, as occurs on the Farne Islands.

Different subcolonies were often at different stages of the breeding cycle, though this rarely varied by more than a few weeks. Such differences have been recorded in several other species, including the Greater Flamingo (*Phoenicopterus ruber roseus*) (Swift 1960), Gentoo Penguin (*Pygoscelis papua*) and Rockhopper Penguin (*Eudyptes crestatus*) (Roberts 1940), White Pelican (*Pelecanus erythrorhynchos*) (Behle 1944), Common Terns and Common Murres (*Uria aalge*) (Salomonsen 1943), Arctic Terns (Bullough 1942), and Gannets (*Morus bassanus*) (Nelson 1967). Most of these reports were merely general impressions from brief visits, with no attempt to record the differences between the reproductive stages of the groups, but they do suggest that synchronized groups are common in colonial birds.

How this synchronization is achieved is not known. It may be that pairs in a similar physiological state aggregate into prebreeding flocks that subsequently form subcolonies, and that the dense flocking and nesting behavior may allow displaying pairs to influence one another and so further increase the synchrony. Such social stimulation was first suggested by Darling (1938) in colonies of Herring Gulls, but critical assessment of his data failed to reveal any significant difference in the onset and duration of laying in large and small colonies (Coulson and White 1960). In the Sandwich Tern subcolonies, the duration of laying was not related to size, except that very small subcolonies (< 10 nests) had short durations of laying. The average duration of laying in the subcolonies was 18–21 days, but the range was very wide in the small colonies of 1965 and 1966, as several small subcolonies had very brief laying durations, with standard deviations of $\pm$ 15 and $\pm$ 12.5 days respectively. In 1967 the standard deviation was reduced to $\pm$ 5.5 days, so that there seems to be a limit to the difference in maturation states that can be incorporated into a subcolony.

The four species of terns nesting on Coquet Island all exhibit silent coordinated flights from the nesting area called "dreads" or "panics"

(Marples and Marples 1934) that are derived from escape behavior, but may help to synchronize early reproductive behavior (Lind 1963). The Sandwich Tern has a closer and more integrated flocking formation than the other terns, taking the form of a silent collective upflight, followed by much "chattering" as the birds resettle. In this species these upflights occurred with each subcolony acting as a separate unit, which also has been recorded in the Roseate Tern (Serventy and White 1951). It seems that this close flocking behavior could provide a mechanism for greater synchronization than is possible in the other species of terns studied.

The average clutch size normally showed a small rise and then a decline, or a progressive decline through the laying season with minor variations in the other tern species, but in the Sandwich Tern it tended to reach a maximum when most individuals in a subcolony were laying. Since the period when the largest clutches were being laid did not occur at the same time in different subcolonies, as they were at different stages of the breeding cycle, it cannot be correlated closely with abundant food supply. What determines that a large clutch is laid when most birds are laying is not known, but it might be that birds capable of laying two eggs can synchronize their laying time more effectively.

Synchronization of laying in a subcolony was an advantage when hatching success was considered. Desertions account for the major failure of eggs, and this was more prevalent in the remaining nests when most of the birds had hatched their eggs and led their chicks out of the subcolony. Therefore coordination of breeding activities was an advantage in a dense group of birds.

The significantly higher hatching success among the clutches in the middle of a subcolony compared with those on the perimeter, and the tendency for a compact subcolony to have a higher hatching success than a diffuse one, suggested a gradation in the quality of nest sites that probably reflected the quality in fitness of the birds involved. Similar differences have been found in Black-headed Gulls (Patterson 1965) and Kittiwakes (Coulson 1968). In the Sandwich Tern subcolonies of less than 20 nests hatching success was significantly lower than those with more than 20 nests because of desertion by less synchronized birds. If poorer quality birds are forced to nest in small subcolonies, rather than on the edge of large ones, this may represent a failure of the individuals to synchronize their breeding sufficiently to be able to join the large group. So far no examination has been made of the adults that comprise the different subcolonies of Sandwich Terns.

The asynchronous hatching exhibited by all the tern species resulted in a differential mortality favoring the first hatched chicks. Nevertheless increased clutch size resulted in more young being fledged per pair.

As Lack's hypothesis (1947, 1948) is that the normal clutch size corresponds to the maximum average number of young that the parents can successfully raise, a selection for the larger clutch sizes might be expected. Lack (1966) has argued that increased productivity as far as the fledging stage may be misleading, in that postfledging mortality may be greater in larger broods. There was some indication that chicks fledged from larger broods weighed less than those in smaller broods, at least in the Common Tern (Langham 1968).

Terns exhibit some postfledging care of the young (Ashmole and Tovar 1968; pers. obs.), mainly involving feeding until the young can fish for themselves. Where there are more than two young, this limits the care one parent can spend on one chick, which is very likely to affect survival. Whether two chicks present a similar problem, notably in the Roseate and Sandwich Terns, is not known, but obviously one chick with two parents looking after it is at a definite advantage.

All species showed a decline in the number of chicks produced per pair with time, which was most noticeable in the Sandwich Tern and least so in the Common Tern. As there was no evidence of a decline in hatching and fledging success with time, this reflected a decline in clutch size that has already been considered. Presumably such a decline was a result of deteriorating environmental conditions, but this has yet to be demonstrated for a seabird.

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Summary

The breeding biology of the Sandwich Tern was examined and briefly compared with that of the Roseate, Common, and Arctic Terns. The nest site preferences were described and related to the vegetation and topography of the island study area.

The Sandwich, Arctic, and Common Tern tended to occupy the island simultaneously, followed in a few days by the Roseate Tern. The Sandwich Tern began laying almost at once, and its nests were associated with Black-headed Gulls' nests. The Common and Arctic Tern did not lay until 2 weeks later, and the Roseate Tern about 3 weeks later. The Sandwich Tern formed discrete subcolonies in which the laying was highly synchronized, permitting this species to spend less time in the nesting area than the other species.

The average clutch size for all species was highest in 1965 and lowest in 1966. Although the average clutch size declined during the laying season in the other species, that of the Sandwich Tern varied within subcolonies and showed a tendency to reach a maximum when most birds were laying. Since subcolonies were not at the same stage of the breeding cycle, clutch size variation was not consistent throughout the whole colony.

All species exhibited asynchronous hatching that led to differential survival of chicks. Hatching success varied within Sandwich Tern subcolonies, being significantly higher in the center than on the perimeter.

Fledging success did not decline noticeably with season, though chick production dropped as a result of a decline in clutch size. This was lowest in the Common Tern where the breeding season was the longest.

Although larger clutches produced more offspring, these tended to fledge at lower weights. As postfledging care is important in terns, large broods may be at a disadvantage and suffer a higher mortality.

The results are discussed with particular reference to synchronization in the subcolonies of the Sandwich Tern.

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