OCCURRENCE AND TIMING OF SECOND CLUTCHES IN COMMON TERNS

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ABSTRACT.—Eighteen pairs of Common Terns (*Sterna hirundo*) at three different colonies laid second clutches while still feeding young from their first broods. Seven clutches were laid before the chicks from the first brood fledged, and 11 were laid after the chicks from the first brood fledged. In each case, parents alternately fed chicks from the first brood and incubated the second clutch. Sixteen of the 18 clutches disappeared, were addled, or were deserted. Young hatched from the two other second clutches, but all chicks died or disappeared 2–4 days after hatching. We suggest that a second clutch, laid before chicks from the first brood fledged, probably results from a physiological miscue associated with chick loss from the first brood and stimulated by an unusual surplus of food. Conversely, when laid after chicks from the first brood fledge, a second clutch might function as insurance, permitting a pair to raise young late in the season if chicks from the first brood are lost. In either case, parents must partition care between eggs and chicks from the second clutch and fledged chicks from the first brood. Accordingly, the successful fledging of chicks from two broods in a single season is unlikely unless exceptionally favorable conditions occur. *Received 20 January 1983, accepted 15 December 1983.*

CHICKS of gulls and terns generally require brooding and feeding by both parents, activities that usually continue for several weeks or months after the chicks fledge (Nisbet et al. 1978, Burger 1980). Common Terns (*Sterna hirundo*) normally lay a single clutch during a breeding season, and both parents attend and feed the chicks for at least 6 weeks after fledging, even when only one chick has been raised (Nisbet 1976 and unpubl. obs.). Individual pairs of several colonially nesting species [e.g. Common Terns, Nisbet and Cohen 1975; Silver Gulls (*Larus novaehollandiae*), Wooller and Dunlop 1979; Herring Gulls (*L. argentatus*), Parsons 1976; Black-legged Kittiwakes (*Rissa tridactyla*), Wooller 1980] are known to produce a second clutch a minimum of 6–12 days after the artificial removal or loss of their first clutch. Silver Gulls, however, are unique among colonially nesting seabirds in that they routinely fledge two successive broods during a year (Nicholls 1974). Wooller and Dunlop (1979) proposed that a refractory period of 6–7 weeks, equivalent to the fledging period of Silver Gull chicks of the first brood, functions to prevent subsequent clutches from being produced until after the first brood is independent.

Although the advantages of raising a second brood during a single breeding season are potentially substantial, parents face several constraints. In Common Terns, late nesters realize reduced reproductive success (Morris et al. 1976 Nisbet and Welton in press). Parents should produce a second clutch as early in the breeding season as possible. The laying of the second clutch, however, should not interfere with the production of chicks from the first brood (Wooller and Dunlop 1979). In addition, parents face the difficult task of partitioning parental care between eggs and chicks from the second clutch and chicks from the first clutch.

We have independently observed 18 incidents, at three different colony sites, in which pairs of Common Terns laid second clutches while still feeding young from their first brood. The purpose of this paper is to describe these cases in detail and to comment upon their probable proximate and ultimate causes.

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TABLE 1. Timing of clutch starts and fate of eggs and chicks from Common Tern pairs at Port Colborne (PC), Monomoy (M), and Wickford Light Tower (WLT). No eggs hatched from second clutches. Years of observation were: PC—1982, M—1979, WLT—1981.

Pair number (colony)	First clutch					Second clutch	
	Clutch size	Laying dates	Hatching dates	Number of chicks fledged	Date of fledging	Clutch size	Laying dates
S6 (PC)	2	15, 17 May	7, 8 June	1	4 July	1	14 June
S7 (PC)	3	8, 9, 11 May	1, 2 June	1	1 July	2	23, 26 June
S8 (PC)	3	9, 11, 13 May	4, 5 June	1	2 July	2	15, 18 June
S10 (PC)	3	11, 12, 14 May	5, 6 June	1	3 July	2	15, 18 June
11 (M)	3	23, 25, 26 May	20, 21, 22 June	1	14 July[a]	2	3,[a] 5,[a] July
137 (M)	3	20,[a] 22, 23 May	17, 17 June	1	9 July	2	3,[a] 5,[a] July
3 (WLT)	2	—[b]	3,[a] 4[a] June	1	29 June[a]	3	21,[a] 23,[a] 24 June

[a] Approximate date.
[b] Before first visit on 21 May.

STUDY AREAS AND METHODS

Of the 18 cases, 14 were observed in 1982 and 1983 by DAW and RDM at a colony near Port Colborne, Ontario (42°53'N, 79°16'W) (see Morris et al. 1976 for colony description), 3 cases were observed by ICTN in 1979 at a colony at Monomoy National Wildlife Refuge, Massachusetts (41°38'N, 69°58'W), and 1 case was observed in 1981 by TWC at a colony on Wickford Light Tower, Rhode Island (41°34'N, 71°26'W). The observations were made in the course of studies that included the marking of eggs and chicks in sequence of laying and hatching (328 nests at Port Colborne over the 2 yr, 125 nests at Monomoy, and 82 nests at Wickford). All the pairs whose behavior is described here were studied at close range (<8 m) from blinds. The most intensive observations were at Port Colborne, where DAW and RDM individually color-marked both members of 13 (1982) and 14 (1983) pairs and studied their parental behavior for at least 3 h each day from 1 May to 10 July (1982) and to 24 July (1983). At Monomoy, the colony was visited daily from 22 May to 9 July and on 20, 21, and 28 July 1979 (see Nisbet and Welton in press). Behavioral observations were made for up to 6 h on most visits, but only 11 birds were individually marked. At Wickford, the colony was visited twice weekly from 21 May to 7 July and 14 and 23 July 1981. About 35 unmarked pairs were observed for up to 3 h on each visit.

RESULTS

The laying of second clutches occurred in two contexts. Seven clutches were laid before the fledging of chicks from the first brood, and 11 were laid after the fledging of chicks from the first brood. This difference in the temporal spacing of broods is considered important, and the two cases, therefore, will be treated separately.

Second clutches before fledging of first-clutch chicks.—The timing of egg laying and fates of eggs and chicks from each of the two clutches of the seven pairs that laid second clutches while prefledged young from the first brood were still at the nest site are given in Table 1. At Port Colborne, two eggs hatched from each of the four first clutches. In the three-egg clutches, the third egg disappeared or was addled before hatching. The second chick in each brood disappeared between 2 and 10 days after hatching. Each of the single surviving chicks from the four first clutches was seen flying 25–30 days after hatching. At Monomoy, the two pairs hatched 3 and 2 eggs, but only one chick from each brood survived to fledging age. The other chicks died of exposure or were killed by ants shortly after hatching. At Wickford, the single pair hatched both eggs in the clutch about 3 and 4 June. The first chick died of unknown causes about 9 June, but the second chick survived and fledged about 29 June. Thus, in all seven cases, a second clutch was laid while a single chick from the first clutch was still being fed by the parents (Table 1).

At Port Colborne (1982) and Monomoy, copulations were seen in two pairs (one at each colony) after the eggs in the first clutch hatched and a few days before the second clutches were laid. Common Terns normally stop copulating a few days after clutch completion (Morris and Nisbet unpubl. obs.). At Port Colborne, pair S7

TABLE 2. The amount of incubation effort given by male and female partners of each of the four study pairs at Port Colborne during incubation of their first and second clutches.

Pair number	Incubation time [min ($\bar{x}$ ± 1 SD) per 3 h]					
	First clutch			Second clutch		
	Hours observed	Male	Female	Hours observed	Male	Female
S6	36	87.0 ± 43.7	82.2 ± 36.5	48	23.1 ± 37.5	53.0 ± 56.8
S7	21	74.0 ± 54.7	99.5 ± 47.8	36	12.3 ± 22.3	120.5 ± 63.5
S8	45	81.3 ± 59.0	94.3 ± 55.1	63	18.0 ± 29.6	57.0 ± 43.4
S10	42	65.3 ± 47.6	112.0 ± 45.2	51	19.1 ± 42.1	38.0 ± 32.9

was seen copulating once on 17 June, 15 days after chicks from the first clutch hatched. The frequency of copulations (one observed in one of four pairs watched for 3 h daily throughout the laying period for second clutches) was well below that recorded in 1981 among pairs before completion of first clutches (mean = 0.83 copulations·pair^{-1}·h^{-1}, Morris unpubl. obs.). At Monomoy, pair 137 was seen copulating several times on 30 June 13 days after chicks from the first clutch hatched. One of the copulations took place just after the chick had refused a fish offered to it by the male. The male then fed the fish to the female and copulation followed shortly thereafter.

At Port Colborne, shortly after the eggs from the first clutch hatched and before the disappearance of the second chick, the female partner in each of the four pairs performed characteristic "food-begging" behavior. The behavior was directed at her mate upon his return to the nest site with a fish. Females of the other nine color-marked pairs under observation were seen occasionally to take and eat fish from their mates when chicks were present. This was recorded only on nine occasions, however, was restricted to periods when the chicks were very young (1–2 days of age), and was never associated with "food-begging" behavior by the female. The rate at which males fed fish to partners during the laying of the second clutch in 1982 (0.07 ± 0.06 feeds·male^{-1}·h^{-1}) was well below comparative rates of males at the same colony during the laying of first clutches in early May 1982 (0.42 ± 0.45 feeds·male^{-1}·h^{-1}). "Food-begging" was not noted at Monomoy or Wickford.

At Port Colborne, first eggs of the second clutches were laid in the original scrape sites 6, 9, 10, and 21 days after eggs from the first clutch hatched (Table 1). Incubation effort given by each partner to their first and second clutches was not equivalent. Whereas both partners incubated the first clutch with approximately equal frequency, the male partner rarely incubated the second clutch, and three of the female partners did so for relatively short periods (Table 2). In two cases (pairs S6, S10), eggs from the second clutch disappeared or were found outside the scrape 5–11 days after they were laid and before the remaining chick from the first clutch fledged (Table 1). In the other two cases (pairs S7, S8), eggs in the second clutch were deserted 6 days after the single chick from the first clutch first flew freely.

At Monomoy, second clutches were laid in new scrapes 3 and 10 m away from the nest sites. In both cases, the eggs in the second clutches were smaller than those in the first clutches (weights of first eggs were 20.4 and 20.7 g in second clutches vs. 21.3 and 21.0 g in the first clutches). As at Port Colborne, the second clutches were not incubated continuously, and one member of each pair spent more time on the eggs than the other. In pair 11, the female (which was individually marked) sat on the eggs for short periods on 7 July, and the nest was deserted the next day. In pair 137, both parents were observed on 7 and 8 July sitting on the eggs and attending the chick from their first clutch, while one parent periodically brought fish and fed the chick. On 9 July the chick was flying for the first time, and both parents flew in and out of the study plot with it; neither attended the second clutch during the 6-h period of observation. By 28 July, both of the second clutches had been deserted. None of the eggs showed any visible signs of embryonic development when opened, although most were too old and dessicated for early develop-

Fig. 1. Common Tern chick from first brood begging while its parent incubates the second clutch.

ment to have been detected if it had occurred. At Wickford, the second clutch was laid in the same scrape as the first. On 5 visits between 24 June and 14 July, one parent was observed sitting on the eggs while the chick begged from it. On 23 July the chick had fledged, and the eggs were gone.

Second clutches after fledging of first-clutch chicks.—The timing of egg laying and fates of eggs and chicks from the two clutches of the 11 pairs that laid clutches after successfully fledging at least one chick are given in Table 3. Ten of these pairs were at Port Colborne, and six of the second clutches were laid in the same scrape location as the first clutches. Pairs S2 and S5 (both members of each pair color-banded) hatched one and two eggs, respectively, from their first clutches. Each of these chicks was seen flying 25–30 days after hatching. Although hatching and fledging dates were not determined, the other eight pairs each fledged at least one chick from their first clutch. At Monomoy, all three eggs in the first clutch of pair 199 hatched. The first two chicks were killed by ants, but the third survived and fledged on 9 July.

Fledged chicks were never seen at nests S2 and S5 after the second clutches were laid, although both pairs were seen standing with their fledged chicks elsewhere in the colony. The female of pair S2 incubated the second clutch for long periods ($\bar{x} = 35.5 \pm 23.9$ min/h) over 17–18 days, but the male incubated for only a short time (12 min/h) on one day. Neither member of pair S5 was ever seen incubating their second clutch, although both birds continued to defend the nest site. The second clutch of pair S2 was deserted on 19 July and of pair S5 on 1–2 July.

In the other eight cases at Port Colborne, parents alternately fed fledged chicks from their first brood at the nest site and incubated second clutches. No detailed data on incubation duration were collected for these eight pairs. In pair 199 at Monomoy, one parent sat on the second clutch for most of 9 h of observation on 20 and 21 July, 11–12 days after the first chick fledged, although the chick persistently begged from it (Fig. 1). Of these nine second clutches, four (2, 3, 7, 8) disappeared, two (1, 199) were deserted, one (6) was addled, and two (4, 5) hatched young (Table 3). Both chicks from clutch 5 disappeared between 25 and 27 July, 2–4 days after hatching. The single chick from clutch 4 was found dead near its nest on 16 July, 2 days after hatching. The parents of the latter chick had attempted to feed it on 14 July, but their single fledged chick from the first brood monopolized every feeding.

DISCUSSION

The observations summarized above indicate that each of the 18 pairs had laid a second clutch while still feeding a chick from their first brood. An alternative explanation, that the second clutches might have been laid by other females, can be excluded in most cases. All of the 18 pairs were observed regularly (in 14 cases,

TABLE 3. Timing of clutch starts and fate of eggs and chicks from Common Tern pairs at Port Colborne (PC) and Monomoy (M). No young fledged from second broods. Years of observation were: PC—1983, M—1979.

Pair number (colony)	First clutch					Second clutch		
	Clutch size	Laying dates	Hatching dates	Number of chicks fledged	Date last chick fledged	Clutch size	Laying dates	Hatching dates
1 (PC)	—	—	—	1[b]	—	2	2, 3 July[a]	—
2 (PC)	3	8, 10, 12 May	1, 2 June[a]	3	1 July[a]	3	1, 2, 3 July[a]	—
3 (PC)	—	—	—	1[b]	—	2	20, 24 June	—
4 (PC)	—	—	—	1[b]	—	2	22, 23 June	14 July
5 (PC)	3	9, 10, 12 May	2, 3 June[a]	2	2 July[a]	2	1, 2 July[a]	23, 24 July
6 (PC)	3	12, 14, 16 May	5, 6 June[a]	1	3 July[a]	1	6 July	—
7 (PC)	—	—	—	1[b]	—	2	11, 12 July	—
8 (PC)	—	—	—	1[b]	—	1	21 July	—
S2 (PC)	3	8, 10, 12 May	30 May	1	25 June	1	1 July[a]	—
S5 (PC)	2	2, 4 May	27, 27 May	2	22 June	1	28 June	—
199 (M)	3	21, 23, 24 May	3, 3, 4 June	1	9 July	2	20, 21 July[a]	—

[a] Approximate date.
[b] Only one fledged chick at nest site.

daily) from blinds, and they vigorously defended their territories against intruders; 7 of the 18 pairs were individually marked, and 11 of the second clutches were laid in the same scrapes as the first clutches.

The phenomenon of second-clutch production while chicks from the first are still being fed could readily be overlooked without detailed observations from a blind, because it requires evidence that the same parents are attending chicks and eggs and that the chick(s) is being raised by its own parents. Even in the absence of such observations, however, it is known that Common Terns that start their clutches in June and July normally do so outside the areas where earlier nesters are raising young. For example, at Port Colborne, Common Terns traditionally begin nesting on the western end of the breakwall and pairs nesting later occupy areas further east along the wall as the preferred substrate at the west end becomes saturated with nests (Morris et al. 1976). From notes on studies of 600 pairs of Common Terns in Massachusetts, Nisbet determined that only 20 late clutches were started close to active territories and that only 2 or 3 of these were deserted at the time when nearby broods were fledging (unpubl. obs.). Accordingly, we conclude that the laying of second clutches while prefledged or fledged chicks are still at the nest site is a relatively rare phenomenon in Common Terns.

The common features of the seven pairs that laid a second clutch before chicks from the first brood had fledged were that they all nested early and that they all lost 1 or 2 chicks shortly before or shortly after hatching. Thus, each was raising only one chick, despite the fact that food was sufficiently abundant at all three colonies for other pairs to raise 2 or 3 chicks successfully (Nisbet and Welton in press; unpubl. obs. of DAW, RDM, and TWC).

For these pairs, the laying of the second clutch was probably not a "serious" attempt to raise a second brood toward the end of the breeding season. This is supported by the limited investment of the parents in the second clutch, as indicated by reductions in copulation frequency, fish-feeding rates of males to their partners, egg size, clutch size, and incubation behavior (especially by the males). All eggs in these clutches either disappeared, rolled out of the nest, or were deserted after the chick from the first brood fledged. Our interpretation of these cases is that a physiological miscue occurred that resulted in the female initiating "food-begging" behavior while a chick from her first brood was still present. The miscue may have been stimulated by an unusual surplus of food available to the pair that resulted from the loss of all but one chick while sufficient food was available to raise more than one. This, in turn, may have led to the resumption of female begging behavior, which, in turn, led

to laying and incubating activities. We suggest, therefore, that an underlying physiological mechanism, in place to permit the laying of a second clutch following a refractory period after loss of a first clutch (or brood) within the same breeding season, was stimulated at an inappropriate time. The proximate cause for this is unknown at present, although unusual food availability may have been a stimulus.

For those pairs ($n = 11$) that laid a second clutch after chicks from the first brood had fledged, second clutches might function as "insurance," permitting a pair to raise young late in the season if the chicks from their first brood are accidentally lost after fledging. We note that second clutches were observed primarily in pairs that were raising only one chick, circumstances in which the chance of its accidental loss are substantial (Nisbet 1976). Although data on incubation effort are limited, two pairs were successful in hatching eggs and five other pairs incubated eggs for at least 16 consecutive days. As no chicks from these second clutches fledged, it seems clear that Common Tern parents attempting to raise two successive broods in a single season face several problems. The most signficant of these is that the adults must partition parental care between eggs and chicks from the second clutch and fledged chicks from the first brood (see Fig. 1). Fledged Common Tern chicks are normally accompanied by their parents during postfledging dispersal (Nisbet 1976) and appear to require prolonged parental care for optimal postfledging survival, as do the chicks of several other tern species (Ashmole and Tovar 1968). Conversely, newly hatched Common Tern chicks require constant brooding and defense, as well as having specialized food requirements (very small fish). Common Tern parents would be hard pressed to perform both of these roles simultaneously and successfully. An additional problem is that recently fledged tern chicks often remain at the nest site and are able to monopolize feedings intended for their newly hatched siblings from second clutches. Thus, a parent-offspring conflict (Trivers 1974) over the partitioning of resources would work against the successful raising of two broods by a pair of Common Terns during one breeding season.

Among monogamous seabirds, active participation by both parents is generally necessary for successful breeding (Hunt 1980, Pierotti 1981, Burger 1981). Both partners participate fully in incubation, brooding, and chick-feeding behavior, and successful raising of chicks by a single parent has rarely been reported (Nisbet et al. 1978). Mechanisms that prevent the production of a second clutch before the successful raising of chicks from a first clutch should therefore be under active selection. In view of these considerations, it is unlikely that second clutching by Common Terns serves any substantial adaptive function. Nonetheless, the 11 pairs that delayed production of a second clutch until chicks from the first brood fledged exhibited greater potential for successfully raising two broods than the seven pairs that laid a second clutch before fledging chicks from the first brood. It is possible, therefore, that under exceptionally favorable conditions second clutching might result in the successful fledging of chicks from two broods during a single breeding season.

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