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Consequences of Renesting in Common Terns (*Sterna hirundo*): Changes in Clutch Size, Egg Mass, and Productivity

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Abstract.—Some previous studies of seabirds have suggested that birds renesting after earlier failures may lay smaller clutches and smaller eggs than the same birds in their first nestings. Common Terns (*Sterna hirundo*) were studied at a site where most first clutches and broods were destroyed by high seas from a hurricane on 22 June 1972. Most or all pairs renested 8-17 d (mean 11.2 d ± 2.1SD) after failure. Renesting pairs had lower clutch size than first-nesting pairs (means 2.11 vs 2.85), lighter eggs (20.08 vs 21.89 g for first eggs in the clutch) and lower productivity (≤ 1.24 vs 2.07 chicks raised to fledging). Two of 34 fledglings from renestings were subsequently encountered as breeders, versus 2 of 30 from surviving first nestings in 1972 and 5 of 73 from the same site in 1971. Hence, renesting contributed offspring to the next generation, although it must have entailed physiological, energetic and temporal costs to the parents. *Received 27 May 2019, accepted 9 September 2019.*

Key words.—clutch size, Common Tern, egg mass, growth, renesting, *Sterna hirundo*

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In most bird species, pairs that lose clutches or broods to predation or other causes renest and often successfully rear young in their second or third attempts. Small passerines and other species at the 'fast' end of the 'fast-slow' life-history continuum (Jones *et al.* 2008) can fit two or more successful breeding attempts into the seasonal period suitable for breeding. Most seabirds, however, are at the 'slow' end of the 'fast-slow' continuum (Weimerskirch 2001), and pairs whose first attempts fail may not have time to fit a second breeding attempt into the available breeding season. The probability that pairs that fail in their first breeding attempt will renest and will then be successful in raising young to the point of fledging depends on the species, the date of failure, the quality of individual birds, and other factors (Hipfner *et al.* 1999; Wendeln *et al.* 2000; Becker and Zhang 2011).

Brown and Morris (1996) described an incident in which flooding simultaneously destroyed eggs of about 80% of pairs in a colony of Ring-billed Gulls (*Larus delawarensis*) around the middle of the incubation period. Most or all of the pairs that failed renested synchronously about 12 d later: they laid smaller clutches and smaller eggs than those in the first nesting, but their productivity was as high as that of early-nesting pairs at the same site two years later. Here, I report on a similar incident in a colony of Common Terns (*Sterna hirundo*), in which flooding simultaneously destroyed about 90% of broods early in the chick-raising period; most of the pairs that failed renested about 11 d later. I measured renesting synchrony, and compared clutch-sizes, egg masses, hatching success, chick growth rates, asymptotic masses, fledging success, and productivity between first nestings and renestings.

Three other papers have reported data on renesting Common Terns. Arnold *et al.* (2004) conducted an experimental study of Common Terns at the same site, which included a group of birds whose clutches were removed immediately after clutch completion and renested 11-12 d later, compared to a control group matched for original laying dates. Two other multi-year studies of renesting Common Terns involved smaller numbers of birds that failed for other reasons (predation on eggs or chicks, food shortage) at various times during the nesting cycle (Wendeln *et al.* 2000; Becker and Zhang 2011). Both studies reported characteristics of the parents that did or did not renest, and productivity of the renesting pairs in several years; Wendeln *et al.* (2000) also reported clutch sizes and egg masses; Becker and Zhang (2011) also reported survival to recruitment; neither paper reported chick growth.

METHODS

Study Area and Field Methods

I studied Common Terns (hereafter, terns) at Bird Island, Marion, Massachusetts, USA (41° 40′ 10″ N, 70° 43′ 02″ W) in 1972. Terns had been studied at Bird Island in 1970 and 1971 (Nisbet and Drury 1972), and studies have been continued for 47 years thereafter (Breton *et al.* 2014; C. S. Mostello, unpubl. data). Data collected in 1972 were reported briefly by Nisbet and Cohen (1975) and Nisbet (1978a) but are reported and analyzed more fully here. In the first nesting, about 310 pairs of terns nested at Bird Island; 52 nests were studied in detail and 48 of these were included in an egg-exchange experiment (Nisbet 1978a). On 22 June, high seas from hurricane 'Agnes' washed over most of the island and destroyed most tern broods and late clutches. However, about 30 broods of chicks on the highest parts of the island survived the hurricane, including 17 study broods. The surrounding areas were immediately reoccupied, and many new nests were started 4-22 days after the hurricane, with a peak of laying in my study-plots between days 8 and 17 (mean 11.2 d ± 0.3 SE, *n* = 55; Fig. 1). I estimated that about 240 new nests were established on the island at this time, of which I marked 60 at the time of laying in the same area as my original study-plots or adjacent to them and studied 28 in greater detail. I estimated that almost all of the nests started between days 8 and 17 in my study-plots were renestings by pairs that had lost eggs or chicks in the hurricane, although a few may have been first nestings by pairs that were naturally late (see Discussion for elaboration).

All study-nests were enclosed within low wire fences to facilitate chick studies (Nisbet and Drury 1972). Study-plots were visited daily during the first egg-laying period and every 1-3 d during the re-laying period; all nests and eggs were marked when first encountered. Laying dates in the re-laying period were estimated based on the dates at which successive eggs in the clutch were found, plus in some cases back-calculation from dates of hatching, using data on laying and hatching intervals and incubation periods summarized by Nisbet and Cohen (1975); almost all estimated laying dates are thought to have been accurate to within ± 1 d.

Eggs were weighed to ± 0.1 g with a Pesola® spring balance within 3 d of laying; in cases where the egg was not weighed on the laying date, the fresh weight was estimated using the mean rate of weight-loss of 0.12 g d^{-1} (Rahn *et al.* 1976). Nests were checked daily during the first hatching period and every 2-3 d while eggs from the renesting period were hatching. Chicks were banded when first encountered, and dates of hatching were estimated to ± 1 d based on weight. Within each clutch and brood, eggs and chicks were denoted *A*, *B* and *C* in order of laying or hatching, respectively. Chicks from the first nesting period that survived the hurricane were weighed daily until they were found dead, disappeared,

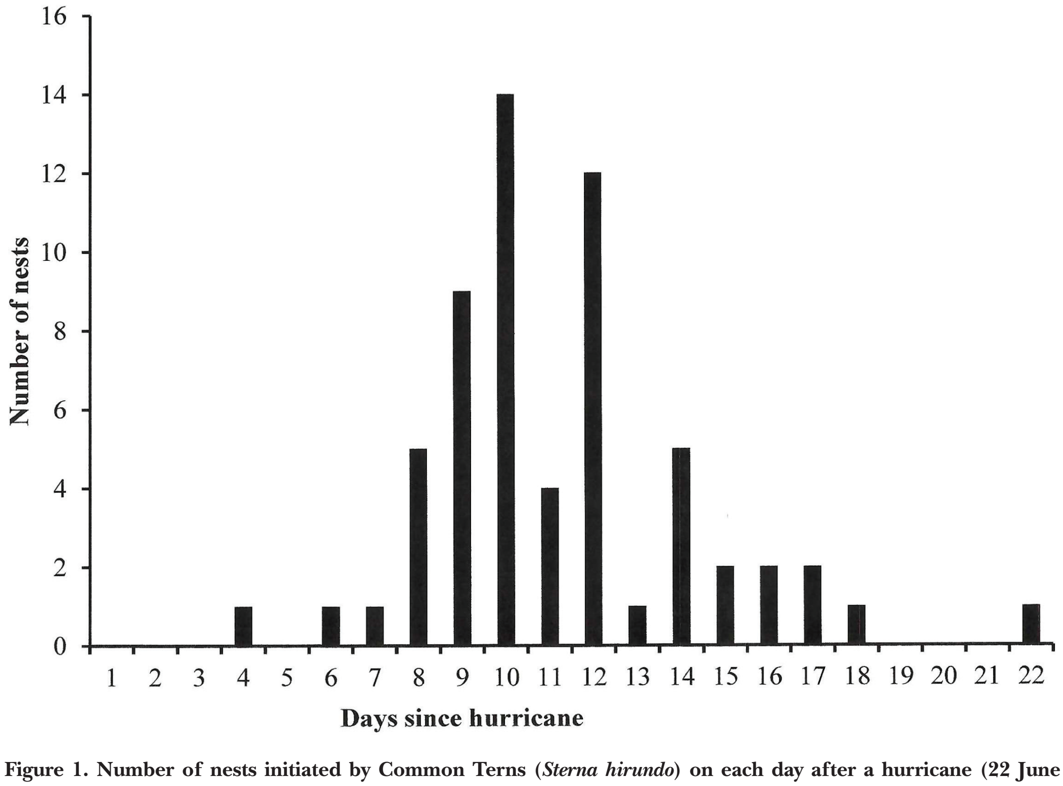

Figure 1. Number of nests initiated by Common Terns (*Sterna hirundo*) on each day after a hurricane (22 June 1972). Laying dates (first egg in each clutch) were estimated ± 1 d.

or fledged (last encountered at age ≥ 21 d). In the renesting period, study-plots were visited and chicks were weighed every 2-3 d until 28 July, and then on five dates until 11 August, when the surviving chicks were 13-21 d old (mean 16.1 d ± 2.8 SD, $n = 37$). Chicks were deemed to have survived to fledging if they weighed > 80 g when last encountered. This and subsequent studies at this site have indicated that most tern chicks that reach ages > 13 d and masses > 80 g survive to fledging (Nisbet 1978a; Nisbet *et al.* 2002; Tims *et al.* 2004; I. C. T. Nisbet, unpubl. data). However, none of these studies followed chicks until mid-August, so it is possible that this criterion may have overestimated survival; hence, estimates of productivity of renesting pairs are presented here as maxima.

For each nest included in the egg-exchange experiment, egg parameters pertain to the eggs laid in the nest; chick parameters pertain to the chicks that hatched in the nest (although these chicks were derived from eggs laid in other nests), because chick growth and survival appeared to be determined by the parents that raised the chicks (Nisbet 1978a).

Returns

Seven adults that attended marked nests in the first nesting period were individually marked with colored patagial tags. I searched for tagged adults during the renesting period and attempted to trace them to marked nests.

In 1975 (Nisbet 1978b), 1983 (Nisbet *et al.* 1984) and from 1986 onwards (Nisbet and Cam 2002; Breton *et al.* 2014), I trapped adults at Bird Island and several other nearby colonies, to search for banded terns that had survived from fledging in 1972 or other years to enter the breeding population from 1975 onwards. Although sampling was not rigorously randomized in any site or year until 1995 (Nisbet and Cam 2002), it was designed to sample birds from all parts of each colony site in each year and is thought to have yielded unbiased comparisons between cohorts of chicks banded in prior years, including the two subsets of the 1972 cohort.

Statistical Analysis

For each chick for which sufficient data were available, I calculated the linear growth rate (LGR) as the slope of a linear regression of body mass vs age between ages 4 and 14 d, and the asymptotic mass (AM) as the mean body mass over all encounters from age 17 d onwards (Nisbet *et al.* 2002; Tims *et al.* 2004). Although I have previously limited calculation of LGR to cases with ≥ 4 data points and of AM to cases with ≥ 2 data points (Nisbet *et al.* 2002; Tims *et al.* 2004), in this study only two weights and one weight, respectively, were available for many chicks in the renesting group, so I used these data to estimate LGR and AM for those chicks. Chicks that were known to have died before the hurricane are excluded from calculations of LGR; all chicks that survived the hurricane are thought to have fledged. Clutch-size, hatching success, fledging success, productivity and the probability of subsequent encounter as a breeder were compared between clutches, broods, and fledglings in the first and renesting periods using χ^2 tests, Fisher Exact tests, Mann-Whitney tests or ANOVA; egg mass, LGR and AM were analyzed using two-way ANOVA with Tukey's tests to identify significant differences between groups and among *A*-, *B*- and *C*-eggs and chicks. Because no *C*-chicks from renestings survived to fledging, comparisons for LGR and AM were limited to *A*- and *B*-chicks. Although the egg exchanges during the first nesting period resulted in changes in LGR and chick survival (Nisbet 1978a), those changes were reciprocal among groups, so that mean values would not have been changed.

Because few banded chicks survived to fledging from the first nesting in 1972, I also used data from chicks raised to fledging in first nestings at the same site in 1971 (Nisbet and Drury 1972) for the analysis of post-fledging survival. I used Fisher Exact tests to compare chicks raised in the renesting period in 1972 with (a) chicks raised in the first nesting period in 1972; and (b) chicks raised early in the season in 1971.

RESULTS

Characteristics of Surviving Pairs

Pairs in the first nesting that survived the hurricane laid significantly earlier than those that were washed out, reflecting the fact that the earliest-nesting pairs in the colony nested at the highest elevations. There were no significant differences in egg mass or clutch size (Table 1).

Table 1. Comparison of nest characteristics of Common Tern (*Sterna hirundo*) pairs in the first nesting whose clutches and broods survived the hurricane (in June 1972) with those that were washed out. Entries are in the form mean ± SE.

	Survived	Washed out	$F_{1,45}$	P
n	17	30[1]		
Laying date (*A*-egg) (1 May = 1)	20.50 ± 0.80	26.40 ± 1.40	7.96	0.007
Egg mass (*A*-egg) (g)	21.65 ± 0.28	21.83 ± 0.27	0.56	0.46
Clutch size	2.82 ± 0.09	2.73 ± 0.09		0.62[2]

[1]Excluding two clutches broken by a human intruder and three broods that were partially destroyed in the hurricane.
[2]χ^2 test comparing clutches of 3 eggs with clutches of 2 eggs, the latter including one clutch of one egg in the Washed out group.

Frequency of Renesting

Among seven adults that had been marked with patagial tags during the first nesting, three attended broods that survived the hurricane (see below for their breeding performance). Three of the remaining four birds were identified in the nesting area during the renesting period and probably renested there, but I was not able to determine the specific nests that they were attending. About 280 pairs lost their clutches or broods during the hurricane, and I estimated that about 240 new clutches were started subsequently; although a few of these may have been late-nesting birds that had not started nests before the hurricane (see Discussion), this suggests that at least 80% of the early-nesting pairs renested at Bird Island. Some of the remainder may have moved to renest in a colony at Ram Island, 10 km WSW of Bird Island: numbers nesting at Ram Island were higher in July than in May, but I did not make precise counts.

Breeding Performance

Compared to pairs in the first nesting, renesting pairs had smaller clutch-sizes, lighter eggs, and lower productivity (Table 2). Within-clutch differences in egg-mass were greater in renesting pairs (~6% difference between *A*- and *C*-eggs, vs ~2.5% in first-nesting pairs). Growth rates (LGR) were similar among groups, except that *C*-chicks from first nestings grew significantly more slowly than those in any other group (Table 2). LGR was also low in *B*-chicks in the renesting period, but the difference from *A*-chicks was not significant ($P = 0.08$, Tukey's test), probably because of small sample sizes. Asymptotic masses (AM) were similar among groups, except that *B*-chicks of renesting pairs had significantly lower values of AM. Most pairs in the first nesting that survived the hurricane were able to raise two chicks to fledging in good condition, and four pairs raised three. In contrast, most renesting pairs raised only one chick to fledging in good condition: five pairs raised two chicks,

Table 2. Comparison of breeding performance parameters between first nestings and renestings by Common Terns (*Sterna hirundo*) after a hurricane in June 1972. All entries except those for hatching success and survival to fledging are in the form mean ± SE (*n*). Data for egg-mass, LGR and AM are analyzed using two-way ANOVA with Tukey's tests for multiple comparisons; entries in the same block without a letter in common are significantly different ($P < 0.05$). The right-hand column gives *P*-values for pairwise comparisons between first nestings and renestings (χ^2 tests, Fisher exact tests, Mann-Whitney tests, or ANOVA; significant at $P < 0.05$); ns = not significant; nd = no data.

Parameter	First nesting	Renesting	*P*
Laydate (*A*-egg) (1 May = 1)	22.9 ± 0.6 (52)	64.2 ± 0.3 (55)	< 0.001
Clutch-size	2.85 ± 0.05 (52)	2.11 ± 0.08 (55)	< 0.001
Egg-mass (g):			
A-egg	21.89 ± 0.21 (52)a	20.08 ± 0.23 (55)b	< 0.001
B-egg	21.64 ± 0.22 (50)a	19.47 ± 0.25 (49)b	< 0.001
C-egg	21.30 ± 0.24 (41)a	18.88 ± 0.43 (13)b	< 0.001
Hatching success (%)	99% (116/117)[1]	94% (47/50)	ns
Linear growth rate (LGR) (g d^{-1}):			
A-chick	7.37 ± 0.33 (35)a	7.64 ± 0.49 (16)a	ns
B-chick	6.93 ± 0.34 (33)a	6.08 ± 0.80 (6)a	ns
C-chick	4.10 ± 0.52 (14)b	nd	—
Asymptotic mass (AM) (g):			
A-chick	122.6 ± 2.5 (10)a	122.4 ± 3.7 (8)a	ns
B-chick	120.6 ± 2.3 (12)a	88.9 ± 4.6 (4)b	< 0.001
C-chick	113.5 ± 4.0 (5)a	nd	—
Survival to fledging	72% (29/40)[2]	≤ 68% (28/41)	ns
Productivity (fledglings/nest)	2.07 ± 0.19 (14)	≤ 1.24 ± 0.15 (21)	< 0.001

[1]Excluding three clutches washed out in the hurricane and two clutches broken by a human intruder.

[2]Limited to broods that survived the hurricane, but excluding four chicks drowned in the hurricane while siblings in their broods survived.

but the survival rate of B-chicks was significantly lower in the renesting period (5/11 vs 11/12; Fisher Exact test, $P = 0.027$), and the surviving *B*-chicks were in poor condition when last encountered (Table 2).

The three marked birds that were traced to nests in both periods all attended nests with three eggs in the first period and two eggs in the renesting period. Their egg masses were 22.0, 22.2 and 22.2 g in the first period and 20.1, 20.7 and 19.3 g, respectively, in the renesting period. Although the sample size is too small for statistical tests, these data indicate that changes in clutch size and egg mass within individual birds were consistent with the group means (Table 2).

Encounters as Adults

Two of 34 chicks (6%) banded in the renesting period in 1972, and thought to have survived to fledging, were subsequently encountered as breeding adults in 1975-1995, vs 2/30 (7%) banded in the first nesting period and monitored after the hurricane in 1972 and 5/73 (7%) banded in 1971. These proportions were not significantly different (Fisher Exact tests, $P > 0.6$).

DISCUSSION

Following the hurricane, the areas where terns had lost eggs or chicks were immediately recoccupied and many new nests were established there. Although I have referred to these new nests as 'renestings' throughout this paper, it is possible that some might have been first nestings by pairs that were naturally late. However, I believe that very few such first nestings could have been included in my sample. In 1970 and 1971, only a few nests were started at Bird Island after 22 June, and almost all of these were located around the periphery of the island (author's unpubl. data). In 1971, laying was completed in my study-plots by 9 June (Nisbet and Drury 1972), and in 1972 the latest nest prior to the hurricane was started on 16 June. Renesting was highly synchronized, and only two nests were established in the study-plots outside the period from 6-18 d after the hurricane (Fig. 1). I excluded these two nests, and three others started on days 6, 7 and 18, from my analysis, thereby minimizing the chances that my sample could have included more than one or two naturally late pairs.

My observations of renesting in Common Terns were generally parallel to those of Brown and Morris (1996) in Ring-billed Gulls. In both cases most of the breeding pairs failed simultaneously due to extrinsic events (flooding caused by storms), and most or all of these pairs renested synchronously after a latency period of 11-12 d. The main difference was that the gulls studied by Brown and Morris failed in mid-incubation, whereas the terns in my study failed when most pairs had chicks up to 12 d old. In both studies, renesting pairs laid smaller clutches and smaller eggs than the means for the comparable group of birds in the first nesting period, although the differences were larger for the terns in my study than for the gulls in that of Brown and Morris (26% vs 7% for clutch-size; 9-11% vs 3-4% for egg mass or volume; Table 2). The renesting gulls in Brown and Morris's study had productivity similar to that of early and peak breeders in another year, whereas the renesting terns in my study had markedly lower productivity than early breeders that survived the hurricane (Table 2) and breeders at the same site in 1970 and 1971 (Nisbet and Drury 1972), with only slight evidence of differences in characteristics that might reflect differences in intrinsic quality (Table 1). Brown and Morris did not report data on chick growth, but I found marked differences in growth patterns: in the first nesting, *C*-chicks had low growth rates but those that survived to fledging did so in good condition; in renesting birds, *B*-chicks had low survival rates and the few that survived had low body masses when last encountered (Table 2). Hence, the low productivity of renesting birds in my study resulted from both reduced clutch-size and reduced parental performance in raising chicks.

Other studies of renesting in Common Terns are not closely comparable with mine. In Arnold *et al.*'s (2004) experimental study at Bird Island in 1998, the renesting pairs (group R) had lower productivity than the controls (EC) matched for original laying date, but the difference was only marginally significant; there were no differences in clutch size or egg mass. However, the sample of renesting pairs was small ($n = 11$), all re-laid before 30 May, and hatching was delayed by only 12 d (Arnold *et al.* 2004). The renesting Common Terns studied by Wendeln *et al.* (2000) and Becker and Zhang (2011) failed in their first nestings for varied reasons, including predation on eggs and chicks and food shortage; the frequency of failure was much lower (averaging 9% over a 17-yr period), and failures occurred throughout the first half of each season, so that renesting birds established nests among many others that were at later stages in the breeding cycle, and did not nest synchronously. Wendeln *et al.* (2000) found no differences in clutch size between first layings and re-layings by the same birds, and no consistent differences in egg mass (increases in some years, decreases in others). Becker and Zhang (2011, incorporating the data of Wendeln *et al.* 2000), found that productivity of renesting pairs was lower than that of first-nesting pairs in only two of seven years. Neither Wendeln *et al.* (2000) nor Becker *et al.* (2011) reported data on chick growth.

Adult terns in my study initiated their replacement clutches at a later stage in the breeding season than in most other studies of renesting: from 30 June to 9 July, dates at which chicks are starting to fledge in normal years. They were still feeding unfledged chicks at the time of my last visit on 11 August, close to the average date at which adult female terns usually depart on long-distance migration (Nisbet *et al.* 2011; Bracey *et al.* 2018). Terns that renest late in the season must incur significant physiological, energetic and temporal costs, both from the demands of egg-laying and chick-rearing and from delay in entering the post-fledging period when they have to care for fledglings, molt, and prepare for migration (Nisbet *et al.* 2011, 2017). Becker and Zhang (2011) reported that renesting terns had higher lifetime reproductive success and fitness than non-renesting birds, but their study included few birds that renested as late in the season as mine. As in my study, Becker and Zhang (2011) found that offspring from renestings recruited to the breeding population at similar rates to offspring from first nestings. Hence, renesting contributes directly to the fitness of parents, offsetting physiological, energetic and temporal costs for those that renest even late in the season. Renesting birds may also gain indirect benefits, including additional experience in raising chicks and reinforcing pair-bonds that may have been strained by early failures.

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