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FROM TRAGEDY TO TRIUMPH: RENESTING IN RING-BILLED GULLS

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ABSTRACT.—When animals that provide parental care to offspring are faced with actual or potential failure during a breeding bout, the option to continue breeding is countered by the option to cut losses and forego reproduction until the next breeding season. In 1990, we recorded laying date and laying order of eggs in 51 Ring-billed Gull (*Larus delawarensis*) clutches prior to their total loss by flooding. Pairs remained on territory and produced new clutches following a refractory period of 11.6 ± SD of 1.9 days. Post-loss clutches were initiated synchronously ($n = 51$ clutches in four days; 89% of all clutches marked in the 7 × 7 m study plot) but mostly contained significantly fewer and lighter eggs than first clutches. We contrast incubation, hatching and chick survival patterns of these storm-delayed pairs in 1990 with patterns of early-, peak- and late-nesting pairs at the same colony in 1992. The incubation and within-clutch hatching patterns of post-loss clutches 1990 were most similar to those of late nesting pairs in 1992, yet these storm-delayed pairs realized a fledging success similar to that of early-and peak-nesting pairs in 1992. We discuss larid reproductive strategies in the context of conditions that favor successful renesting. *Received 22 August 1994, accepted 27 January 1995.*

IN LONG-LIVED, iteroparous breeders, a given reproductive bout carries both energetic and risk costs that must be weighed against the potential benefits of investment in the present versus future breeding opportunities. Thus, individuals that best play strategies to optimize lifetime reproductive success are expected to weigh the prospects of current reproductive success against the cost to long-term future prospects (Williams 1966). When animals that provide parental care to offspring are faced with actual or potential failure during a breeding bout, they must "decide" whether to continue effort during that breeding season, or to cut their losses and forego reproduction until the next breeding season.

In many temperate-nesting avian species, the timing of breeding is important to seasonal reproductive success and the timing of optimal clutch initiation is believed to coincide with peak food availability for the chicks (Lack 1968). However, many proximate factors operate to influence the onset of breeding in a particular year. A few examples include day length (Parsons 1975b), the physiological state of females (Perrins 1970), and the availability of suitable nesting substrate (Morris and Chardine 1985). Most temperate- and tropical-nesting seabirds normally lay a single clutch and raise a single brood during a given breeding season (except Silver Gulls, *Larus novaehollandiae stephens*; Nicholls 1974). In temperate-nesting larids, the synchrony of clutch initiation, clutch size, and egg size all decrease as the breeding season progresses (e.g. Parsons 1975b, Boersma and Ryder 1983), and later-nesting pairs usually experience lower breeding success than earlier nesters (Nisbet and Cohen 1975, Morris et al. 1976, Massey and Atwood 1981, Boersma and Ryder 1983).

Temperate-nesting *Larus* gulls are indeterminate layers (Parsons 1976) that compensate for the loss of an egg(s) prior to clutch completion by continuing to lay until their clutch contains a definite number of eggs, an ability that terminates shortly after clutch completion. However, following the loss of a completed clutch, both tropical- and temperate-nesting larids are known to lay replacement clutches following a refractory period (Ashmole 1962, 1963, Beer 1966, Maunder and Threlfall 1972, Nisbet and Cohen 1975, Wooller 1980, Hayward et al. 1982, Storey 1987, Massey and Fancher 1989, Mills 1989). The ability to replace lost clutches may be influenced by both seasonal factors (Parsons 1976) and breeding experience (Wooller 1980). When the fledging success of renesting pairs is reported, it is usually "low" or "nil."

In early May 1990, we recorded details on 51 completed Ring-billed Gull (*L. delawarensis*) clutches containing eggs of known lay date and order that were later destroyed by flooding. Pairs remained on territory and produced new clutches following a refractory period. We compare: (1) the egg size, clutch size and laying synchrony of pre- and post-loss clutches; and (2) the incubation, hatching and chick survival patterns of post-loss clutches in 1990 against these patterns for Ring-billed Gulls nesting in the same study area in 1992. We then discuss larid reproductive strategies in the context of conditions that favor successful renesting.

STUDY AREA AND METHODS

An estimated 2,500 pairs of Ring-billed Gulls nest on a limestone rock pile on a breakwall associated with the Welland Ship Canal, 1 km off the north shore of Lake Erie near Port Colborne, Ontario (42°53′N, 79°16′W). In early April 1990, before first clutches were initiated, we marked a 7 × 7 m study area and erected an observation blind near the edge of the plot. With only four exceptions induced by inclement weather, we visited the site daily during egg laying from 13 April to 8 May 1990 to mark new clutches and to number eggs as they were laid. Each egg was measured using Vernier calipers and weighed with a 100-g Pesola scale.

On the morning of 10 May 1990, a violent storm crossed Lake Erie accompanied by winds of 100 km/h and 3-m waves that persisted over the next two days, raising water levels in the vicinity of the colony approximately 1.5 m. About 80% of 2,500 Ring-billed Gull nests on the rock pile were washed away, and large quantities of gravel and large rocks were redistributed over the nesting area. Nesting material, broken eggs, and about a dozen dead adult gulls were scattered throughout the colony. All 51 clutches within our small study plot were completely destroyed (hereafter referred to as pre-loss clutches). On 12 May 1990, we remarked the corners of the study plot and continued to visit the area daily through egg laying, incubation and hatching of all new clutches ($n = 57$) initiated in the area. Clutches initiated after the storm (hereafter referred to as post-loss clutches) were treated as described above. Chicks in all broods were banded with Darvic color bands in unique combinations according to their hatch order.

Two years later (1992) an opportunity arose in the context of another study to contrast various breeding parameters of the birds delayed by the storm in 1990 with those of pairs initiating clutches in the same study plot but in a more normal year. Thus, in 1992, we marked a slightly larger study area (10 × 10 m) in the same location used in 1990. We visited the study site daily, and marked eggs and clutches as described above. All chicks were uniquely color banded or dyed with Rhodamine B with respect to hatch order. Our visits into the study site were terminated on 30 May 1992 when all chicks hatched from the study nests. In both years, we recorded from a blind the fate of chicks and the number of chicks that survived to 21 days posthatching.

In the sections that follow, we compare the incubation, hatching and chick survival patterns for post-loss clutches in 1990 against those for 1992 clutches. Our visitation schedule was the same in these two years, and more comparative data for this comparison were available in 1992 than in 1991 (for visitation schedule and annual objectives, see Brown and Morris 1994).

Although we report means (±1 SD), we used nonparametric statistical tests (which compare medians) to identify differences for both categorical and continuous variables because the eggs within a clutch were not independent (i.e. the clutch was the legitimate sampling unit). We used paired tests (e.g. Freidman ANOVA, Wilcoxon sign-rank test) for within-clutch comparisons. For all tests, the level of significance for rejection of the null was $P < 0.05$.

RESULTS

Egg-laying chronologies in 1990 and 1992.—In 1990, clutch initiation began on 13 April and continued to 4 May ($n = 51$ clutches in 22 days; Fig. 1A). The peak of clutch initiation (peak defined here as mean clutch initiation date ±1 SD = 23.8 April ± 4.9 days) occurred over the 10 days between 20 and 29 April during which 35 (69%) of 51 clutches were initiated. All of these clutches were lost prior to hatching in the storm on 10 May. The mean time between the first egg laid in pre-loss clutches and their destruction on 10 May 1990 was 15.6 ± 5.6 days ($n = 51$, range 6–27 days). The initiation of new clutches began on 14 May. The initiation of post-loss clutches was highly synchronous with 51 (89%) of 57 clutches initiated between 21 and 24 May (Fig. 1B). The mean time interval (i.e. relay interval) between the destruction of pre-loss clutches and the initiation of post-loss clutches was 11.6 ± 1.9 days ($n = 57$, range 4–16 days).

In 1992, clutch initiation in the larger study area (same site in colony) began on 8 April and continued to 11 May ($n = 111$ clutches in 34 days). The peak of clutch initiation was 16 to 29 April (22.2 April ± 6.5 days) during which 77 (69%) clutches were initiated. Clutches initiated prior to 16 April ($n = 22$) were referred to as early clutches while those initiated after 29 April ($n = 12$) were designated as late clutches.

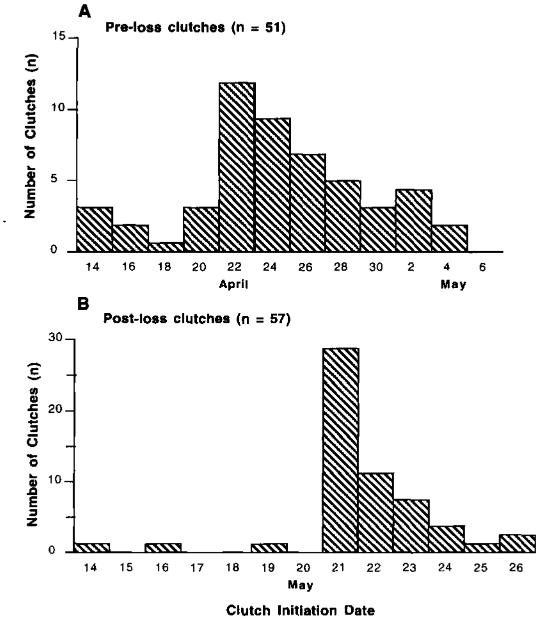

Fig. 1. (A) Pre-loss and (B) post-loss Ring-billed Gull clutch initiation dates at Port Colborne Ontario, 1990. The storm occurred on 10 May. Clutch-initiation dates are given at (A) two-day and (B) one-day intervals.

Characteristics of pre-loss and post-loss clutches in 1990.—In the tabular and statistical results that follow, we include only the 51 post-loss clutches initiated between 21 and 24 May 1990 in an attempt to separate renesting from late-nesting gulls (e.g. clutches initiated 14, 16 and 19 May; see Discussion). We used the mean relay interval ±1 SD as our criteria for choosing the smaller sample of post-loss clutches for analyses.

The distribution of clutch sizes in pre- and post-loss groups showed disproportionately more three-egg clutches in the pre-loss group than in the post-loss group (Fisher exact test, $P = 0.001$; Table 1). In the pre-loss and post-loss groups, respectively, 4 of 35 and 17 of 39 three-egg clutches were completed in three days while the remaining clutches took four or more days to complete (2×2 contingency table, $X^2 = 9.3$, df = 1, $P < 0.01$). The clutches ($n = 3$) initiated on 14, 16 an 19 May each contained three-eggs, while the clutches ($n = 3$) initiated on 25 and 26 May each contained two eggs. All one-egg post-loss clutches ($n = 5$) disappeared within six days after laying.

TABLE 1. Distribution of Ring-billed Gull clutch sizes for pre-loss and post-loss clutches at Port Colborne, Ontario in 1990.

		Clutch size		
Clutch type	*n*	3	1, 2 or 4	$\bar{x} \pm$ SD
Pre-loss	51	50	1[a]	2.98 ± 0.1
Post-loss	51[b]	39	12[c]	2.70 ± 0.7

[a] A two-egg clutch initiated 3 May 1990.

[b] Clutches initiated 21-24 May 1990.

[c] Five one-egg, six two-egg and one four-egg clutches.

There were significant differences among the masses of first-, second- and third-laid eggs within both pre-loss (Table 2; Freidman $X^2 = 10.7$, df = 2, $n = 50$, $P < 0.01$) and post-loss ($X^2 = 22.5$, df = 2, $n = 39$, $P < 0.01$) three-egg clutches. In pre-loss clutches, the third egg was significantly lighter than the first (Wilcoxon sign-rank test, $Z = -2.3$, $P < 0.05$) and second ($Z = -4.0$, $P < 0.01$) eggs. In post-loss clutches, the third egg was also significantly lighter than the first ($Z = -2.0$, $P < 0.05$) and second ($Z = -4.6$, $P < 0.01$) eggs, and the first egg was lighter than the second egg ($Z = -2.8$, $P < 0.01$). First and third eggs from the pre-loss clutches were significantly heavier than first (Mann-Whitney $U = 2.4$, $n_1 = 50$, $n_2 = 39$, $P < 0.05$) and third ($U = -2.9$, $P < 0.01$) eggs in post-loss clutches (Table 2). In summary, post-loss clutches were smaller, completed faster and contained lighter eggs than pre-loss clutches.

Incubation and hatching patterns for post-loss eggs in 1990 and all eggs in 1992.—We defined the incubation period for each egg as the number of days between laying and hatching of that egg (Chardine and Morris 1983). Table 3 provides within-clutch incubation duration data for each egg in all monitored periods. In 1990, the within-clutch incubation periods for first, second and third eggs in post-loss clutches were significantly different (Freidman $X^2 = 23$, df = 2, $P < 0.01$). First eggs in post-loss clutches were incubated significantly longer than the second ($U = -4.8$, $P < 0.01$) and third ($U = -5.0$, $P < 0.01$) eggs; there was no difference between second and third eggs ($P > 0.1$). In 1992, the within-clutch incubation periods for first, second and third eggs were significantly different for early ($X^2 = 18$, df = 2, $P < 0.01$) and peak ($X^2 = 63.6$, df = 2, $P < 0.01$) clutches, but not for late ($X^2 = 5.6$, df = 2, $0.1 > P > 0.05$) clutches. In both early and peak clutches, the incubation period for the first egg was significantly longer than that of the second egg, and the second egg

TABLE 2. Egg mass (g; $\bar{x} \pm$ SD) for first-, second- and third-laid eggs from pre-loss and post-loss Ring-billed Gull clutches at Port Colborne, Ontario in 1990. Same letter denotes significant differences.

Clutch type	n[a]	Mass (g) of Egg 1	Mass (g) of Egg 2	Mass (g) of Egg 3
Pre-loss	50	53.1 ± 4.5^{bd}	54.0 ± 4.4^{c}	51.6 ± 4.1^{bce}
Post-loss	39	50.9 ± 4.2^{dfg}	52.6 ± 3.7^{fh}	49.4 ± 3.7^{egh}

[a] Three-egg clutches.

was incubated longer than the third egg (Wilcoxon sign-rank tests, all $P < 0.01$). In addition, eggs in early clutches took a significantly longer time to hatch than eggs in peak and late clutches regardless of their position in the laying sequence (Mann-Whitney U-tests, all $P < 0.05$).

The incubation patterns for eggs in post-loss clutches (1990) were most similar to those of eggs in late clutches in 1992; there was no difference ($P > 0.1$) in the incubation period for first, second and third eggs between post-loss (1990) and late (1992) clutches. Conversely, the incubation period for first and second eggs in post-loss clutches were significantly shorter than those for first ($U = -3.9$, $n_1 = 27$, $n_2 = 39$, $P < 0.01$) and second ($U = -4.0$, $n_1 = 30$, $n_2 = 39$, $P < 0.01$) eggs from peak 1992 clutches.

The within-clutch hatching patterns of post-loss (1990) and early, peak and late (1992) clutches that hatched all three eggs are given in Table 4. In 1992, the hatching patterns of eggs in clutches initiated early in the egg laying period were relatively synchronous and decreased for clutches initiated later. In 1990, the hatching pattern of eggs in post-loss clutches was most typical of the late-nesting gulls in 1992. In 12 of the 20 post-loss clutches that hatched three chicks, eggs hatched asynchronously at intervals of at least 24 h. In the other eight clutches, the *A*-chick (first-hatched) and *B*-chick hatched on the same day, with the *C*-chick hatching at least 24 h later (Table 4).

Chick survival post-loss 1990 and 1992.—In 1990, pairs laying post-loss three-egg clutches realized a mean fledging success (chick survival to 21 days posthatching) of 1.5 ± 0.7 chicks/pair ($n = 39$; Table 5). The fledging success of these post-loss pairs was not statistically different from pairs that laid three-egg clutches during the early, peak and late nesting periods of 1992 (all $P > 0.05$). Pairs that laid other-sized clutches raised fewer chicks to 21 days regardless of laying period. However, when all clutch types were combined, the fledging success of post-loss pairs was similar to that of both early and peak nesters (both $P > 0.1$). The comparison with late nesters did not reach statistical significance, but was suggestive (Mann-Whitney U-test, $Z = -1.7$, $n_1 = 51$, $n_2 = 12$, $0.1 > P > 0.05$).

In 1990, 20 post-loss clutches hatched three chicks. *C*-chicks realized the poorest survival in both synchronous (1 of 8 fledged) and asynchronous (2 of 12 fledged) broods, while *A*- and *B*-chicks realized equal survival in both synchronous (8 *A*-chicks and 7 *B*-chicks) and asynchronous (9 *A*-chicks and 9 *B*-chicks) broods.

From 1992 through 1994, 15 (23%) of the 65 post-loss fledglings have been sighted at the

TABLE 3. Mean (±SD, with n in parentheses) incubation duration for Ring-billed Gull eggs in post-loss (1990) and early, peak and late (1992) clutches. Same letters denote significant difference between eggs ($P < 0.05$, except u, where $0.1 > P > 0.05$).

Clutch type	Incubation duration (days) Egg 1	Incubation duration (days) Egg 2	Incubation duration (days) Egg 3
1990			
Post-loss	26.0 ± 1.0^{cdkl} (27)	24.7 ± 0.6^{cmn} (30)	24.5 ± 0.8^{do} (30)
1992			
Early	31.0 ± 1.3^{efkpq} (11)	28.0 ± 1.3^{egmrs} (13)	26.1 ± 1.7^{fgotu} (15)
Peak[a]	27.2 ± 1.1^{hilp} (39)	25.5 ± 0.8^{hjnr} (39)	24.5 ± 1.0^{ijt} (39)
Late[b]	26.4 ± 1.3^{q} (5)	24.8 ± 0.4^{s} (5)	24.6 ± 0.5^{u} (5)

[a] Includes only clutches ($n = 39$) where three eggs hatched.

[b] Sample sizes were low because of termination of investigator visits into colony.

TABLE 4. Within-clutch hatching patterns Ring-billed Gull eggs in clutches during post-loss period (1990) and during early, peak and late periods (1992) at Port Colborne. Equal sign (=) denotes eggs hatched on same day, while greater-than symbol (>) denotes eggs hatched more than 24 h apart.

Clutch type	Hatching pattern[a] Synchronous A=B=C	Synchronous A=B>C	Asynchronous A>B=C	Asynchronous A>B>C
	1990			
Post-loss	0	8	0	12
	1992			
Early	5	2	1	0
Peak	4	22	6	7
Late	0	2	0	3

[a] Data includes only clutches in which all three eggs hatched.

Port Colborne lighthouse colony. In 1993 and 1994, 5 of these 15 adults were trapped on their clutches and sexed by discriminate-function analysis (body characters used were head-bill length and gonys depth); all five were males, including two brothers (Brown unpubl. data).

DISCUSSION

In 1990, we recorded details on 51 completed Ring-billed Gull clutches that were destroyed by flooding and 57 new clutches laid in the same area after the storm. We suggest that most of these poststorm clutches were likely laid by renesting pairs and discuss the patterns associated with replacement clutches in the context of larid reproductive strategies and the conditions that favor successful renesting.

Were poststorm clutches laid by renesting pairs?—Renesting by uniquely recognizable individuals (e.g. color banded) has been reported in a number of larids (Austin 1951, Wooller 1980, Hays 1984, Massey and Fancher 1989). While we recognize that individual birds were not uniquely identifiable in our study, several factors suggested that the post-loss clutches were laid by renesting pairs. First, the interval between flooding (10 May) and initiation of post-loss clutches in our study ($\bar{x} = 11.6 \pm 1.9$ days) was similar in duration to known relaying intervals reported for other larids (13.2 ± 0.1 days for Herring Gulls [*L. argentatus*], Parsons 1975b; 12.4 ± 1.4 days for Black-legged Kittiwakes [*Rissa tridactayla*], Wooller 1980; 9 days for Common Terns [*Sterna hirundo*], Hays 1984; 7–9 days for Least Terns [*S. antillarum browni*], Massey and Fancher 1989).

TABLE 5. Number of chicks fledged per pair (survival to 21 days posthatching) according to clutch type (three-egg and other clutches) of Ring-billed Gulls nesting at Port Colborne, Ontario during post-loss period in 1990, and early, peak and late periods in 1992.

Clutch type	No. pairs	Clutch size ($\bar{x}$ ± SD)	Chicks fledged (*n*)	Chicks fledged/pair ($\bar{x}$ ± SD)
		Post-loss 1990		
Three eggs	39	3.0 ± 0.0	58	1.5 ± 0.7
Other	12	1.8 ± 0.8	7	0.6 ± 0.6
Total	51	2.7 ± 0.7	65	1.3 ± 0.8
		Early 1992		
Three eggs	17	3.0 ± 0.0	27	1.6 ± 1.0
Other	5	2.4 ± 0.8	1	0.2 ± 0.4
Total	22	2.9 ± 0.5	28	1.3 ± 1.1
		Peak 1992		
Three eggs	75[a]	3.0 ± 0.0	110	1.5 ± 0.9
Other	1	2.0 ± 0.0	2	2.0 ± 0.0
Total	76	3.0 ± 0.1	112	1.5 ± 0.9
		Late 1992		
Three eggs	8	3.0 ± 0.0	10	1.2 ± 1.0
Other	4	2.2 ± 0.0	0	0.0 ± 0.0
Total	12	2.8 ± 0.8	10	0.8 ± 1.0

[a] One nest deleted because vegetation obscured visibility of chicks from blind.

Second, nest-site tenacity is common to many larids (Austin 1949, McNicholl 1975, Southern 1977, Blokpoel and Courtney 1980, Cuthbert 1988) and likely facilitated the resettling of pairs in close proximity to their pre-loss nesting location. Parsons (1975a) found that experimental egg removal caused little movement of nest sites by banded Herring Gull pairs. Furthermore, we now know that 80 of the 104 Ring-billed Gull adults that were color banded in our study area (10 × 10 m) during 1992 returned to the same area to breed in 1993 ($\bar{x}$ between year nest distance = 1.1 ± 0.9 m, $n = 24$ stable pairs; Brown unpubl. data).

Third, the similarity in the number of pre-loss ($n = 51$) and post-loss ($n = 57$) clutches, coupled with the high degree of nesting synchrony of pairs after flooding, suggests that most post-loss clutches were laid by renesting gulls. Rapid and synchronous renesting also has been reported in Forster's Terns (*S. forsteri*); in two different years, 77 and 100% of renesting pairs did so in less than 10 days after flooding (Storey 1987). Accordingly, we believe it likely that repeat clutches were laid by pairs that remained on territory after the loss of their first clutch. However, since it was also likely that a few post-loss clutches were laid by opportunistic late-nesting pairs (in particular, the three-egg clutches initiated on four, six and nine days after the storm), we considered only the 51 post-loss clutches initiated from 21 through 24 May to be replacement clutches.

Patterns associated with replacement clutches.—Several factors influence the patterns associated with clutch replacement in larids, including laying date (Parsons 1975b, 1976), clutch age (Parsons 1975b, 1976, Wooller 1980), and breeding experience (Wooller 1980). In our study, most post-loss clutches (89%) were initiated synchronously over a four-day period, suggesting that neither the ages of the pre-loss clutch (range 6–27 days) nor their laying dates (13 April–4 May) controlled the relay interval. However, since there were disproportionately more one- and two-egg replacement clutches, and the three-egg replacement clutches contained lighter eggs than pre-loss clutches, females probably had lower energy reserves to invest in replacement clutches. This interpretation is consistent with that of other authors who have proposed that: (1) Herring Gulls stopped laying eggs when egg size was below a threshold value (Parsons 1975b); (2) egg size in Western Gulls (*L. occidentalis*) was influenced by female physiological condition (i.e. energy reserves) and possibly food availability (Pierotti and Bellrose 1986); and (3) female Ring-billed Gulls in poor body condition lay smaller clutches containing smaller and lower-quality eggs (Meathrel and Ryder 1987a). In our study, it appears that females did not delay replacing lost clutches in order to increase body condition. Based on the numerous observations that avian clutch sizes decrease with season, Rowe et al. (1994) constructed a model to show that a benefit of female body condition (and, hence, clutch size) gained by a delay would, at some point, be outweighed by a cost of lower offspring value. Our data support the prediction that the storm-delayed gulls reduced clutch size and egg mass, and did not delay relaying. While egg size in larid clutches usually decreases with position in the laying sequence (Vermeer 1969, Parsons 1975b, Meathrel and Ryder 1987b), *A*-eggs were lighter than *B*-eggs in replacement clutches. This suggests that females may be able to partition energy reserves among the eggs in an attempt to optimize clutch size.

In larids that lay multi-egg clutches, effective incubation is usually delayed until the clutch is complete (Vermeer 1970, Parsons 1972, Nisbet and Cohen 1975), resulting in a more synchronous hatching pattern with the *A*- and *B*-chicks hatching on same day, and the *C*-chick hatching 24 to 48 h later (Courtney 1979). As the breeding season progresses, effective incubation begins at clutch initiation, and within-clutch hatching patterns become more asynchronous (Morris 1988). The incubation and hatching patterns of eggs in replacement clutches in our 1990 study more closely resembled those of late-nesting Ring-billed Gulls in 1992. Renesting pairs began incubation at clutch initiation, as reflected by the shorter incubation durations ($P < 0.05$) of *A*- and *B*-eggs in replacement clutches than early and peak nesters (1992), resulting in a more asynchronous hatching pattern (i.e. eggs hatched >24 h apart). An asynchronous hatching pattern has been viewed as a parental adaptation that facilitates brood reduction when food availability is low and unpredictable (Lack 1968); older and larger offspring within a brood gain competitive and survival advantages at the expense of their younger siblings (see Parsons 1975a). These expectations were realized in that *C*-chicks realized poor survival in comparison to their older siblings, and all pairs that hatched at least on egg (44 of 51) raised at least one chick to 21 days.

Conditions that favor successful renesting.—Following the complete loss of their clutches on 10 May 1990, each Ring-billed Gull pair had the option to either cut their losses and save further investment for future breeding opportunities, or try again. In larids, first-time and renesting pairs that breed later in a season usually realize lower breeding success (e.g. Hayward et al. 1982). While egg mass, clutch size, incubation, and hatching patterns of the replacement clutches that we monitored reflected those associated with late-nesting larids in a normal year, nest synchronization was greater. Furthermore, the average fledging success of renesters was similar to that of peak breeders recorded at this colony in other years (Table 5; see also Brown and Morris 1994).

During our study, four factors likely contributed to successful renesting including: (1) the large number of renesting pairs; (2) the high degree of nest synchrony; (3) the timing of renesting was early enough in the season and conditions were at least adequate for successful breeding; and (4) that renesters were delayed early breeders, and likely to be older and more experienced breeders rather than typical late nesters. Similarly, late-nesting Herring Gull pairs experimentally delayed as a group realized breeding success equal to that of peak nesters (Parsons 1975a). In Herring and Ring-billed gulls, respectively, nesting synchrony has been correlated with hatching and fledging success (Parsons 1975a), and to lower levels of aggression; aggression was negatively correlated with fledging success (Fetterolf 1984). In Red-billed Gulls (*L. novaehollandiae scopulinus*), the mean egg and clutch sizes of early-nesting pairs, that lost a clutch and relayed, were larger than those of peak birds laying first clutches at the same time, indicating that early nesters were better quality birds than late nesters (Mills 1979).

Severe weather and flooding (Parsons 1975b, White et al. 1976, Montevecchi 1978, McNicholl 1982, Storey 1987), as well as predation (Nisbet and Welton 1984, Massey and Fancher 1989), are often major causes of nest failure among ground-nesting larids, and such single events can have catastrophic effects on nesting success of breeding pairs. While most ground-nesting larids lay a single clutch and raise a single brood, the potential for rapid renesting may have evolved in response to such unpredictable events where there is the opportunity to renest in synchrony with other breeders. Larids may follow a simple rule—replace lost clutches as quickly and often as possible. Thus, while the timing of breeding may coincide with peak food availability, early breeding permits a second breeding attempt within a season for older more experienced breeders that have a lower future survival and residual reproductive value. Since larids usually experience greater productivity with age (Mills 1973, Pugesek 1983, Pugesek and Diem 1983), renesting may add an important component to the fitness of aging breeders. This explanation is consistent with: (1) the negative correlation between laying date and age observed in larids (Ryder 1975, Haymes and Blokpoel 1980, Massey and Atwood 1981, Nisbet et al. 1984); (2) the fact that reproductive effort of California Gulls (*L. californicus*) increased with parental age and was associated with higher mortality of older parents (Pugesek 1983); (3) the fact that ability to replace lost clutches increased with breeding experience of female Black-legged Kittiwakes (Wooller 1980); and (4) the observation that young Ring-billed Gulls at Port Colborne, identified by black markings on the tail feathers, sometimes abandon one- and two-egg clutches shortly after completion (Brown pers. obs.). Renesting also may contribute to future reproductive success through proximate mechanisms such as territory and partner retention. While renesting can have some selective value in the short term, the long-term costs and benefits of renesting on longevity and lifetime reproductive success of males and females of different age classes require further study.

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