

REPRODUCTIVE ECOLOGY OF THE WESTERN GULL: THE IMPORTANCE OF NEST SPACING

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GULL colonies usually exhibit considerable variation between pairs in both territory size and timing of breeding. This variation is subject to natural selection, and timing of breeding and territory size can be correlated with reproductive success (Paynter 1949; Paludan 1951; Vermeer 1963, 1970; Brown 1967; Kadlec and Drury 1968; Kadlec et al. 1969).

Patterson (1965) and Kruuk (1964) showed that for the small Black-headed Gull (*Larus ridibundus*) the principal source of egg and chick mortality was predation. For these birds, optimum predator defense resulted from nesting during that period when the maximum number of birds were breeding. Pairs breeding either earlier or later suffered greater loss of chicks to predation. Patterson (1965) also postulated that there should be an optimal spacing of nests, based on a balance between clumping of nests for enhancement of group defense and scattering of nests for effectiveness of the cryptic coloring of eggs and chicks (Tinbergen et al. 1967).

For the larger *Larus* gulls neighboring pairs may be a more important source of chick loss than predators (Paynter 1949, Emlen 1956, Parsons 1971). For these species large territory size may reduce the chance that a chick will trespass into a neighbor's territory. It has also been found that adults defend their territories more actively when they have chicks than when they are incubating (Hunt and Hunt MS, also this study, see below). Thus in these species early nesting may be advantageous as a means of minimizing chick loss to neighboring pairs.

In light of the conflicting selective pressures on territory size and timing of breeding, it is reasonable to expect that the optimum territory size and time for breeding will vary from one colony to another, depending upon the relative importance of predators or neighbors for chick loss. The colony of Western Gulls (*Larus occidentalis wymani*) nesting on Santa Barbara Island, California, provided an opportunity to test this hypothesis, as the only potential chick predators there are adult Western Gulls. In the present study we identified the causes of chick mortality and related the reproductive success of pairs to aspects of spacing of nests and timing.

STUDY SITE AND METHODS

We conducted our study on Santa Barbara Island, Channel Islands National Monument, Santa Barbara County, California. Santa Barbara Island is a 260-ha (1 square mile) island 61 km (38 miles) from the nearest mainland and 39 km (24 miles) from

the nearest island, Santa Catalina Island. Philbrick (1972) provides an account of the history and flora of the island, while its avifauna is described by Hunt and Hunt (1974).

The colony of Western Gulls was divided into three separate segments: two-thirds of the 1510 pairs counted on territory in July 1972 nested on the western plateau, while another 25% utilized the southern third of the eastern slopes and plateau. The remaining pairs nested on the northeast corner of the island.

Our two study sites were on the western plateau where the gulls nested in fields of ice plant (*Mesembryanthemum crystallinum*). The places chosen for our studies appeared to have a relatively high concentration of nests, but they cannot be classified as clearly representing either colony edges or central areas, as the colony was patchily distributed and poorly defined.

From 15 May until 23 July 1972, we lived on the island and made daily visits into the colony. To determine territory size we plotted two grids during the incubation phase, placing numbered stakes at 5-m intervals outlining two tracts of 125 × 65 m and 125 × 85 m respectively.

A total of 63 nests were staked in the two grids, but hatching failure, desertion, or egg loss reduced to 39 the total number of nests on which our statistics are based. In each nest the eggs were marked and measured (see Hunt and Hunt 1973). Chicks were banded and weighed on the day of hatching and reweighed subsequently every fifth day. Growth rates of the chicks on the basis of weight were calculated from the straight line portion of the growth curve between ages 10 and 20 days (Spaans 1971, Hunt 1972).

Observations were made from blinds with eye level 11 feet high, which facilitated watching the gulls' interactions and made pinpointing the birds' locations within our grids relatively easy. Data for the mapping of territories included places where either adults or chicks stood, points from which intruding birds were driven, and the sites of agonistic interactions. Classified as agonistic interactions were grass pulling, supplanting, attacks, and fights. During the chick phase the grids were each watched on 25 days for between 1 and 15½ h at a time (mean = 4.0), for a total of 224.75 h or 3406.3 nest hours of observation. At 20-min intervals the number of parents present on each territory was recorded, as were arrivals and departures of parents between these intervals.

RESULTS

Chick survival.—Although the chicks in our study sites hatched over a period of 38 days (22 May to 28 June), 85% of the broods hatched during the first 2 weeks (Fig. 1). The distribution of hatching dates in our study plots appeared to be representative of the colony as a whole.

Of the 99 chicks hatched within our study grids, 84 (84.8%) survived to a weight of 500 g, our criterion for survival (see Hunt 1972). Of those 84 surviving to 500 g, only two were known to have died before fledging. The causes of chick loss are presented in Table 1. Although the numbers are too few for statistical analysis, it is clear that killing by neighbors and starvation (as judged by loss of weight or failure to grow) were the most important causes of mortality. Table 1 also shows that chicks of any age

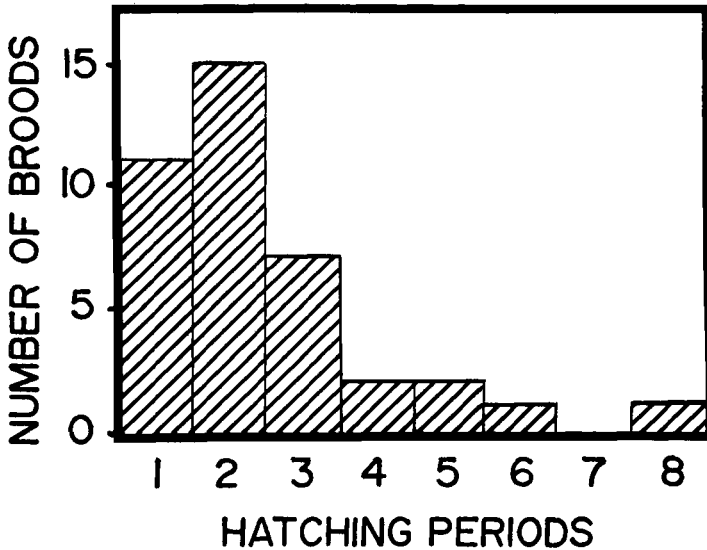


Fig. 1. Hatching dates of the first chick of 39 broods in our study areas vs. the number of broods hatched in those periods. 1, 22-26 May; 2, 27-31 May; 3, 1-5 June; 4, 6-10 June; 5, 11-15 June; 6, 16-20 June; 7, 21-25 June; 8, 26-30 June.

were likely to be killed by neighbors, while starvation took its toll primarily among chicks older than 10 days.

Causes of mortality were not uniformly distributed with respect to the date of hatching of the first chick in a brood (Table 2). It appears that more chicks were killed from late broods than from early broods and that starvation may have been less frequent in the late broods than in the early. No statistically significant correlation was evident between time of hatching and either chick survival (Fig. 2) or the number of chicks killed by neighbors.

Territory size.—Territory size and behavior associated with maintain-

TABLE 1
CAUSES OF MORTALITY AND AGE AT DEATH OF WESTERN GULL CHICKS

	Age in days				Total
	1-10	11-20	21-30	≥31	
Killed by neighbors	3	2	2	1	8
Killed by own parent	1	0	0	0	1
Starvation	1	4	1	0	6
Missing	1	0	0	0	1
Unknown cause	1	0	0	0	1
TOTAL	7	6	3	1	17

TABLE 2
DATE OF HATCHING¹ AND CAUSE OF DEATH OF WESTERN GULL CHICKS

	22-26 May	27-31 May	1-5 June	6-28 June	Total
Killed by neighbors	1	0	7	0	8
Starvation	3	3	0	0	6
Other	0	2	1	0	3
Total died	4	5	8	0	17
% mortality of total hatched	12.5	13.5	44.4	0	17.2

¹ Of the first chick in each brood.

ing territory varied during the breeding season (Table 3). For 16 pairs for which adequate information on territory size during incubation was available, increase in territory size was statistically significant between the incubation phase and the first 10 days of the chick phase ($P = 0.038$). No statistically significant change occurred in territory size between the first 10 days and the period between 11 and 20 days, although the areas occupied shifted considerably (see Fig. 3). These shifts appeared to be moves away from portions of the territory where parent gulls frequently had hostile interactions with neighbors, and additions of unoccupied places where the chicks hid. As the chicks became increasingly mobile the parts of the territory that were most frequently occupied changed.

Although we found a significant correlation between time of breeding and territory size in the first 10 days after hatching ($r = 0.477$, $P < 0.01$), there was no correlation between territory size and either chick survival or the number of chicks killed during their first 10 days. Apparently even the smallest of chick territories were large enough so that chicks were not significantly more exposed to attack by neighbors than chicks on large territories. The distance from a nest to that of the nearest neighbor, which varied from 1.75 to 21.0 m (mean 10.9 ± 4.9 m), was important in affecting chick survival. Pairs that had chicks killed by neighbors nested closer to their neighbors than those pairs that had no chicks killed (Mann-Whitney U-test, $P = 0.021$).

TABLE 3
TERRITORY SIZE DURING INCUBATION AND THE CHICK STAGE

	N	m ²			% showing increase from previous time period
		Mean	SD	Minimum Maximum	
Incubation	17	150	± 126	31 514	—
Chicks 1-10 days	38	211	± 124	48 551	75
Chicks 11-20 days	39	191	± 141	29 573	34
Chicks 21-30 days	37	214	± 167	24 803	49

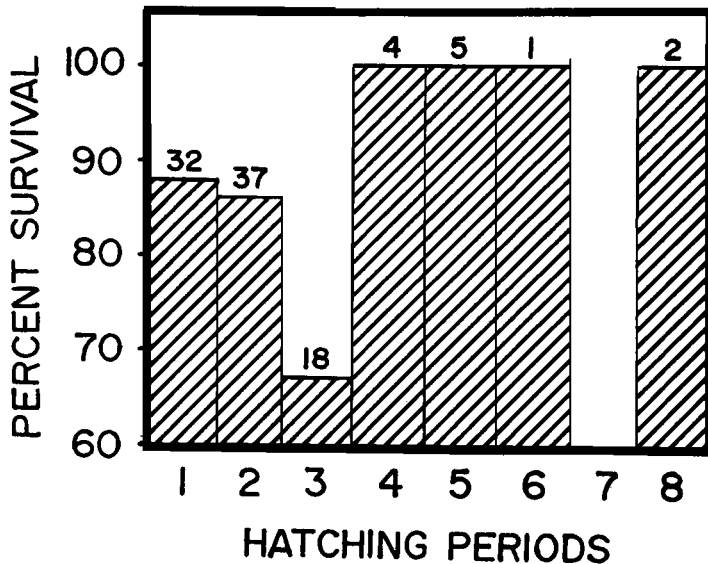


Fig. 2. Percent survival of chicks hatched in different time periods. The number of chicks in the sample is indicated at the top of each column. Hatching periods of the first chick in each brood are as follows: 1, 22-26 May; 2, 27-31 May; 3, 1-5 June; 4, 6-10 June; 5, 11-15 June; 6, 16-20 June; 7, 21-25 June; 8, 26-30 June.

Growth rates.—Chicks that survived to reach 500 g grew at a faster rate (mean = 25.9 g/day \pm 4.7 g) than did chicks that failed to survive (mean = 16.5 g/day \pm 7.2 g; Mann-Whitney U-test, $P = 0.026$). The minimum growth rate of any chick surviving to criterion was 13.2 g/day while the fastest rate of growth of a chick that failed to survive to criterion was 25.0 g/day. We found no correlation between the date of hatching and the growth rate of the fastest growing chick in a brood ($N = 39$, $r = 0.127$, $P > 0.05$). While average growth rates were lower in larger broods, the growth of the fastest growing chick was similar in broods of one, two, or three chicks (Table 4).

Parental behavior.—Young in their first 10 days were left unattended 0-11% of the time by their parents with an average of $1.6 \pm 2.6\%$. Although in other studies (Hunt 1972, Hunt and Hunt MS) we have found that chick mortality was correlated with the amount of time chicks were left unattended, in the present study we found no statistical correlation between the percent of time chicks were left unguarded and either the number of chicks killed (Mann-Whitney U-test, $P = 0.34$) or the overall survival of chicks ($P = 0.30$). Likewise we found no statistically significant correlation between the date of hatching of the first

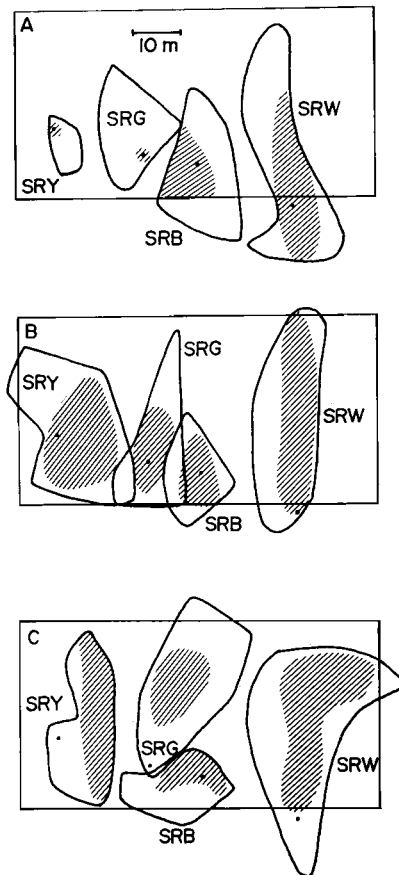


Fig. 3. Territory shifts of four neighboring pairs of gulls during three consecutive 10-day periods: A, 25 May–3 June; B, 4–13 June; C, 14–23 June. The dates of hatching of the first chick in each brood were: SRW, 25 May; SRB, 26 May; SRY, 1 June; SRG, 4 June. The dot in each territory indicates the nest site. Areas of overlap in B and C were places from which intruders were chased by both neighbors. Striped areas indicate where the adults and chicks spent most of their time.

chick in a brood and the percent of time that brood was left unattended ($r = 0.282$, $P > 0.05$).

Attending parents generally attacked all intruding adults and chicks. The number of aggressive acts per hour increased from an average of 0.14 per pair during the incubation stage to 0.61 per pair during the first 10 days of the chick stage in 30 of 32 pairs for which information is available ($P < 0.001$), indicating a higher level of aggression towards trespassers once the chicks were hatched.

TABLE 4
GROWTH RATES¹ OF CHICKS FROM BROODS OF DIFFERENT SIZES

	Brood size		
	1	2	3
Average, all chicks	28.4 ± 2.7	26.1 ± 4.1	24.2 ± 6.3
Fastest growing chick only	28.4 ± 2.7	28.3 ± 3.1	28.0 ± 4.5
Number of broods	5	16	18

¹ g/day gained.

In five instances chicks were able to avoid being driven from the territory they had invaded and subsequently were adopted by the adults of that territory. In all but one of these cases the adopted chicks were over 2 weeks old at the time of adoption. While the foster parents eventually showed complete acceptance of the adopted chicks, their own chicks often continued to harass the adopted chick for a day or so after its acceptance by the adults. While one such adoption resulted in a brood of four chicks, we were unable to obtain evidence that such adoptions reduced fledging success in the original brood.

DISCUSSION

With the knowledge that the Western Gull colony on Santa Barbara Island was subject to no predation by other species and that neighbors were a potential source of chick mortality, we expected that birds nesting early in the season and holding large territories would enjoy the greatest reproductive success. This prediction was based on our hypothesis that opposing selective pressures on territory size and timing of breeding caused by predators and dangerous neighbors will be reflected in patterns of reproductive success as discussed in the introduction. But, unlike the situation with Glaucous-winged Gulls (*Larus glaucescens*) on Mandarte Island, British Columbia (Hunt and Hunt MS), we found no correlation between chick survival and either date of hatching or territory size for the Western Gulls on Santa Barbara Island. While these results at first inspection appear to provide evidence against the general applicability of our hypothesis, we do not believe this to be the case.

Territory size was much greater on Santa Barbara Island than it was on Mandarte Island. The smallest territory on Santa Barbara Island (48 m² during the first 10 days of the chick phase) was larger than the largest territory (34 m²) found on Mandarte Island. On Santa Barbara Island all territories were apparently large enough so that variations in territory size were less important than differences in the distance to the nearest neighbor's nest for predicting killing of chicks by neighbors. We hypothesized that as territory size increases, chick loss from killing by

neighbors should decrease. A decrease in chick loss with increase in territory size might be expected to approach an asymptote close to but somewhat above zero chick loss. This residual chick loss to neighbors would not be influenced by territory size but rather by other factors such as the temperament of neighbors or the distance between nests, which would affect the probability of contact between young chicks near their nests and neighbors. This may be the reason for our finding of a negative correlation between distance to the nearest neighbor's nest and the killing of chicks by neighbors, but it is not a completely satisfactory explanation in view of the shift of adults and chicks to portions of their territories removed from contact with neighbors (Fig. 3).

The lack of a correlation between time of hatching and chick survival on Santa Barbara Island (Fig. 2) is reasonable in view of the freedom from predation and the relatively insignificant number of chicks killed by neighbors. Under these circumstances timing would not be expected to play an important role in reproductive success (Hunt and Hunt MS). In contrast, other investigators who have studied timing of breeding have found greatest chick survival in a distinct restricted portion of the breeding season (early: Paynter 1949; Paludan 1951; Vermeer 1963, 1970; Nisbet, *in litt.*; middle: Brown 1967, Kadlec and Drury 1968, Kadlec et al. 1969). Many of these cases documented severe chick loss to neighboring gulls and predators.

Most of the Western Gulls on Santa Barbara breed early in the season (Fig. 1). In contrast the Black-headed Gulls studied by Patterson (1965), which were subject to heavy predator pressure, showed a peak of breeding in the middle of the season. The difference between the two colonies may represent a shift to earlier breeding on the part of the Western Gulls in response to past pressures to avoid exposure of young to neighbors in an environment lacking counterbalancing pressures from predation.

Factors other than timing and territory size will have to be taken into account before our understanding of the determinants of reproductive success will be complete. In past studies high growth rates have been positively correlated with both chick survival and early breeding (Kadlec et al. 1969, Hunt 1972). In the present study high growth rates are correlated with survival but not with timing of breeding, and thus may have a significance apart from one related to seasonal fluctuations in food supplies. Because on Mandarte Island chicks killed by neighbors had lower growth rates than those that survived (Hunt and Hunt MS) and because the data of Smith and Hunt (*in Kadlec et al. 1969*) show that chicks that grow slowly can survive as long as they are not starved, other explanations for the significance of growth rates must be sought.

One possibility that requires further investigation is that if parents fail to provide adequate food, hungry chicks may show greater activity and thereby have a greater tendency to wander from their territories.

The expansion of territory size between the incubation and chick phases (Table 3 and Fig. 3), which has also been found to a lesser extent for Glaucous-winged Gulls on Mandarte Island (Hunt and Hunt MS), is of selective advantage insofar as it provides the chicks with a maximum safety zone between them and potentially dangerous neighbors, while allowing the adult gulls to conserve energy by defending less ground during incubation. Likewise shifting the places most frequently occupied to a portion of the territory removed from frequent clashes with neighbors (Fig. 3) should both increase the safety of the chicks and conserve the energy of the adults by reducing agonistic encounters. Thus territory in the Glaucous-winged Gulls and especially in the Western Gulls on Santa Barbara Island does not have the stability classically associated with territorial behavior (Tinbergen 1960, and others). Instead, these shifts in territory size, like those Meyerriecks (1960) found in the Green Heron (*Butorides virescens*), allow for a more efficient use of energy and time in that the amount of territory defended is continuously adjusted to the actual requirements of the bird within the limits imposed by the availability of space. These changes in reproductive territory size are different from those reported by Gibb (1956) and Drury and Smith (1968) for changes in foraging territories in Water Pipits (*Anthus spinoletta*) and Herring Gulls (*Larus argentatus*). Breeding territories should never collapse into a dominance hierarchy as a result of crowding or the existence of a desirable resource, as may happen with foraging territories.

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SUMMARY

In a study of the breeding biology of the Western Gull (*Larus occidentalis wymani*) on Santa Barbara Island, California, territory size was very large (mean > 200 m² during the chick stage) and chick survival was high (85%). While chick survival was positively correlated with growth rates and negatively correlated with the distance to the nearest neighbor's nest, there was no correlation between survival and either

territory size or timing of hatching. These results are applied to a hypothesis relating chick survival to territory size and timing of breeding.

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