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Authors
Hunt, George L
Hunt, Molly Warner

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GULL CHICK SURVIVAL: THE SIGNIFICANCE OF GROWTH RATES, TIMING OF BREEDING AND TERRITORY SIZE[1]

GEORGE L. HUNT, JR. AND MOLLY WARNER HUNT
Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717 USA

Abstract. In a 2-yr study of the survival of Glaucous-winged Gull (*Larus glaucescens*) chicks, pecking of trespassing chicks by neighboring adults was the major cause of chick mortality. In years of both low and high food availability chick survival was strongly correlated with growth rates. Chicks that grew slowly were more likely to be killed by neighbors than fast-growing chicks. In the year of low food availability, among slow-growing chicks, those hatched early in the season on large territories had better survival rates than chicks hatched late in the season on small territories. In the year of high food availability, timing of breeding and territory size had little bearing on chick survival.

A model of chick survival in relation to timing of breeding predicts that when neighbor interference is the major cause of chick mortality, chicks hatched early in the season will have the highest probability of surviving. When predators are the major cause of chick mortality, chicks hatching in the middle of the breeding season will have highest survival. A second model relates chick survival to territory size. Chicks raised on large territories will most likely avoid neighbor interference, while predation will select for either small or large territory size, depending upon the effectiveness of group mobbing against the predator.

Key words: Colonial nesting; fledging success, gulls; Glaucous-winged Gull; growth rates; Larus glaucescens; *model, breeding timing and gull chick survival; model, territory size and gull chick survival; mortality; predation.*

INTRODUCTION

Social systems and spacing patterns of breeding vertebrates have received considerable attention in recent years (see reviews by Brown 1964, Lack 1968, Orians 1969*a*, Brown and Orians 1970). Colonial breeding has been described as a response to abundant or unpredictable food resources (Orians 1961, Crook 1964, Horn 1968, Lack 1968, Emlen 1971, Krebs 1974, Hunt and Hunt 1975), to short breeding seasons and reduced food resources (Barash 1974), or to predation pressure (Cullen 1960, Ashmole 1963*a*, *b*, 1971, Kruuk 1964, Patterson 1965, Tinbergen et al. 1967, Parsons 1971, Alexander 1974). These are works dealing with factors external to the breeding situation; little information is currently available concerning the internal factors that determine spatial and temporal configurations of breeding colonies. The roles of age relative to position or timing (Coulson 1966, 1968, MacRoberts and MacRoberts 1972) and of mutual stimulation (Collias et al. 1971, MacRoberts and MacRoberts 1972, Victoria and Collias 1973) have been examined. Interference between colony members is another internal factor of possible importance.

In some social vertebrates interference between colony members can be as extreme as the killing of young by adults. Crushing and biting by adult northern elephant seals (*Mirounga angustirostris*) are major factors in pup mortality (LeBoeuf et al. 1972). In large *Larus* gulls, killing of chicks by neighbors is an important cause of chick mortality (Paynter 1949, Drury and Smith 1968, Parsons 1971, Hunt 1972). Less extreme interference includes behaviors such as stealing nest material (Ytreberg 1956, Cullen 1957, Sladen 1958) or food (various gulls which we have observed) from other colony members. Reproductive patterns that might reduce these forms of interference by neighbors should exist.

In the present study we initially set out to determine the relative importance of various causes of chick mortality, including killing by neighbors, in the Glaucous-winged Gull (*Larus glaucescens*), and the characteristics of parents successful in rearing young. Parameters examined included territory size, growth rates and timing of hatching. In the second year we attempted to separate the effects of seasonal changes on reproductive success from effects related to the age or experience of the parents through exchange of eggs between birds laying at different times. We examined the significance of the internal temporal and spatial structure of a colony in relation to food availability for individual reproductive success. Then, we integrated these factors into an hypothesis that predicts optimal timing and spacing of nesting in relation to conflicting needs for protection against external predators and avoidance of interference by neighbors. This hypothesis may have applicability to other colonial vertebrates.

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METHODS

The study was carried out on Mandarte Island, British Columbia, Canada during June–July 1971 and May–August 1973. For descriptions of the island and its nesting seabirds see Vermeer (1963) and Drent et al. (1964). Methods during the 2 yr differed, and are described separately below.

In 1971 two study sites were chosen: one was an area of rocks and tall grass surrounded by bushes on the southeast side of the island, designated C meadow after the system of Vermeer (1963), and the second, Hoh meadow (not studied by Vermeer), was a more exposed area on the northwest side of the island, dominated by large rocks interspersed with short grass.

In each meadow 25 nests were marked with a coded stake during incubation. All eggs in these nests were numbered and measured. Due to egg loss the sample was reduced to 23 nests in C meadow and 18 nests in Hoh meadow. When chicks hatched, each chick was weighed and color-banded to identify its nest of origin and its position in the hatching sequence. When known, the number of the egg from which it hatched was recorded. Thereafter each chick was weighed every 5 days.

In each meadow we observed gulls from wooden blinds which were high enough (eye level at $\approx 2\frac{1}{2}$ m) to enable us to see interactions in the low vegetation and rough terrain. Continuous dawn to dark observations were made in each meadow every 4–6 days from just prior to the hatching of the earliest chicks until those chicks had almost fledged, yielding a total of 123 nest-days of observation during incubation and 235 nest-days during the chick stage. This represented 1,425 nest-hours and 4,056 nest-hours respectively.

During day-long observations we recorded presence or absence of each parent at 15-min intervals. Between 15-min checks observations were made on arrival or departure of adults, hostile interactions and feeding of chicks. From these data we calculated length of absence of adults from their territory and percent of time chicks were left unattended. When chicks were attacked, note was taken of the chick's location, whether or not it survived, and other circumstances such as defense by the chick's parents. As a supplement to day-long observations, Hoh meadow was checked from the blind four times daily for 15–45 min. During these checks only presence or absence of the chicks was noted.

Territories were mapped using a grid laid out at the end of the breeding season and landmarks observed throughout the breeding season. Territory boundaries were determined by the location of fights and other agonistic encounters between adults on neighboring territories. For each nest we measured the distance to all nests on contiguous territories.

"Surviving" chicks attained a weight of 500 g usually prior to age 25 days. "Nonsurviving" refers to all forms of mortality and also to 10 chicks which grew so slowly that they failed to attain criterion weight by the time we left the island at the end of July. Due to their undernourished condition these birds were unlikely to fledge. Chicks referred to as killed were destroyed by neighboring gulls.

In 1973 we designed an experiment to separate timing of breeding (both within the season and relative to neighboring pairs), territory size, and parental quality as factors governing reproductive success in individual gull pairs. We exchanged eggs between pairs breeding at different times during the season and compared survival of chicks, growth rates and territory sizes between the different groups.

Six areas of the island were used for the study: B, C, D_3, and E meadows (Vermeer 1963), Hoh meadow, and East meadow on the southeastern tip of the island. During the incubation period in each area a grid of numbered stakes at 4-m intervals was set up to include all the nests within view from a blind. The grids ranged from 72 to 196 m^2 in area and varied in shape according to topography and visibility. A detailed map was made of each grid, showing the positions of nests, rocks, and bushes.

The grids were each observed for 2 h a day for 25–29 days between 12 June and 3 August. During each observation period territories were mapped using data on places where chicks and adults stood and location of interactions with neighboring gulls. The territory measured for statistical purposes was an aggregate of all points mapped for a pair and their chicks during the 30 days after the first chick hatched, bounded by a line drawn between peripheral points, taking into account topography and the configuration of neighboring territories. Excluded from this measured territory were large areas of bushes at the edges of the grids where the chicks often hid but which the adults tended to avoid. If a nest were inside the bushes, the nest was included in the measurement, but adults as a rule remained in the open once their chicks hatched.

We determined the date of first egg in each nest by checking 371 nests daily in the six grids and surrounding areas. When the pattern of laying became apparent, we divided 104 nests within the grids into eight categories of about equal size such that 50% of the pairs were given eggs due to hatch earlier or later than their own eggs, and the other 50% were controls (Table 1). The controls (groups A and C) either were allowed to keep their own eggs or were given eggs which hatched within 2 days of their own eggs. Pairs in the B groups received eggs that hatched

TABLE 1. Design of egg-exchanging experiment in 1973. Numbers in parentheses refer to the dates with day 1 = 10 May 1973

Category	Control or experimental	Sample of nests	Dates of clutch commencement	Dates of hatching of first chick in a brood	Hatching dates relative to ⩽ 3 neighboring pairs
A1	C	17	Early (1–10)	Early (30–36)	Before 60% of neighbors (50% for A2)
A2	C	8	Middle (11–14)	Middle (40–45)	
B3	E	19	Middle (11–19)	Early (30–36)	
B4	E	9	Late (20–23)	Middle (41–45)	
C5	C	8	Middle (12–19)	Middle (43–48)	Later than or contemporary with all neighbors
C6	C	15	Late (20–29)	Late (51–56)	
D7	E	8	Early (3–10)	Middle (43–47)	
D8	E	20	Middle (11–18)	Late (51–57)	

8–15 days before their own eggs, and those in the D groups received eggs that hatched 8–15 days after their own eggs. Given these time constraints, it was possible to arrange egg switches only between the middle period and the other two groups, and not directly between the early and late groups. The egg-hatching was arranged so that a gap of 2 or 3 days separated consecutive time categories (Table 1).

In organizing these categories we also considered the timing of hatching relative to neighboring pairs. The 104 nests chosen for the experiment all had at least three contiguous neighboring territories. Pairs in the A and B categories hatched eggs at least 8 days before two or more neighbors, while the C and D groups hatched contemporaneously or later than all neighbors (Table 1). This effectively divided the middle-hatching group into an earlier period (A2 and B4) and a later period (C5 and D7), although the range of dates overlapped.

The eight categories were distributed throughout the six grids. To provide the desired environment for the 104 pairs under study, we exchanged the eggs of other pairs without regard to the time and neighbor constraints defined for the eight categories.

In the egg exchanges pairs received unpipped eggs if we knew the laying date of the foster eggs, or cracked or pipping eggs if the laying date of the foster eggs was not known. The nests of pairs under study were never left without eggs, so that incubation was not interrupted. Birds in the eight categories received three eggs whenever possible. We measured the length and breadth of the eggs laid by and received by these birds, and avoided using as replacements very small eggs which might produce weak, underweight chicks. At least two chicks hatched in all but five nests, although those chicks were not always biological siblings. All exchanged eggs were accepted by adults, and regardless of whether incubation was shortened or prolonged, adults exhibited normal parental behavior.

Chicks were banded and weighed on the day they hatched. Every 6–9 days we weighed all banded chicks in each area until they reached at least 500 g. Growth and survival data were treated the same as in 1971, although in 1973 there were no underweight chicks that had not reached 500 g by the time we left the island.

The growth rates of individual chicks in both years were calculated from the straight-line segment of the growth curve between day 5 and day 20 (Spaans 1971, Hunt 1972). For interbrood correlations of growth rates with survival and other parameters we used two measures: the growth rate of the fastest-growing chick, and the mean growth rate of all chicks in a brood for which data were available. These measures permitted inclusion of mortality data for small chicks that died before growth data were obtained. The growth rate of the fastest-growing chick provides an index of the maximum capability of a pair in feeding its chicks, while the mean growth rate may reflect the overall well-being of the brood.

RESULTS

Chick mortality

In 1971, 49 (48%) of 99 chicks failed to reach 500 g, our criterion for survival, while in 1973 only 75 (26%) of 288 chicks failed to reach 500 g. Most chicks that died were killed by neighbors, most frequently before chicks reached 10 days of age (Table 2). The distribution of territories throughout the six grids in 1973 precluded intensive observations required to determine causes of death. In 1973, 57% of the chick mortality occurred before chicks were more than 10-days-old, and at least 49% of chick deaths was caused by neighbors. The latter figure may be low, however, as we do not have data on the reasons for disappearance of 34 of the 75 chicks that we know did not survive.

In 1971, 10 chicks were found dead in their neighbors' territories, and we witnessed the killing of 9 other chicks by neighboring adults. Usually a

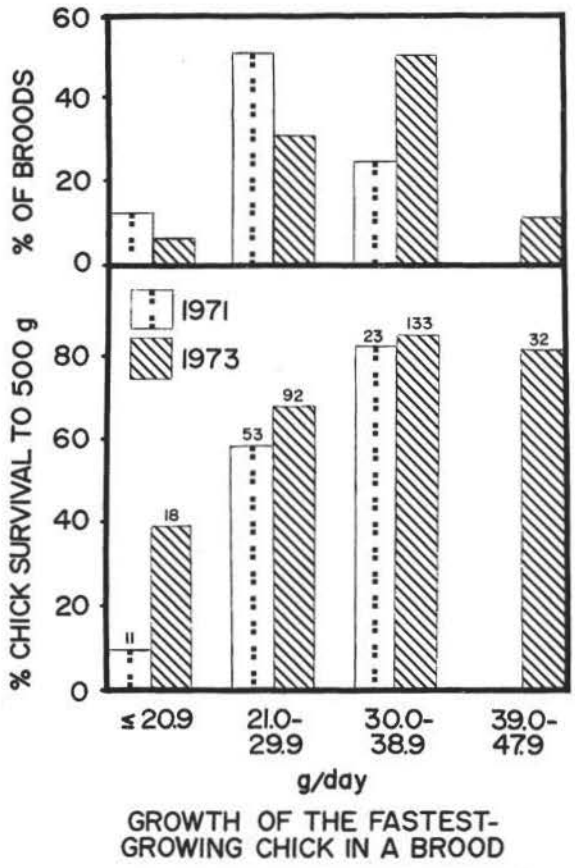

FIG. 1. Percent chick survival vs. the growth of the fastest-growing chick in each brood, and the distribution of those growth rates among broods in our samples. Number of chicks in sample is indicated at top of each column. High growth rates were positively associated with high chick survival in both years (1971—$\chi^2 = 16.58$; 1973—$\chi^2 = 22.45$; 2 df; $p < 0.001$ in both years).

chick was seized by the head or neck and dragged toward the center of the attacker's territory. If the chick did not escape, it would be pummeled about the head and back until motionless. We also observed 105 nonfatal attacks on chicks, 96 of which were against chicks older than 10 days.

The observed killings occurred primarily when chicks were at the edge of their own territory or had entered a neighbor's territory. All but one observed attack in the 2 yr apparently related to territorial conflict, and only occasionally were chicks eaten after being killed. Cannabilistic predation of chicks, reported as a potentially significant form of chick mortality by Parsons (1971), was seen only once when an adult flew into a territory, grabbed a small chick, and flew off with it.

In general, the parents of a chick that was attacked outside their territory limited defense to vigorous grass-pulling and long-calls. In 1971, of 50 observed attacks on chicks outside their territories when at least one of its parents was present, only seven times did a parent enter the attacker's territory to defend its chick. In all seven instances the chick escaped.

Northwestern Crows (*Corvus caurinus*) killed one small chick in our study area in 1971 and five small chicks from nests adjacent to the territories studied in 1973. Five of these chicks hatched early, while the sixth hatched in the middle of the 1973 season. Fragments of other dead chicks were encountered under crow roosts primarily early in both years. Although predation was apparently only a minor cause of chick loss in this colony, it was concentrated on the earliest hatching chicks and decreased in magnitude as the season progressed.

Other causes of chick mortality in 1971 included late spring storms that were particularly damaging to 5–10-day-old chicks hatched early in the season (Table 2). From our study plots and from information supplied by John Ward about other areas of the colony, it was clear that these chicks which are too large to be brooded adequately can be sufficiently wetted and chilled by a 2–3-day storm that they cannot recover. We also observed seven instances of inappropriate parental behavior that resulted in chick mortality, including failure to shift from incubation to feeding and brooding of chicks, and the

TABLE 2. Causes of mortality vs. age of chick in 1971 (excluding 10 underweight chicks defined as having not survived)

Cause of death	Age (days) 1–10	11–20	21–30	Total dead chicks
Killed by neighbors	13 (34.2%)	5 (13.2%)	1 (2.6%)	19 (50.0%)
Killed by crow	1 (2.6%)	0	0	1 (2.6%)
Inappropriate parental behavior	6 (15.8%)	1 (2.6%)	0	7 (18.4%)
Exposure to storm	3 (7.9%)	0	0	3 (7.9%)
Apparent starvation	0	0	2 (5.3%)	2 (5.3%)
Disease	0	0	1 (2.6%)	1 (2.6%)
Missing	4 (10.6%)	1 (2.6%)	0	5 (13.2%)
TOTAL	27 (71.1%)	7 (18.4%)	4 (10.5%)	38 (100.0%)

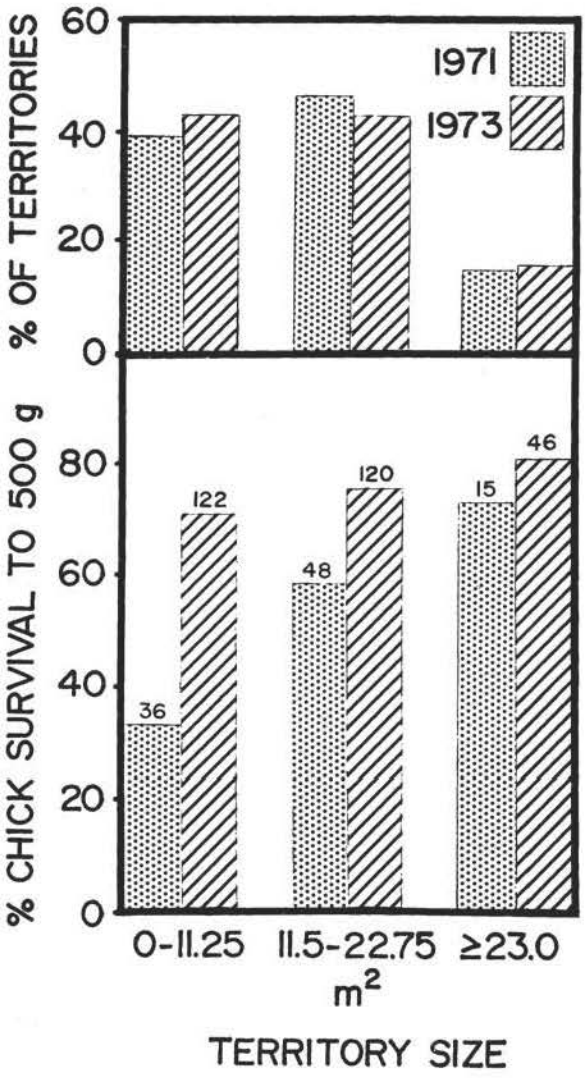

FIG. 2. Percent chick survival vs. territory size during the chick phase, and the distribution of those territory sizes among the pairs under study. Number of chicks in sample is indicated at top of each column. Within the small and medium territory categories, survival was significantly higher in 1973 than in 1971 (1971 vs. 1973: small $\chi^2 = 16.29$, $p < 0.001$; medium $\chi^2 = 4.55$, $p < 0.05$; large $\chi^2 = 0.34$, $p > 0.05$).

carrying of a chick over the water and dropping it as though it were an eggshell (Tinbergen et al. 1962).

Growth rates

In both years chicks that survived to 500 g grew faster than those which died (Table 3). The major direct cause of death of slow-growing chicks was not starvation but killing by neighbors. In 1971 the 10 underweight chicks still alive at our departure grew between 13.5 and 18.3 g/day. Data from these chicks was not included in tests of the relationship

TABLE 3. Growth rates of chicks (g/day gained)

	1971 Growth rate		1973 Growth rate	
	n	($\bar{x}$ and SD)	n	($\bar{x}$ and SD)
All chicks	62	23.9 ± 6.4	223	27.6 ± 7.9
Surviving chicks	51	26.9 ± 3.9[a, c]	202	28.5 ± 6.9[b, d]
Chicks that died	11	18.2 ± 5.2[a]	21	18.4 ± 10.8[b]
Chicks killed by neighbors	7	20.1 ± 3.7[c]	12	19.9 ± 6.9[d]
Mean—				
1-chick broods	8	24.5 ± 7.6	18	28.7 ± 7.5
2-chick broods	42	24.0 ± 6.0	58	29.0 ± 7.0[e]
3-chick broods	21	24.6 ± 4.6	147	26.8 ± 8.5[e]
Fastest—				
2-chick broods	21	27.0 ± 4.7	30	31.9 ± 7.2
3-chick broods	7	27.8 ± 4.3	50	32.5 ± 6.4

[a, b and d] $p < 0.001$, t-test.
[c] $p < 0.01$, t-test.
[e] $p < 0.05$, t-test.

between growth rates and chick survival. Growth rates of the fastest-growing chick in a brood were positively associated with the percent survival of chicks in those broods during both years (Fig. 1).

In 1971 chicks in small broods grew no faster than chicks in larger broods (Table 3). This indicates that growth rates in general were not dependent upon brood size during either year, with the possible exception of the difference between two- and three-chick broods in 1973.

Territory size and territorial behavior

The distribution of territory sizes during the chick stage was similar for the 2 yr (Fig. 2). In 1971 mean chick territory size of 41 territories was 14.3 ± 7.5 (SD) m², range 1.8–34.0 m²; in 1973 for 104 territories it was 14.8 ± 9.5 m², a range 2.3–46.7 m². In the smallest territories chicks had little room in which to move safely, but in large territories they usually had refuges in which to hide as well as space to move about.

Percent survival of chicks was positively associated with the size of their territory in both years, but the relationship was statistically significant only in 1971 (1971: $\chi^2 = 8.51$, 2 df, $0.02 > p > 0.01$; 1973: $\chi^2 = 1.70$, $0.2 > p > 0.1$; Fig. 2). On small and medium-sized territories chick survival was significantly greater in 1973 than in 1971 (Fig. 2). There was no statistically significant difference in survival on the larger territories between the 2 yr. In 1971 the killing of chicks by neighbors occurred more frequently among broods on small territories than on large territories (Mann-Whitney U-test, $p = 0.007$).

Inter-nest distance did not relate to chick survival in either year, possibly because nests in large territories were frequently close to the territory boundary

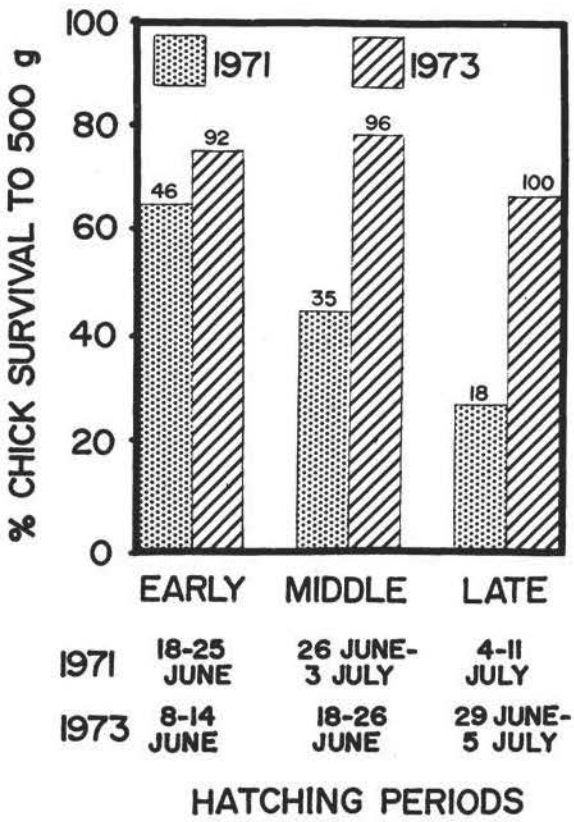

FIG. 3. Percent chick survival vs. date of first chick hatching in each brood. Number of chicks in sample is indicated at top of each column. Within each hatching category, chick survival was significantly greater in 1973 than in 1971 only in late-hatching chicks (1971 vs. 1973: early $\chi^2 = 1.31$, $0.30 > p > 0.20$; middle $\chi^2 = 3.64$, $0.10 > p > 0.05$; late $\chi^2 = 8.29$, $p < 0.01$).

rather than in the center, or because chicks left their nests shortly after hatching and thereafter used most of their territory (Hunt and Hunt 1975).

Territory size appeared to be important for survival of both slow- and fast-growing chicks in 1971 (Table 4). In 1973, territory size may have been more important for chick survival in broods having low average growth rates (Table 4).

The territory sizes did not always remain constant throughout the nesting season. In 1971 11 territories did not change in size between the egg and chick stages, 23 of 41 territories increased in size, while only 7 became smaller (Sign Test, $p = 0.003$). Territory increase was accomplished mostly by annexation of unoccupied areas between territories and to a lesser extent by taking over part of neighbor's territories. The mean change in size (including those that did not change) was 4.1 ± 7.23 m^2 with a range of -3.1 to 27.9 m^2. Since in 1971 there was no statistically significant correlation between chick survival and territory size during the incubation phase ($\chi^2 = 1.91$, 2 *df*, $0.50 > p > 0.30$), these shifts in size were important in determining the probability of chick survival.

One aspect of behavior possibly related both to changes in territory size and to chick survival was the change in aggressiveness of parents switching from incubating eggs to chick care. Incubating birds appeared quite tolerant of trespass and would rarely leave their nests to drive out an intruder. In contrast, birds with chicks vigorously defended territory boundaries and drove all other gulls from them. In 1971 frequency of defense behaviors increased from 0.13/h per pair during the incubation stage to 0.48/h during the chick stage (Wilcoxon matched pairs test, $p = 0.034$). Thus, a neighbor with chicks was potentially more dangerous to a wandering chick than was an incubating neighbor.

Influence of timing

Hatching dates of the first chick in each brood (hereinafter referred to as hatching date) for 41 broods in 1971 ranged from 18 June to 10 July, with a mean date of 28 June. In 1973 the mean hatching date of the original eggs in 371 nests was 23 June (range 8 June–27 July), based on an interpolation from laying dates. The difference in mean hatching dates between the 2 yr is statistically significant (*t* test, $p < 0.001$).

Chicks hatched early in the 1971 season had a higher probability of surviving than those hatched later (Table 5, Fig 3; $\chi^2 = 7.99$, $p < 0.02$). Broods hatched early more often suffered no mortality (Mann-Whitney *U*-test, $p = 0.06$) or no killing by neighbors (Mann-Whitney *U*-test, $p = 0.07$) than broods hatched late in the season.

Differences in survival between chicks hatched on different dates in 1973 were much less than in 1971 (Fig. 3). There was no statistically significant difference in survival between chicks hatched early and those hatched in the middle of the 1973 season. Broods hatched late in the 1973 season had lower survival than those hatched in the middle ($\chi^2 = 3.75$, $0.1 > p > 0.05$).

Birds hatched in mid- and late-season 1973 survived better than their counterparts in 1971 (Fig. 3). Thus, lack of seasonal differentiation of survival in 1973 was related to improved survival of middle- and late-hatching birds (Tables 6 and 7).

Date of clutch initiation during 1973 did not relate to chick survival in nests where egg exchanges produced similar hatching dates and similar timing with respect to neighbors. Early laying gulls were as successful in raising early hatching chicks as those laying in mid-season (Table 6; $\chi^2 = 0.14$, $p > 0.05$). There was no significant difference in chick survival between late- and mid-season laying birds when both

TABLE 4. Percent survival of slow- and fast-growing chicks on territories of different sizes

	Year	Growth measure[a] (g/day)	Territory size (m^2)			Broods (N)	χ^2[b]
			< 11.5	11.5–22.9	≤ 23.0		
Chicks in slow-growing broods	1971	average ≤ 25	15.4 (13)[c]	48.0 (25)	40.0 (5)	17	---
	1971	fastest ≤ 28	31.8 (22)	43.5 (23)	60.0 (5)	20	3.65
	1973	average ≤ 25	60.4 (48)	68.4 (38)	80.0 (10)	32	1.59
	1973	fastest ≤ 28	56.3 (48)	58.3 (36)	55.5 (9)	31	0.04
Chicks in fast-growing broods	1971	average > 25	66.7 (15)	84.2 (19)	90.0 (10)	19	---
	1971	fastest > 28	60.0 (5)	86.9 (23)	80.0 (10)	16	---
	1973	average > 25	84.4 (64)	78.0 (82)	79.4 (34)	66	1.90
	1973	fastest > 28	88.5 (61)	81.6 (87)	85.3 (34)	67	1.45

[a] See Methods section of this paper for explanation of these measures.
[b] χ^2 refers to a comparison of chick survival on different territory sizes within each growth category. In all groups in which the sample sizes for each cell were large enough for a 2×3 χ^2 test, $p > 0.05$.
[c] Numbers in parentheses indicate the number of chicks in each sample.

groups hatched young during mid-season (Table 6; $\chi^2 = 1.62$, $p > 0.05$).

In 1973 survival of chicks hatched early with respect to neighbors was similar to those from broods hatched late (Table 6; A & B groups—77.5% vs. C & D groups—70.5%). At least 60.5% of mortality in the C and D groups was caused by neighbors, while only 37.5% of mortality in the A and B nests was from killing ($\chi^2 = 5.50$, $p < 0.05$). Likewise, of chicks hatched in mid-season that failed to survive, seven of nine killed came from nests that were late with respect to their neighbors. Similar percentages of survival and the large number of chicks for which cause of death is not known dictate the use of caution in interpreting these results.

TABLE 5. Date of hatching of the first chick in a brood and causes of mortality in those broods in 1971. Percentages given in parentheses

	18–25 June	26 June–3 July	4–11 July
Total chicks hatched	46 (100.0)	35 (100.0)	18 (100.0)
Killed by neighbors	6 (13.0)	6 (17.2)	7 (38.9)
Killed by crow	1 (2.2)	0	0
Inappropriate parental behavior	1 (2.2)	4 (11.4)	2 (11.1)
Exposure to storm	3 (6.5)	0	0
Apparent starvation	0	2 (5.7)	0
Disease	0	0	1 (5.5)
Missing	2 (4.4)	2 (5.7)	1 (5.5)
Total died	13 (28.3)	14 (40.0)	11 (49.9)
Slow growth rate[a]	3 (6.5)	5 (14.3)	2 (11.1)
Total 'not survived'	16 (34.8)	19 (54.3)	13 (61.0)

[a] See definition of 'nonsurvival' in Methods section this paper.

Late-nesting parents in 1971 left their chicks unguarded more often than early nesters during the first 10 days after hatching ($r = 0.43$, $p < 0.01$). Broods in which chicks were killed by neighbors were left unguarded a greater percentage of the time than broods in which no chicks were killed (Mann-Whitney U-test, $p = 0.0053$).

In both years chick growth rates and territory size during the chick stage were related to time of hatching. Growth rates for the fastest-growing chick in a brood were greater in early-hatching than in late-hatching broods (1971: $r = 0.49$, $p < 0.01$; 1973: $r = 0.22$, $p < 0.05$). Similar correlations in both years were found between the date of hatching and the average growth rate of a brood.

In 1973, the correlation between date of egg laying and growth of the fastest-growing chick was not statistically significant ($r = 0.16$, $p > 0.05$). Date of egg laying may reflect both the foraging ability and reproductive experience of parents (Coulson 1966, Perrins 1970, Perrins and Moss 1974), but the stronger correlation in 1973 between growth rates and hatching dates than with laying dates indicates that growth rates of gulls may be more strongly in-

TABLE 6. Chick survival in different laying and hatching categories, 1973. Overall survival by laying categories was as follows: Early—77.1%, Mid—77.2%, Late—60.3%. $\chi^2 = 4.84$; 2 df; $p > 0.05$. For overall survival by hatching categories, see Fig. 3 this paper

Category	Laying period	Hatching period	Chicks hatched (N)	% survival
A1	Early	Early	47	74.5
A2	Mid	Mid	24	87.5
B3	Mid	Early	45	77.8
B4	Late	Mid	26	73.1
C5	Mid	Mid	23	73.9
C6	Late	Late	43	58.1
D7	Early	Mid	23	82.6
D8	Mid	Late	57	73.7

TABLE 7. Percent survival of fast- and slow-growing chicks hatched at different times during the season

	Year	Growth measure[a] (g/day)	Hatching dates			Broods (N)	χ^2[b]
			Early	Middle	Late		
Chicks in slow-growing broods	1971	average ≤ 25	53.8 (13)[c]	38.9 (18)	16.7 (12)	17	----
	1971	fastest ≤ 28	53.8 (13)	45.0 (20)	25.0 (16)	20	2.70
	1973	average ≤ 25	73.3 (15)	75.7 (33)	55.3 (47)	32	4.12
	1973	fastest ≤ 28	57.9 (19)	60.0 (30)	53.3 (45)	31	0.53
Chicks in fast-growing broods	1971	average > 25	80.6 (31)	87.5 (8)	60.0 (5)	19	----
	1971	fastest > 28	82.1 (28)	77.8 (9)	100.0 (1)	16	----
	1973	average > 25	76.7 (73)	84.2 (57)	80.4 (51)	66	1.06
	1973	fastest > 28	81.2 (69)	91.7 (60)	81.1 (53)	67	3.40

[a] See Methods section of this paper for explanation of these measures.
[b] χ^2 refers to a comparison of survival of chicks hatched at different times within each growth category. In all groups in which the sample sizes for each cell were large enough for a 2×3 χ^2 test, $p > 0.05$.
[c] Numbers in parentheses indicate the number of chicks in each sample.

fluenced by seasonal variation in the availability of food than by the foraging ability of parents. Ainley and Schlatter (1972), however, suggest for the Adelie Penguin (*Pygoscelis adeliae*) that foraging experience of adults is correlated with chick growth and survival, and Ashmole (1963*a*) suggests foraging experience is of considerable importance in determining reproductive success of tropical seabirds.

The growth rates of chicks may influence the relationship between survival and date of hatching (Table 7). Chicks in broods with high growth rates during 1973 showed little change in percent survival as the season progressed. During 1971, chicks in broods with high average growth rates showed slightly lower survival only late in the season, as was the case for chicks with slow growth rates in 1973. In contrast, chicks with slow growth rates in 1971 showed a rapid decline in survival as the season progressed (Table 7).

TABLE 8. Correlation matrices for survival, growth of the fastest growing chick in a brood, timing of breeding, and territory size during the chick phase

	Survival	Growth	Hatching date	Territory size
1971				
Survival	1.00	----	----	----
Growth	0.70	1.00	----	----
Hatching date	–0.46	–0.48	1.00	----
Territory size	0.20	0.05	–0.38	1.00
1973				
Survival	1.00	----	----	----
Growth	0.42	1.00	----	----
Hatching date	–0.16	–0.22	1.00	----
Territory size	0.10	0.19	–0.44	1.00

Territory size during the chick stage was greater for early hatching broods in both years (1971: $r = -0.35$, $n = 41$, $p < 0.05$; 1973: $r = -0.45$, $n = 104$, $p < 0.01$). In 1973 we also examined the relationship between laying date and territory size during the chick stage because the egg exchange allowed a partial separation of the normally linked parameters of laying and hatching dates. Laying date and chick territory size were correlated, but to a lesser extent than territory size and hatching date ($r = -0.23$, $n = 104$, $p < 0.05$).

Growth rates, time of hatching and chick territory size are all highly correlated (Table 8). Stepwise multiple regression analysis showed growth rates to be the best predictor of chick survival followed by time of hatching and territory size (Table 9). It is not clear how useful these measures of relationship are, however, since the contingency analyses presented in Tables 4 and 7 indicate that territory size and timing may vary in importance between slow

TABLE 9. Results of stepwise linear multiple regression of growth (of the fastest-growing chick in a brood), date of hatching, and territory size (during the chick phase) on chick survival. r^2 is adjusted for degrees of freedom

Independent variables	Regression coefficients	β
1971		
Growth	0.0457	0.65
Hatching date	–0.0058	0.09
Territory size	0.0072	0.14
Constant	–0.436	0
Survival analysis: $r^2 = 0.485$		
1973		
Growth	1.53	0.41
Hatching date	–0.221	0.07
Territory size	0.0097	0.00
Constant	37.4	0
Survival analysis: $r^2 = 0.155$		

and fast growing chicks and between years of differing food availability. Furthermore, it appears likely that territory size and chick survival may be related in a nonlinear manner.

Although growth rates appear to be the overriding determinant of chick survival, we were able to factor out the effect of growth rates by examining the combined influence of territory size and timing of breeding on the survival of slow-growing chicks in 1971. Among broods with low average growth rates (< 26 g/day), chicks raised early in the season on large territories had a higher rate of survival (83% of 6) than chicks hatched late in the season on small territories (25% of 12; Fisher Exact Probability Test, $p < 0.05$).

Discussion

It is legitimate to compare results obtained in 1971 with those obtained from an experimentally manipulated population in 1973 for three reasons. First, no observed abnormalities in behavior were displayed by parents given eggs that accelerated or delayed the normal time of hatching. Second, only minor differences existed in chick survival between experimental and control pairs. Third, the correlation of unusually high chick survival [compared to chick survival found by Vermeer (1963) and Ward (1973)] with higher growth rates suggest that 1973 results were the product of natural events. Post-hatching disturbance of the colony was similar in both seasons and did not affect the comparison of chick survival in the 2 yr.

The comparison of results between 1971 and 1973 allows us to evaluate the importance of timing of breeding and territory size in a year of food scarcity and a year of food abundance. Food was more easily obtained by Glaucous-winged Gulls breeding on Mandarte Island in 1973 than in 1971.

Although direct measures of food availability were not obtained in either year, indirect measures were possible. In 1973 the gulls laid eggs an average of 5 days earlier than in 1971, a difference perhaps related to the degree of food availability (Perrins 1970). Also, growth rates of chicks in 1973 were higher than in 1971 (Table 4), presumably reflecting the greater food abundance. In addition, during 1973 we often saw large flocks of gulls feeding on schools of fish within sight of Mandarte, but in 1971 we never saw this happen.

The differences between the years provide a striking example of how changes in food availability may affect the importance of factors such as territory size that may, in a colonial species, appear unrelated to food availability (Tinbergen 1952, Klopfer 1973:55–56). In 1971 low food availability was accompanied by low chick survival (Ward 1973), and both territory size (Fig. 2, Table 4) and date of hatching (Fig. 3, Table 7) were important to chick survival. In contrast, during 1973 when food seemed plentiful time of hatching and territory size had little relationship to chick survival.

The difference in survival of slow- and fast-growing chicks (Fig. 1) may in part be related to behavioral differences between hungry and satiated chicks. Hunt and McLoon (1975) found that chicks that have failed to obtain food upon begging are more active and move further from their parents than recently fed chicks. Unfed chicks wandered near their territory boundaries and were attacked by neighboring adults more frequently than chicks that had obtained food. Thus, for Glaucous-winged Gulls breeding on a large territory early in the season (so that hatching occurs when neighboring pairs are still incubating and, therefore, relatively tolerant of trespass on portions of the territory distant from the nest) may be particularly important when food is not abundant (1971, Tables 4 and 7). Although the correlation of territory size with chick survival in 1971 is not statistically significant when the contribution of growth and timing are accounted for (Table 9), the fact that adults expend much energy defending and enlarging their territories during the chick stage suggests that territory size is of biological importance to chick survival (Hunt and Hunt 1975).

We can now better understand the results of several previous studies: Kadlec et al. (1969) and Hunt (1972), Herring Gulls (*L. argentatus*); Ward (1973), Glaucous-winged Gulls; and Hunt and Hunt (1975), Western Gulls (*L. occidentalis*). These studies all showed that chicks with high growth rates had higher survival rates than slow-growing chicks. Starvation was not a major factor in any of these studies, but hunger may have induced behaviors in chicks which increased mortality. Hunt (1972) found lower chick survival in a population where adults made longer trips to foraging areas than in a population where adults made short trips. Growth rates of chicks were similar in both instances, but the difference in the length of intervals between returns of parents with food may have resulted in differences in chick behavior. Increased wandering by chicks also may have been responsible for higher mortality in chicks left unattended by their parents (late nesting pairs in 1971, this study; Little Green Island population, Hunt 1972).

Nettleship (1972) found that young Common Puffins (*Fratercula arctica*) when hungry may move to the enrances of their burrows, thereby increasing exposure to predation by gulls. Gordon Orians (*personal communication*) has also observed that young blackbirds may call more frequently when hungry, possibly attracting predators to the nest. It

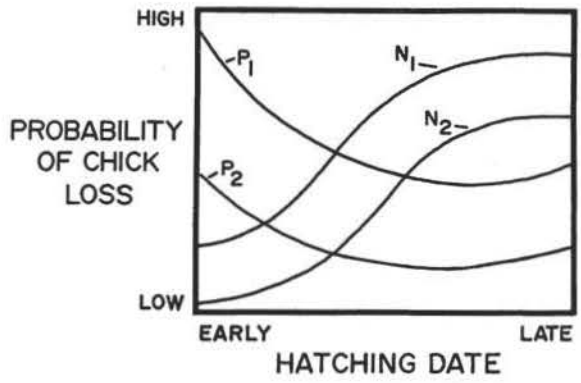

FIG. 4. A model of optimal hatching date in which timing for maximum chick survival is predicted by probability of chick loss to predators and to neighbors. P_1 = loss due to heavy predation pressure; P_2 = loss due to light predation pressure; N_1 = loss due to very dangerous neighbors; N_2 = loss due to moderately dangerous neighbors. For justification of shapes of curves, see text.

is possible that the elevated mortality rates of the juveniles of many species (Lack 1946) are caused not only by their ineptness at obtaining food (Recher and Recher 1969, Orians 1969*b*) but also because behaviors related to hunger may increase their vulnerability to predation. Differences in foraging success may also affect adult behavior toward chicks, but we have no data on this problem.

For colonial species, factors other than hostile neighbors affect optimal timing and space requirements for successful breeding. Predation accounts for a major portion of all egg and chick loss in the small Black-headed Gull *L. ridibundus* (Kruuk 1964, Patterson 1965, Tinbergen et al. 1967) and for the Herring Gulls studied by Parsons (1971). Predation is also a factor in the evolution of nest spacing in terns (Cullen 1960) and weaver finches (Crook 1964). Therefore, an examination of interaction between internal interference and external predation in determining optimal timing and spacing of breeding may be useful.

Figure 4 presents a model in which the optimal timing of hatching for maximum chick survival is predicted by minimizing the probability of chick loss to predators and to neighbors. Since adult aggressiveness in territorial defense increases at chick hatching, the probability of chick loss to neighbors is minimal early in the season when few pairs have chicks. Risk to chicks increases rapidly at the time of maximum hatching, and remains high and relatively constant once hatching is complete. Chick loss to predation has a different seasonal distribution. Predators are likely to take the highest percentage of available chicks early in the season when chicks are relatively scarce, and chicks hatching at peak hatching will be at increasingly lower risk. The probability of late hatching chicks being taken by predators may be lower than for early hatching chicks because late in the season numerous chicks of all sizes are available to predators, depending on the type of predator. We have observed that late hatching chicks will not be the only juveniles in the colony at the end of the breeding season as early hatching chicks do not leave the colony as soon as they can fly. The optimal time for breeding will occur when $[1-(1-N)(1-P)]$ is at a minimum, where N is the probability of chick loss to neighbors and P is the probability of chicks being killed by predators. The neighbor and predator curves need not intersect for this relationship to hold.

All individuals in a colony do not breed at the optimal time each year because individuals may not obtain sufficient energy to breed at the same time (Perrins 1970). The optimum time to breed may vary depending upon fluctuations in food supplies. In the absence of significant chick loss to predation, inclement weather may partially offset the advantages of breeding early (1971 season, this study).

Kruuk (1964) and Patterson (1965) found highest chick survival in mid-season for Black-headed Gulls which suffered the major portion of their chick loss to predators. The percentage mortality of Common Tern (*Sterna hirundo*) chicks was greatest early in the season when chicks were small and few in number (Fig. 4), while the biomass of chicks taken was nearly constant (Nisbet 1975). Parsons (1971, 1975) found that both early- and late-hatching Herring Gull chicks suffered higher mortality due to predators (cannibalistic gulls) than chicks hatched in mid-season. During one season these cannibalistic gulls took a constant number of chicks despite fluctuating numbers available to them. Parsons (1975) concluded that synchrony of hatching with other birds in the same area rather than seasonal changes in food supply determined this pattern of chick survival.

Paynter (1949) and Vermeer (1970) found the greatest success in early nesting Herring Gulls and California Gulls (*L. californicus*), respectively, where the major known source of chick loss was killing by neighbors. In a Ring-billed Gull (*L. delawarensis*) colony Vermeer (1970) found predation and killing by neighbors equally important causes of chick mortality. Success in his colony was greatest early in the season. Our model predicts greatest success in early mid-season, and without more information on the timing of chick mortality we cannot determine whether our prediction is accurate in this case.

Brown (1967), working with Lesser Black-backed Gulls (*L. fuscus*), found that birds nesting in the open had highest chick survival early in the season, while those nesting in dense cover had highest chick

survival in the middle of the season. On the basis of our model we expect that in the open areas the major cause of chick mortality would be neighbor interference; while in the dense cover, the visually-oriented neighbors would be less important than the crepuscular and nocturnal mammalian predators that rely on scent. Brown (1967) does not present the data necessary to test this hypothesis.

Post-fledging survival may also be related to date of hatching (Perrins 1965, 1968, Lack 1966, Fretwell 1969, Nisbet and Drury 1972). Nisbet and Drury (1972) showed that early hatching Herring Gull chicks had higher post-fledging survival than chicks hatched midway through or toward the end of the hatching period. They suggest, "the earliest chicks establish dominance over younger chicks and maintain dominant status throughout the winter" (Nisbet and Drury 1972:169, Fretwell 1969). Such post-fledging selective pressures would increase the overall selective pressure for early breeding in large species of gulls having dangerous neighbors.

Past attempts to relate gull chick survival either to average minimum inter-nest distance (Fordham 1970) or to average density of nests (Vermeer 1963, Patterson 1965, Fordham 1970, Dexheimer and Southern 1974) have failed to show significant correlations. Parsons (1971) measured the average number of nests within fixed distances of individual nests and found maximum breeding success among pairs nesting at the most common density. These measures are not equivalent to measures of actual territory size and provide no means for differentiating the quality of individual territories within a colony. In two areas with the same density of nests it is possible to have very different distributions of territory size. Furthermore, young of most species of Laridae leave their nests soon after hatching. Since in gulls the chicks generally remain within their own territories, it may be necessary to examine territory size directly if the role of spacing within a gull colony is to be understood.

Large territory size is important for the survival of young skuas (*Catharacta maccormicki* and *C. skua lonnbergi*), both to protect them from potentially dangerous neighboring adults and to allow a younger chick to escape the attacks of its older sibling, a major cause of chick mortality (Stonehouse 1956, Burton 1968, Spellerberg 1971, Wood 1971).

Figure 5 presents a model of optimal territory size given the potentially conflicting requirements of providing sufficient space for chicks to avoid molestation by neighbors and sufficient clumping for effective group defense against predators (Parsons 1971). Chick loss to aggressive neighbors is greatest on small territories and decreases as area increases up to some asymptote above which further increase would provide little or no additional protection. The threshold above which increase in area will not affect chick loss will vary with terrain, availability of hiding places, aggressiveness of neighboring adults, tendency of chicks to move away from their nests, and how well chicks are fed (Hunt and McLoon 1975). Burger (1974) found that spacing of Franklin's Gull (*L. pipixcan*) nests increased with greater internest visibility.

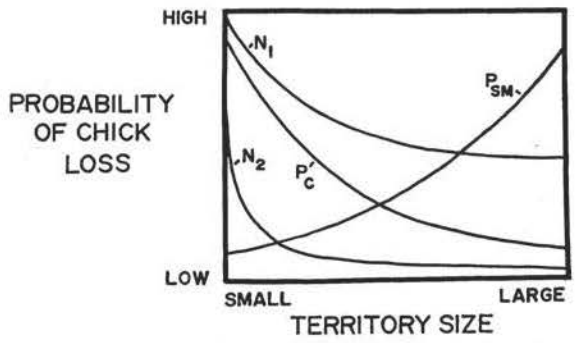

FIG. 5. A model for optimal territory size in which territory size for highest chick survival is predicted by probability of chick loss to predators and to neighbors. N_1 = loss due to very dangerous neighbors; N_2 = loss due to relatively harmless neighbors; P_c = loss to predators due to failure of cryptic components of defense; P_{sm} = loss to predators due to failure of swamping or mobbing strategies of defense.

The relationship between territory size and chick loss to predators is more complex (Fig. 5). Defense of chicks either by mobbing adults or through swamping of predators by large numbers should be most effective when nests are clumped (Kruuk 1964, Patterson 1965, Parsons 1971). However, protection derived from cryptic coloration should be more effective if nests and chicks are widely spaced (Cullen 1960, Crook 1964, Patterson 1965, Tinbergen et al. 1967, Lack 1968, Croze 1970, Ward and Zahavi 1973). Sooty Terns (*Sterna fuscata*) which have no defense against frigatebirds (*Fregata aquila*) (Ashmole 1963*a*:327) are preyed upon chiefly in the denser colonies when "fairly large numbers of chicks were about" (Ashmole 1963*a*:326). Patterson (1965) first suggested that the interaction of the two types of defense should result in an optimal spacing of nests. The optimal chick territory size will be when $[1-(1-N)(1-P_{sm})(1-P_c)]$ is at a minimum, where P_{sm} is the probability of loss to a predator due to the failure of swamping or mobbing strategies of defense, P_c is the probability of loss of chicks due to the failure of the cryptic components of defense, and N represents the probability of loss of chicks to neighbors. As in the model for optimal timing, there is no requirement that the curves for loss to predation and loss to neighbors intersect.

All birds in a colony are unlikely to hold chick territories of optimal size. Population pressures, differences in the aggressiveness of adults and timing of effort to obtain a territory may ultimately influence chick territory size. The optimum territory size within a given colony may change on a yearly basis depending upon food availability to chicks with dangerous neighbors (Hunt and McLoon 1975). Seasonal fluctuations in the size of individual territories may reflect varying needs for exclusive space at different stages of the reproductive cycle (Hunt and Hunt 1975).

Vermeer's (1970) evidence that there is an inverse correlation between size of gull species and the tendency to clump their nests supports our model for optimal territory size. In the small Ring-billed Gull, nests were clumped, similar to the pattern found by Patterson (1965), while in the intermediate-sized California Gull, the nests are randomly spaced, and in the larger Glaucous-winged Gull they are more uniformly spaced. Larger gull species are potentially more dangerous as neighbors and thus they have their nests widely spaced.

Franklin's Gulls were never observed by Burger (1974) to engage in cannibalism, and left eggs uneaten which had been displaced from nests during the stealing of nest material. Of 87 nearest neighbor nest distances documented in her paper, 49 were $\leqslant$ 2 m apart. Close spacing of nests is apparently common in this small gull which is inoffensive to neighbors and which defends against predators by mobbing.

When not affected by predation and lack of available space, large species may nest in colonies with very low density. Western Gulls nesting on Santa Barbara Island, California hold territories averaging 211 ± 124 m^2 (range 48–551 m^2) during the first 10 days of the chick period (Hunt and Hunt 1975). There are no predators on the island, and killing by neighbors is minimal. On the Farallon Islands, California, Western Gulls breed at much higher densities (we have observed), due to space limitations imposed by an increasing population (Ainley and Lewis 1974). At present we lack the data needed to apply our model to this population.

While the models presented were developed specifically for Laridae, with suitable modification they may be applicable to a variety of colonial vertebrates, particularly those which may be dangerous to the young of their own species. In the crow (*Corvus corone*) cannibalism by nonbreeding birds and neighbors is a major cause of chick loss, when nests are close together (Yom-Tov 1974 and references cited therein). For this and other corvids the model may provide understanding of colony structure. Many kinds of fish are known to eat the eggs and young of their own species, and although they are not colonial, the high density of nests in some spawning grounds may create an analogous situation.

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