COLONY SIZE: A TEST FOR BREEDING SYNCHRONY IN HERRING GULL (*LARUS ARGENTATUS*) COLONIES

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ABSTRACT.—The role of social facilitation in breeding synchrony was examined in detail in 8 Herring Gull colonies during one field season in New Jersey and was compared with 4 colonies in the same area during other seasons and 5 colonies from other geographical areas described in the literature. In the eight colonies, mean egg-laying date was inversely related to colony size, the length of the egg-laying period increased with colony size, the variation (standard deviation) in egg-laying date decreased with colony size, and hatching success increased with colony size. As no significant differences occurred in mean egg and clutch size, age variables were eliminated as a cause of the breeding synchrony. Comparing all colonies, the length of the egg-laying period was not correlated with colony size, and the standard deviation of the egg-laying dates decreased as colony size increased up to a size of 200 pairs and increased thereafter. I propose that social facilitation functions to increase synchrony up to a critical number of pairs. Further increases in the number of breeding pairs result in a breakdown of the colony into separate "subcolonies" that function as colonies. Breeding success, as measured by hatching success, increases continuously with colony size. The synchrony, however, increases only up to a critical limit and decreases thereafter, as the synchronies of the subareas occur at different times, making the entire egg-laying period longer. *Received 17 April 1978, accepted 21 May 1979.*

OVER 40 years ago, Fraser Darling (1938), working in a colony of Herring Gulls (*Larus argentatus*) and Lesser Black-backed Gulls (*L. fuscus*), suggested that in colonial species, increased "social facilitation" produces breeding synchrony, resulting in earlier egg-laying, a shorter egg-laying period, and larger clutches. The greater synchrony presumably increases breeding success because the increased number of eggs present at one time swamps predators. That is, an area may support only a certain number of predators all year, and the predators cannot make use of the temporary superabundance of food. Some predators switch from one food source to another when birds are not available, but other food sources are not usually as abundant as a colony of birds. Presumably predators take a relatively constant biomass of prey throughout the breeding season. Thus, relative predation rates should be lowest during the central part of the nesting cycle because more chicks and eggs are available to be eaten. Nisbet (1975) found this to be the case in Common Terns (*Sterna hirundo*), and Parsons (1971, 1975), working in a colony of Herring Gulls, showed that cannibals selected nests that were in less dense areas than normal. He also found that although four particular cannibals ate about the same number of chicks during the season, early and late chick groups suffered a significantly higher mortality than those hatching in the middle of the season.

Considerable controversy has developed among ornithologists over the occurrence of synchrony in breeding colonies. Several authors have presented evidence for increased synchrony with increased colony size (see Coulson and White 1956 for a review). This effect, however, might be a result of differences in age composition in colonies of different sizes (Fisher 1954, Coulson and White 1956, 1958, 1960). Other authors have failed to find any correlation between colony size and synchrony (Weidmann 1956, Orians 1961, Vermeer 1963). Further, Coulson and White (1956)

reported that the temporal spread of breeding increased with colony size. Parsons (1976) showed that small groups of birds (subcolonies) in the colony showed synchronized laying. Others examining synchrony within parts of breeding colonies have also found greater synchrony within these areas than over the colony as a whole (Paynter 1949, Feare 1976, Veen 1977, Gochfeld 1979). In Bank Swallows (*Riparia riparia*), reproductive success was correlated with synchrony (as measured by the standard deviation of the mean hatch date, Emlen and Demong 1975). Egg-laying dates, however, were not considered as a function of colony size in this study, so Darling's hypothesis relating colony size to the occurrence of synchrony was not directly tested.

Several variables are thus involved in the realtionships of colony size and breeding synchrony, including the spread in egg-laying dates, the mean date of egg laying, breeding density, mean clutch sizes, mean egg sizes, and breeding success. Clearly these parameters must be examined in several colonies during the same year in one species to test adequately for the effects of social facilitation, but most studies have considered only a single colony, comparing their results with others in the literature. Further, Darling proposed that the mechanism whereby large colonies had larger clutches, a short egg-laying period, and high breeding success was social facilitation, and this relationship is not usually evaluated.

Here I examine several features of breeding biology and relate them to colony size in 8 Herring Gull colonies ranging in size from 20 to 543 pairs. I was interested in comparing mean egg-laying dates, ranges of egg laying, clumping of egg laying, egg size, clutch size, and hatching success.

STUDY AREAS AND METHODS

In 1977 I examined eight colonies located on salt marsh islands within 20 km of each other in Barnegat Bay, New Jersey. This area contains two large barrier beach islands facing the Atlantic Ocean: Long Beach Island and Island Beach. Numerous low salt-marsh areas and islands, bisected by natural chanels and mosquito ditches, lie behind the barrier beaches and against the mainland. Barnegat Bay separates the barrier beaches from the mainland. Colonies examined, with the number of breeding pairs in parentheses, included: House (543), Egret (343), Experimental (242), Sandy (110), Carvel (108), Big Sloop (85), Little Sloop (28), and Harvey Sedge (20). House, Egret, and Experimental islands are part of a series of islands named Clam Island on local maps. With the exception of Harvey Sedge, which was first formed in 1975, all other colonies were at least 8 yr old, but all were established within the last 25 yr. Therefore, wide differences in population age structure as a function of colony formation dates were not expected.

The gulls founded all colonies on low salt-marsh islands that were subject to tidal inundation during high storm tides. The mean percentage of cover on the islands was 7.8% water (SD = 7.64, range = 0–20), 11.5% bushes (SD = 13.2, range = 2–40), 42.2% *Spartina alterniflora* (SD = 25.9, range = 4–74) and the rest *S. patens*. The islands selected by gulls varied in elevations. *Spartina alterniflora* areas frequently become inundated. The gulls preferred the higher areas of bushes and *S. patens,* as 61% of the gulls nested under bushes, 32% nested in *S. patens,* and only 7% nested in *S. alterniflora*. Thus, for all colonies examined in this study, tide did not play a role in synchronizing nesting, because high tides did not inundate these areas.

The colonies were visited 2–4 times a week from 10 April until 30 June 1977. The islands were carefully searched for new nests during the egg-laying period. I numbered each nest and marked all eggs to determine clutch size. Egg size, calculated by multiplying the breadth times the width (after Grossfeld 1938), was measured for all eggs in randomly selected clutches in each colony. For all nests, I measured the distance to the closest neighbor to get an estimate of colony density. I used the standard deviation of egg-laying date as a measure of synchrony (after Emlen and Demong 1975). Regular nest checks continued during incubation to determine the number of nests in which gulls actually laid eggs and the hatching rate.
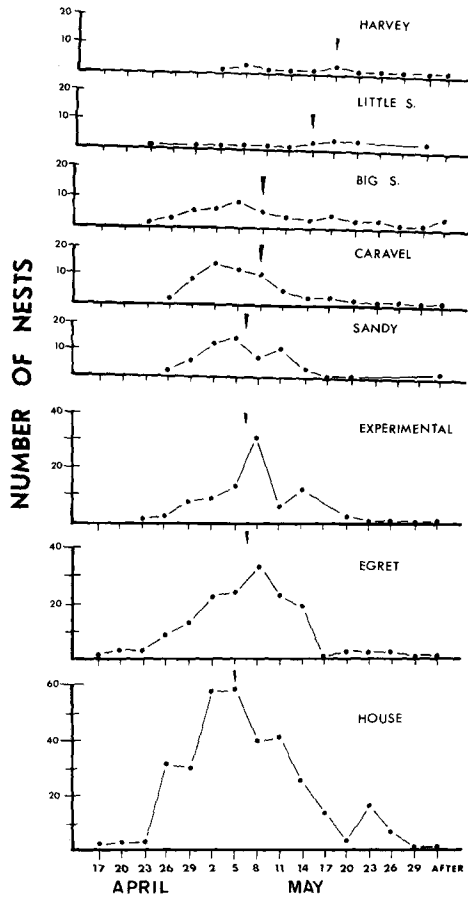
Fig. 1.   Initiation of egg laying on eight Herring Gull colonies in New Jersey. The arrow indicates the mean date of egg laying for each colony.

RESULTS

Egg-laying period for the study islands.—For all islands, egg-laying began 15 April and extended until 18 June. Although I assume that nests initiated in June were probably renesting attempts because they occurred in recently constructed nests, I did not exclude them from the sample. The number of nests initiated in each 3-day period is shown in Fig. 1, where initiation refers to the day the gulls laid the first egg in each nest. The mean date of egg laying was negatively correlated with colony size ($r = 0.74$, df = 6, $P < 0.05$); larger colonies had an earlier mean date of egg laying than smaller colonies. As Fig. 2 indicates, the range of egg laying was not correlated with colony size for the entire sample ($r = 0.43$, df = 6).

Few previous studies have computed any measure of central tendency. That is, they have not compared the standard deviations of the egg-laying dates. This measure allows a comparison of the temporal clumping tendency among groups or colonies. Computing standard deviations for the colonies indicates that the standard deviations were negatively correlated with colony size ($r = -0.74$, df = 6, $P < 0.05$). Thus, for colonies of fewer than 500 pairs, larger colonies have more clumping
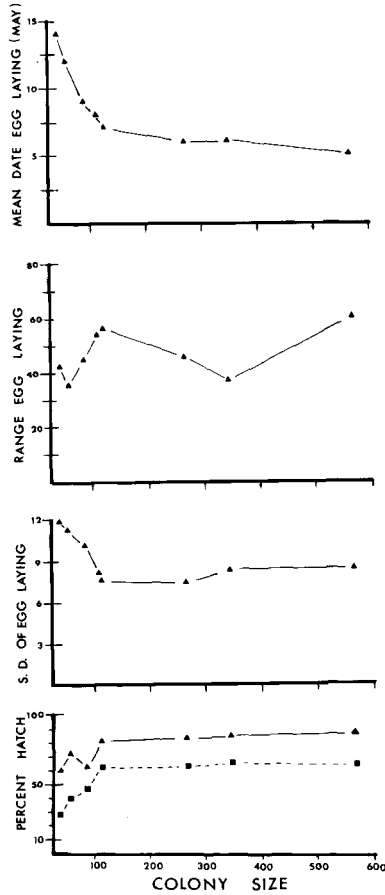
Fig. 2.   Parameters of colony formation as a function of colony size.

or synchrony in nest initiation than smaller colonies. The lowest standard deviations, however, occurred in colonies of 100–250 pairs.

Breeding density.—In general, early pairs nested under bushes, and later nesting pairs nested in *S. patens* adjacent to the bushes. The mean nearest neighbor distances varied from 5.43 to 8.38 m, but there were no significant differences among the islands (*F*-test).

Although mean clutch size varied among islands, there were no significant differences (Table 1, ANOVA; $\bar{x} = 2.76$, range $= 2.51$–2.90). Most nests initiated contained 2 or 3 eggs. I also examined 21 other Herring Gull colonies in the Barnegat Bay area. For the 29 nesting colonies, ranging in size from 5 to 950 pairs ($\bar{x} = 82.6$ $\pm$ 204), there was no significant correlation of mean clutch size with colony size.

Although egg size varied among islands ($F = 2.41$, df $= 7$, 1,668, $P < 0.05$), only the eggs from Harvey Sedge were significantly smaller than those from other islands (Table 1). Harvey Sedge is the only island containing a Herring Gull colony in 1977 that did not contain one in 1975. In the other colonies, significant differences in egg size did not occur, suggesting that there were no significant differences in age structure.

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TABLE 1. Mean clutch and egg size for Herring Gull colonies on eight islands in New Jersey.

Island	Colony size	Clutch size[a]	(n)	Egg size[a]	(n)
Harvey Sedge	20	2.54 ± 0.60	13	120.0 ± 17.0	33
Little Sloop	28	2.74 ± 0.51	22	175.6 ± 17.0	60
Big Sloop	85	2.60 ± 0.63	79	176.1 ± 17.0	205
Carvel	108	2.75 ± 0.69	77	176.5 ± 18.0	211
Sandy	110	2.51 ± 0.73	66	180.3 ± 15.0	165
Experimental	242	2.74 ± 0.68	195	177.6 ± 16.0	534
Egret	343	2.78 ± 0.55	229	173.5 ± 17.0	636
House	543	2.90 ± 0.58	350	177.2 ± 17.0	1,015

[a] $\bar{x}$ ± SD

Two measures of hatching success were recorded: the percentage of nests having at least one egg hatch (nest success) and the percentage of all eggs that hatched (hatching success). In the study islands, nest success was positively correlated with colony size (Fig. 2, Table 2; $r = 0.77$, df = 6, $P < 0.05$). Nest success was negatively correlated with mean egg-laying date ($r = -0.88$, df = 6, $P < 0.01$) and with the percentage of nests containing eggs ($r = -0.67$, df = 6, $P < 0.05$). Hatching rate also was correlated with colony size (Fig. 2; $r = 0.70$, df = 6, $P < 0.01$). Thus, Herring Gulls nesting in colonies with earlier mean egg-laying dates had higher hatching success than those in colonies that laid eggs later.

Given the small number of colonies, and the colinearity of the variables, it is not desirable to run a multiple regression analysis. However, regressions for the two success measures were run on each variable (Table 2). This procedure indicates that colony size, the mean date of egg laying, and the standard deviation of egg laying all contribute substantially to the variability in the success measures. These three variables accounted for 75% of the variability in the percentage of nests having one egg hatch and for 94% of the variation in the hatching success.

DISCUSSION

The pattern of synchrony.—In the colonies I examined, mean egg-laying date was related inversely to colony size, the length of the egg-laying period increased with colony size up to 200 pairs, the standard deviation decreased up to 250 pairs, there were few differences in clutch or egg size, and hatching success increased with colony size.

One of Darling's contentions was supported by these data, as the mean date of egg laying was correlated with colony size. The length of the laying period, however, did not decrease with increasing colony size, as Darling's theory would predict, although the length of the laying period may not be an adequate measure. An inspection of Fig. 2, however, indicates that the greatest synchrony (lowest SD) existed in colonies of 100–250 pairs. Above 250 pairs, overall synchrony decreased. This suggests that the relationship between synchrony and colony size is not linear.

To examine this hypothesis in more detail, I examined data from 1976 for four other Herring Gull colonies in New Jersey (Burger 1977a) and for five colonies described in the literature. The salt-marsh colonies examined in New Jersey were Little Gull (20 pairs), Islajo (140 pairs), Middle (900 pairs), and Little Heron (120 pairs). The colonies examined from the literature were: (1) Brothers Island on Lake Ontario, U.S.A. (47 pairs, Teeple 1977), (2) Skokholm in Wales (1969 data, 400

TABLE 2. Regression of success measures against colony characteristics. Given are t values testing for the importance of each characteristic to the variation in the success measure and the correlation coefficient of each characteristic with the success measure.

	t	P	r	P
Nest success:				
Colony size	2.82	0.02	0.755	0.001
$\bar{x}$ date of egg laying	4.65	0.005	−0.885	0.001
Range	1.08	N.S.[a]	0.404	N.S.
SD	4.35	0.005	−0.872	0.001
Hatching rate				
Colony size	2.38	0.05	0.697	0.005
$\bar{x}$ date of egg laying	9.38	0.001	−0.697	0.005
Range	1.32	N.S.	0.474	0.05
SD	7.71	0.001	−0.953	0.001

[a] N.S. = not significant

pairs, Davis 1975), (3) Skokholm in 1962 (400 pairs, Harris 1964), (4) Kent Island in New Brunswick, Canada (1,000 pairs, Paynter 1949), and (5) Walney in England (1969 data, 9,000 pairs, MacRoberts and MacRoberts 1972). All of these colonies were on dry land above any danger of high tides. All colonies except Walney were island areas isolated from mammalian predators. For these colonies I computed the range, mean, and standard deviation of egg laying. I only examined these colonies as a tentative test of the hypothesis that synchrony increases with colony size up to 100–250 pairs and that synchrony decreases thereafter.

Figure 3 shows the ranges and standard deviations of the egg-laying periods for the eight colonies in the present study, for New Jersey colonies I studied previously, and for the colonies reported in the literature. There was no correlation between egg laying and colony size. The range was positively correlated, however, for colony size below 200 pairs ($r = 0.91$, df = 6, $P < 0.01$), but not above 200 pairs ($r = -0.19$). The standard deviations were negatively correlated with colony size below 200 pairs ($r = -0.78$, df = 6, $P < 0.05$). Thus, synchrony increased as colonies approached 100–200 pairs and decreased thereafter.

I suggest that social facilitation increased for pairs nesting in colonies up to 200 pairs and that thereafter the group size was so large that individuals no longer interacted with the whole group, but began to interact in smaller groups. To an individual in a small colony, the addition of new individuals no doubt increases its perception of the frequency of sexual and territorial displays. To a gull in a larger colony (>200 pairs), an increase in the number of pairs no longer increases its perception of increased reproductive or display activity. When the critical number of pairs is reached, it seems likely that new pairs entering the colony select nest sites in areas with pairs that are also displaying and building nests. An unmated male might find more unmated females in an area with other unmated males than in an area with all incubating pairs. Thus, after a colony reaches 100–200 pairs, it acts as a series of small colonies, resulting in the occurrence of greater synchrony in sub-colonies of the colony compared with the whole colony. The critical size of the group that acts as a "colony," and the size that results in the creation of "subcolonies," might well vary among species and among habitats.

Several factors might control the relative group size of the gulls that act as a sub-colony: breeding density, physical characteristics, vegetation, and colony stability. Breeding density may influence the size of the group, because displays would be
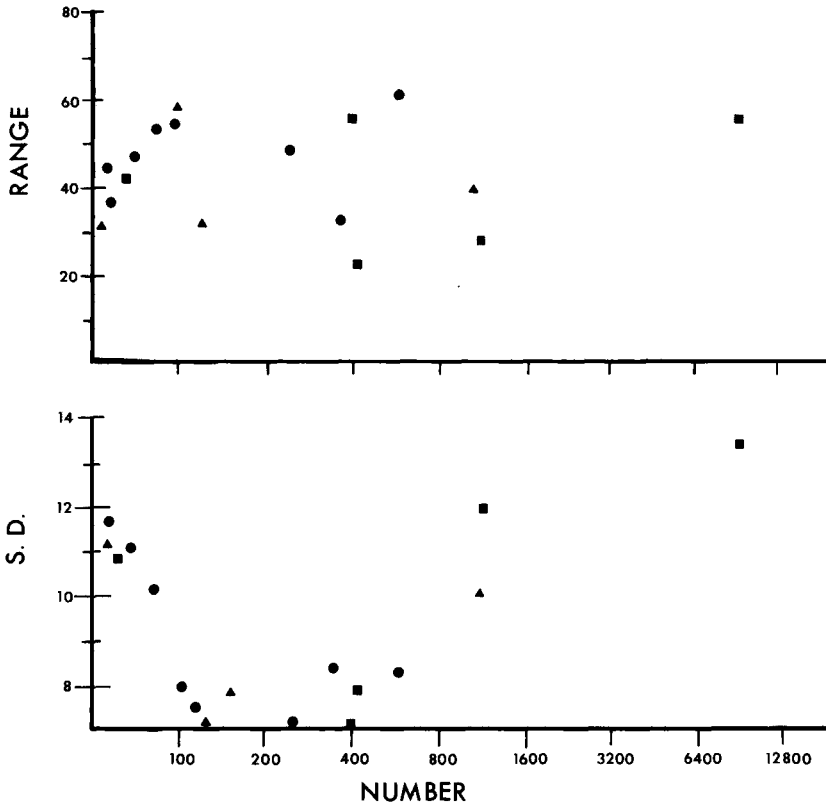
Fig. 3. Standard deviation and range of egg-laying date as a function of colony size for the 1977 New Jersey data (●), the 1976 New Jersey data (▲), and colonies from the literature (■).

visible to more pairs in dense groups (see Parsons 1976). Additionally, increased density might lead to more territorial displays (Patterson 1965), which could lead to delayed breeding. Similarly, vegetation, hills, and rocks may increase or decrease the visibility of displays. Because gulls respond to vegetation dispersion by spacing nests more closely with reduced visibility (Burger 1972, 1974a, 1976, 1977b), vegetation may also influence social facilitation. Gulls nesting in dense cattails (Franklin's Gulls, *L. pipixcan*) or tules (Brown-hooded Gulls, *L. maculipennis*; Burger 1974b) might have smaller areas of synchrony than those nesting in the open, such as the Herring Gulls on grassy knolls at Walney (Brown 1967). Gulls nesting in areas of dense vegetation resort to more aerial displays (Moynihan 1956), which might function to increase social facilitation.

Several other factors in addition to social facilitation might increase synchrony within subcolonies and between colonies: weather, tides, food supply, age composition, behavioral choice, breeding density, and colony stability. Hailman (1965) and Veen (1977) have suggested that birds seek out pairs that are at a similar reproductive stage. This seems likely only for new recruits into the breeding population, as many species of gulls are known to show nest-site fidelity. Philopatry has been reported for Black-headed Gull (*Larus ridibundus*; Ytreberg 1956, Patterson 1965), Black-tailed Gull (*L. crassirostris*, Austin and Kuroda 1953), Mew Gull (*L. canus*, Onno

1967), Lesser Black-backed Gull (Brown 1967), Herring Gull (Paludan 1951, Tinbergen 1953), and Glaucous-winged Gull (*L. glaucescens,* Vermeer 1963). Given that philopatry generally occurs in gulls, it is unlikely that within a colony old, established pairs seek out pairs that are at the same reproductive stage.

Tides or floods may play an important role in the breeding synchrony of gulls nesting in low areas. The onset of breeding in Laughing Gulls (*L. atricilla*) is influenced by spring tides (Burger and Shisler 1978). Southern (1977) discussed the importance of high water levels of the Great Lakes in colony selection by Ring-billed Gulls (*L. delawarensis*). Other gulls, such as Black-billed Gull (*L. bulleri,* Beer 1966), Franklin's Gull, and Brown-hooded Gull (Burger 1974a, 1974b), also nest in ephemeral habitats where nesting is delayed until the high water recedes. Tides did not synchronize the breeding activities of the Herring Gulls observed in New Jersey in 1977, as none of the colonies studied was inundated immediately before or during the nesting season.

Coulson and White (1956, 1958, 1960) and others have suggested that the synchrony observed in colonies might be due to differences in their age composition. That younger birds lay smaller eggs has been well documented for several species, including the Shag (*Phalacrocorax aristotelis,* Coulson et al. 1969), Black-legged Kittiwake (*Rissa tridactyla,* Coulson 1963), Gannet (*Morus bassanus,* Nelson 1966), Slender-billed shearwater (*Puffinus tenuirostris,* Serventy 1967), Herring Gull (Davis 1975), Common Tern (*Sterna hirundo,* Greenhalgh 1974), and Ring-billed Gull (Ryder 1975). Because I found no significant differences in egg size among seven of the colonies, it seems that age is unlikely to be the cause of synchrony in these colonies.

Finally, food supply may influence the onset of egg laying and breeding. Veen (1977) discussed the problems Sandwich Terns (*Sterna sandvicensis*) have in obtaining sufficient food prior to breeding. Presumably food availability would be a more important synchronizer for those species having a restricted or ephemeral food source. It may be that in temperate regions food is not limiting due to the presence of garbage dumps (Harris 1964, 1970; Drury 1965). Despite the availability of garbage, Herring Gulls in New Jersey feed mostly on natural foods, suggesting that food is not limiting. All of the colonies I examined were within 20 km of each other. Thus, it is unlikely that the temporal availability of food varied between these colonies, and the differences in synchrony seem unrelated to food supply.

Breeding success and synchrony.—The occurrence of synchrony is of little evolutionary significance unless it relates to reproductive success or fitness. In the New Jersey colonies, hatching success correlated with colony size and the mean date of egg laying. It is difficult to separate seasonal effects from colony-size effects, because these two factors are correlated. Differences in breeding success as a function of egg-laying date have been found for Herring Gulls (Paynter 1949, Brown 1967, Kadlec and Drury 1968, Harris 1969, Erwin 1971); Glaucous-winged Gulls, California Gulls (*L. californicus*), and Ring-billed Gulls (Vermeer 1963, 1970); Lesser Black-backed Gulls (Brown 1967); Black-headed Gulls (Patterson 1965); and Sooty Terns (*Sterna fuscata,* Feare 1976). The above differences were found within colonies. Late nesters in the New Jersey colonies might have had lower productivity than early nesters apart from any effects of synchrony.

For Herring Gulls, the percentage of eggs hatching ranges from 28% (Teeple 1977) to 80% (Kadlec and Drury 1968). In this study, the highest percentage of eggs hatching was 80% (House Island). For these colonies, the percentage of nests having

at least one egg hatch and the percentage of eggs hatched both correlated directly with colony size. Thus, the larger the colony, the higher the hatching success. Because larger colonies have synchrony within subareas, even though the synchrony for the entire colony as a whole is low, hatching success should be higher because it reflects the high hatching success in each of the highly synchronous sub-areas. Presumably the effect of synchrony on hatching success related to lower predation rates (see Patterson 1965, Nisbet 1975, Parsons 1976).

Thus, I propose that social facilitation functions directly to produce synchrony up to a critical colony size. During this time, breeding success also relates directly to colony size. Thereafter, increases in colony numbers result in a "break-up" into smaller groups, which are synchronous in themselves and have a high breeding success equivalent to similarly sized colonies. Adding the subcolonies of a colony thus results in decreased total synchrony but high reproductive success.

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