our stay on Colville Island possible, but also gave us considerable encouragement and help during the study.

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EFFECTS OF HUMAN DISTURBANCE ON THE BREEDING SUCCESS OF GULLS

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A number of factors have been suggested as affecting reproductive success in gulls. In this study we have attempted to isolate the effect of human disturbance on breeding success. We held other factors such as age of birds, terrain, and density of colony as constant as was practicable with a varied colony environment. There have been several previous discussions of the possible effect of human disturbance on the breeding success of birds. However, no study has documented this effect with controls. Reid (1968) found that in the Adélie Penguin (*Pygoscelis adeliae*) "banding and close observation during seven summers caused the breeding populations in six colonies . . . to decrease by more than 90%." Nelson (1966), commenting on nests on the fringe of colonies, stated that their lower success rates did not take full account of artifacts introduced by human disturbance. Working with the Sooty Tern (*Sterna fuscata*), Ashmole (1963:324) said that "mortality caused by the pecking of chicks by adults was increased enormously by any human disturbance of the colony." Kadlec and Drury (1968: 657) provided some information on the effect of human disturbance, and compared islands visited occasionally with those being studied in detail. Although they acknowledged an effect, they considered it insignificant compared to environmental variables. Hunt (1972), in studying four small Herring Gull (*Larus argentatus*) colonies, found that two colonies, frequently disturbed by picnickers, had lower hatching success than two undisturbed colonies. He found no difference in the ability of parents to raise young. These latter two studies most systematically approach the problem, but each compares totally different colonies that are, of course, under a variety of environmental conditions.

In 1968 we studied the effects of human disturbance on parts of a single colony of gulls on Southeast Farallon Island, California. Our study demonstrated the quite dramatic effect on breeding success caused by an investigator entering a nesting colony.

THE FARALLON GULL COLONY

The Farallon Islands are a small group located 43 km west of San Francisco, California. The colony of Western Gulls (*Larus occidentalis*) occupies a large proportion of Southeast Farallon Island, the largest of the Farallones, and adjacent Maintop Island, which have a combined land area of about 40 ha (see map in Bowman 1961).

The Western Gull is a maritime species. Its breeding is almost entirely restricted to islands along the Pacific Coast from Washington to Mexico. There are three described races, the subject of this study being the nominate form.

The species is the only gull nesting, or known to have nested, on the Farallones. At present we estimate the colony population at 20,000 individuals. During the breeding season, adults were seen spaced out as if on territory on about 70 per cent (28 ha) of Southeast Farallon and Maintop islands. On study plots

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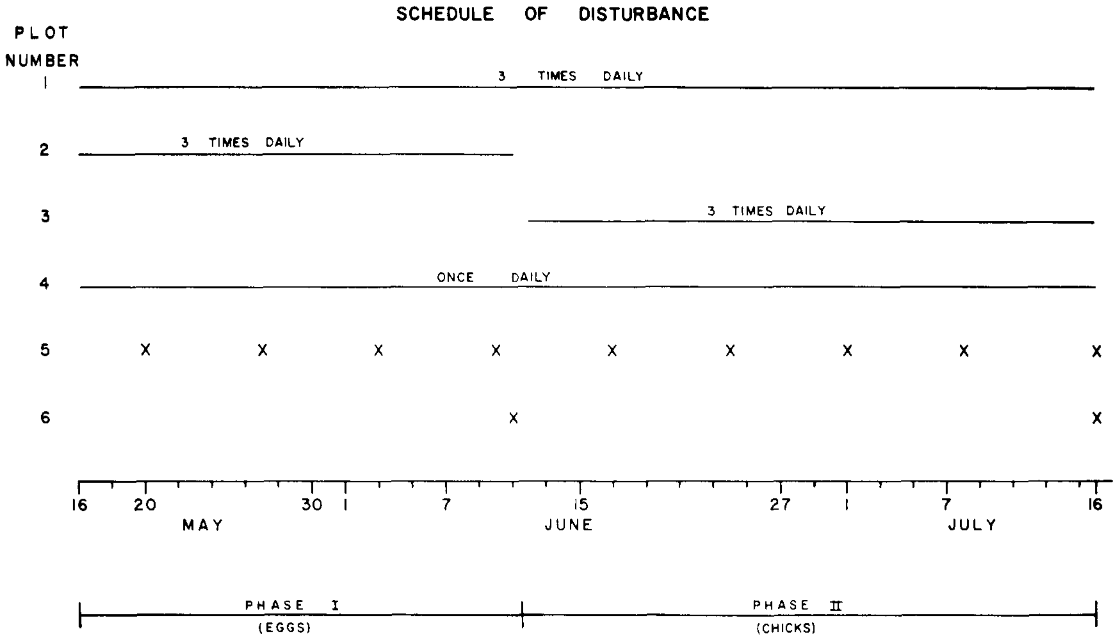

FIGURE 1. Schedule of disturbances of the study plots in the gull colony.

totalling 1.25 ha, 820 nests containing eggs were counted. The average density for the plots was thus 65.6 nests per 1000 m^2. This density was undoubtedly much higher than on most of the colony.

On 3 April 1968 when this study began, the entire population was present on breeding territories. Several nest scrapes were observed at this time. At this stage of the breeding cycle, a person entering the colony causes a "panic flight," sending thousands of screaming gulls into the air. These panic flights also occurred occasionally both during the day and night for undetermined reasons. By mid-April nest building was well under way. As the gulls started laying, their reaction to a person in the colony became less tumultuous and usually only a few hundred would fly above the intruder. During incubation they became reluctant to fly when a person approached. Many ran a short distance from the nest, usually calling loudly. Such birds returned to the nest quickly, and often settled on the eggs only a meter behind the intruder. At this time, gulls flying overhead would sometimes swoop down on persons walking through the colony. As the young began to hatch, the adults became more aggressive, and an intruder might have several diving simultaneously, sometimes striking forcefully on the head.

DESCRIPTION OF SCHEDULED DISTURBANCES

Scheduled disturbances (fig. 1) usually consisted of one person walking slowly (about 0.5 kph) in the study plot for approximately 30 minutes. Plots disturbed three times each day were thus disturbed for a total of approximately 90 minutes. More or less time was spent on each plot depending upon its density, so that each nest received approximately an equal amount of disturbance. The birds were left undisturbed for at least an hour and sometimes several hours between periods of disturbance. During a disturbance the investigator walked slowly through the plot, recording on a map the site and contents of each nest, or the number and location of chicks.

This species is relatively synchronous in its breeding, with most of the colony reaching the same stage within a week. The study was divided into two phases. Phase I included the incubation period, and the very early chick stage, when the chicks are not mobile, and thus do not react to a disturbance. Phase II includes much of the chick period.

Scheduled disturbances of Phase I were begun on 16 May when a check outside the study areas indicated that a majority of the nests contained at least one egg. Later determination revealed that on that day, plot 1 held 75% of the eggs that would be laid there, plot 2 held 61%, and plot 4 held 65%. Disturbances were not started sooner in order to prevent abandonment of nests, since that would have reduced the number available for study.

In plot 2 (disturbed only during Phase I), disturbances were stopped on 11 June when 50% of the nests had at least one young. On the same day, disturbances were begun on plot 3 (disturbed only during Phase II). Seventy-three percent of the nests on this plot had at least one hatched young. There were 92 eggs and 193 young on this plot.

On 16 July disturbances were halted when two young were seen to fly out of a study plot. Counts would have been meaningless after young were capable of flying. On this date counts were made of young on plots 2 and 6, which had not been disturbed since 11 June. Even at this late stage accurate counts of young were possible due to the relative lack of cover on the island. More than 95% of the young on a plot could be found on any single census, and essentially all within two censuses.

DESCRIPTION OF STUDY PLOTS

Six study plots were laid out in the colony (table 1), at least 30 m apart. Human activity in a given plot caused no apparent disturbance in any other plot.

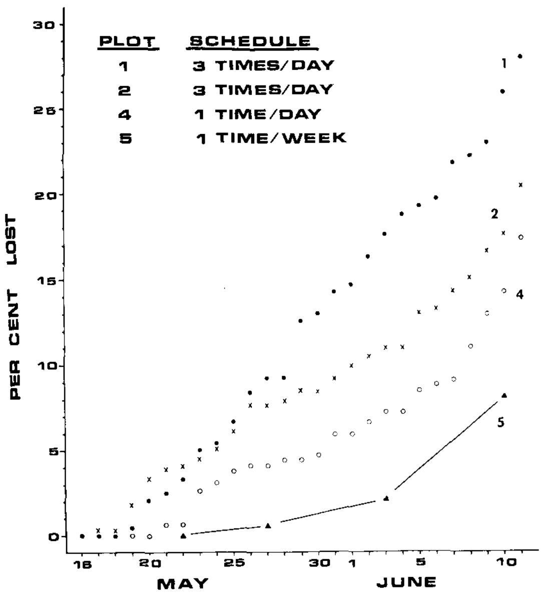

FIGURE 2. Percentage of eggs and/or small young lost of the total number of eggs laid in study plots subjected to varying degrees of disturbance during Phase I (Incubation period). A few eggs were replaced by the gulls after loss, thus these figures differ slightly from those in Tables 1 and 2.

The following criteria determined the selection of the plots: (1) similarity in terrain and exposure to the sun; (2) regular shape, either a broad rectangle or square; and (3) high probability of having at least 100 nests within their boundaries. None of the plots were exactly alike, as expected, but they were reasonably similar.

RESULTS

Phase I survival. The daily loss of eggs or very small immobile young during Phase I was directly proportional to the frequency of disturbance (fig. 2). Each disturbance schedule was highly significantly different ($P < 0.001$) from all other schedules by the Wald-Wolfowitz Runs test (Siegel 1956). Plot 1 had even greater losses than plot 2 although both were disturbed three times daily, probably because of the unscheduled disturbances (see table 1) on plot 1 totalling over 300. The number of these unscheduled disturbances doubled after 29 May, the date the losses on plot 1 suddenly became much greater than plot 2. Calculations of percentage of losses were not carried past 11 June because on that date disturbances, and thus counts, were stopped on plot 2.

Another expression of the effect of human disturbance during Phase I was the reduction of hatching success in plot 1, disturbed three times daily (plus the brief unscheduled disturbances), compared with plot 4, disturbed only once a day (table 2). (Only these two plots could be used for these calculations because they were the only plots visited daily throughout the study, thereby yielding sufficient hatching data.) The plot disturbed three times daily had a significantly greater ($P < 0.01$) loss than the plot disturbed once a day. All significance levels were tested by computing the normal deviate derived from the approximation to the binomial (Snedecor

TABLE 1. Size, disturbance schedule, characteristics, density and survival in study plots.

Plot number	Size	Disturbance schedule	Timing of disturbance	Unscheduled disturbances[1]	Maximum occupied nests	Density 1000 m²	Plot characteristics	% Egg survival	% Chick survival
1	200 × 100 ft. (61.0 × 30.5 m)	Phase I, II	3/day	8–16/day	84	45.1	level, few rocks	72.8	47.1
2	150 × 150 ft. (45.7 × 45.7 m)	Phase I	3/day	none	141	67.5	steeper, most rocks	79.5	42.4
3	200 × 100 ft. (61.0 × 30.5 m)	Phase II	3/day	none	117	62.9	level, few rocks	—	29.9
4	150 × 150 ft. (45.7 × 45.7 m)	Phase I, II	1/day	2/day	115	55.1	somewhat steep & rocky	82.9	35.9
5	150 × 125 ft. (45.7 × 38.1 m)	Phase I, II	1/week	none	127	73.0	somewhat steep & rocky	94.3	27.9
6	140 × 125 ft. (42.7 × 38.1 m)	11 June and 16 July	once each	none	111	68.2	steeper, few rocks	—	45.1

[1] Unscheduled disturbances of about one minute each were caused by persons walking through the plot along a path. These resulted in identical disruption to that caused by an investigator during the planned disturbances. Thus a total of 10 in a day would be approximately equivalent to an additional 10 minutes of disturbance by an investigator.

TABLE 2. Hatching success and survival of young to ten days. Calculations are based on the total number of eggs known to have been laid in each plot.

	Eggs laid	Hatched		To 10 days of hatched	
		%	no.	%	no.
Plot 1 (disturbed 3 times daily)	239	66.5	159	80.5	128
Plot 4 (disturbed once daily)	316	77.8	246	74.0	182
Significance of difference		< 0.01		n.s.	

and Cochran 1967:220). Thus, more frequent disturbance appears to have caused reduced productivity due to loss of eggs or their failure to hatch.

Phase II survival. Unexpectedly, chick mortality was highest on the *least* disturbed plot. Survival of chicks during Phase II (table 3) was 47.1% on plot 1 (disturbed 3 times daily), 35.9% on plot 4 (disturbed once a day), and 27.9% on plot 5 (disturbed once a week). The differences between plots 1 and 5 were significant ($P < 0.05$). Survival of chicks to ten days was higher, although not significantly ($P < 0.15$), on plot 1 than on plot 4 (table 2).

These differences in chick survival should not necessarily be interpreted to mean that human disturbance is beneficial. To the contrary, the adverse effect of human disturbance is probably best shown by comparing plots 6 and 2 (both completely undisturbed after 11 June), with plot 3 (disturbed 3 times daily during that period). The undisturbed plots had a very significantly ($P < 0.0001$) higher chick survival rate, 43.6% than did the disturbed plot, 29.9% (table 3).

DISCUSSION

Phase I (incubation period). Our results suggest that a frequently disturbed portion of a colony had greater egg losses, and thus reduced hatching success, compared with a less frequently disturbed portion of the colony. The principal cause of egg loss was destruction by gulls themselves. Often a gull was seen to take an egg from a nest during a planned disturbance. We could not determine whether the gull taking the egg was one of a breeding pair, or one of the non-breeding adults resident on the island. A few eggs may also have been broken or knocked from the nest when an incubating bird suddenly took flight. An incubating bird when flushed sometimes moved the eggs slightly in the nest. It is also possible that birds on the more frequently disturbed plots were kept off the eggs longer, resulting in a decrease in hatching success.

The hatching success on plot 4 (disturbed once a day) was 77.8%. This was somewhat higher than found in most studies of gulls. For instance, Brown (1967) reported a 65.7% hatching success for Herring Gulls and 72.0% for Lesser Black-backed Gulls (*Larus fuscus*). Degree or frequency of disturbance was not documented in his study. Kadlec and Drury (1968:654) showed some hatching data for Herring Gulls, varying between colonies and years from 68.9–79.3% ($\bar{x} = 76.3$). Hunt's (1972) study of the same species had successes ranging from 19% to 69%. In the Western Gull, Schreiber (1970) reported 57.8% hatching success in 150 nests studied. Vermeer (1963) reported 71.0% success in Glaucous-winged Gulls (*L. glaucescens*) in British Columbia in 1961 and 83.0% in 1962. He suggested that the higher hatching success in 1962 might have been due to better weather conditions. Alternately, it could have been due to the approximately twice as intense disturbance in 1961 as in 1962.

Phase II (chick period). Our data demonstrate that among plots subjected to disturbance, survival of young was better on the more frequently disturbed plots. Although the early part of Phase II included some eggs still in the nest, this would not have affected our results. If disturbance results in lower egg viability, as is probable, this lower viability would have tended to reduce survival in the more disturbed plots during Phase II, rather than increase it. The higher survival is a seemingly incongruous finding. However, we observed that the young, as they became mobile during Phase II were more intensely frightened by the investigator on the less frequently disturbed plots. Thus they were more likely to run greater distances from their territories. These chicks were

TABLE 3. Percentage of young and eggs surviving on all study plots. Calculations are based either on the total number of eggs known to have been laid and/or on counts made on 11 June.

Plot no.	Disturb. schedule	Eggs laid	Eggs or young 11 June	% surviving of eggs laid (Phase I)	Young 16 July	% surviving of eggs laid	% surviving of no. on 11 June (Phase II)
1	3/day	239	174	72.8	82	34.3	47.1
2	3/day (Phase I)	391	311	79.5	132	33.8	42.4
3	3/day (Phase II)	—[1]	298	—	89	—	29.9
4	1/day	316	262	82.9	94	29.7	35.9
5	1/week	334	315	94.3	88	26.3	27.9
6	none	—[1]	244	—	110	—	45.1

[1]Available for only those plots checked daily during incubation.

therefore subject to more attacks by the adults into whose territories they had intruded. (In comparing plots 1 and 4, although the more frequently disturbed plot had higher mortality (table 2), the difference was not significant, as perhaps the threshold of habituation to man had been reached.) On the more frequently disturbed plots the young would generally walk ahead of the investigator, angle off to either side, and circle back without having gone far from the nest. These birds thus tended to avoid attack by adults in other territories. Thinning of the population by the demonstrated higher egg loss and thus lower hatching success might help explain a higher chick survival on the more frequently disturbed plots, especially plot 1, disturbed three times daily throughout the study. When the nesting density has been artificially reduced, surviving chicks might encounter fewer attacks by adults. Chicks might also receive more food as members of smaller broods. The primary motivation for these adult attacks on young may be defense of territory rather than predation. Most of the chicks killed were not utilized for food. It would be advantageous for the brood if the parents kept the territory free of intruding chicks which might appropriate food regurgitated by parents feeding their brood. Not only do adults defend territories, but on many occasions older chicks were seen to do the same, even against intruding adults. Some predation by adult gulls seeking very small chicks as food was occasionally observed. Numerous deaths that could not be attributed to physical attack occurred among young gulls, but the exact cause was not determined.

Plots 1 and 4 had an average survival from birth to ten days of 76.6%. This rate is higher than that found by Brown (1967) in the Herring Gull (66.5%) and the Lesser Black-backed Gull (55.8%).

Although amount of disturbance was the only environmental variable altered by the investigators, there were other characteristics of the plots that varied, as Table 1 indicates. Inspection of that table will show however, that for every trend observed in a few plots, other plots contradict the trend (e.g. high density is correlated with high egg survival, cf. plot 2). It appears that the disturbance schedule overwhelmed the relatively minor variations in success caused by plot characteristics.

An additional variable was unavoidably introduced, that of density of nests (table 1). However the greatest difference between the plots in density was only in the order of 25%. The differences in intensity of disturbance were several-fold. It might therefore seem reasonable to conclude that the effects of the differences in density would be overwhelmed by the disturbance schedule. We feel that this is the case.

SUMMARY

This study suggests that under defined conditions, the presence of an investigator can be strikingly detrimental to breeding success. Hatching failure was found to be directly proportional to the amount of disturbance in a plot. However, mortality of young was inversely proportional to the amount of disturbance. The latter mortality was apparently the result of occasionally disturbed chicks reacting to the presence of the investigator by running into other territories and being attacked by adults. Young gulls that were more frequently disturbed were less frightened, and less subject to attack by adults. Overall mortality of young, comparing the completely undisturbed plot with a disturbed plot, was higher on the disturbed plot. Future studies of the effects of the environment upon breeding success in gulls might well take account of this source of mortality.

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