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Author
Hunt, George L

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INFLUENCE OF FOOD DISTRIBUTION AND HUMAN DISTURBANCE ON THE REPRODUCTIVE SUCCESS OF HERRING GULLS[1]

GEORGE L. HUNT, JR.

Department of Population and Environmental Biology, University of California, Irvine Irvine, California 92664

Abstract. A three year study of Herring Gull (*Larus argentatus*) reproductive success on four islands in Maine indicated that production of young was controlled by different factors operating on the eggs and chicks. Hatching success was inversely related to the disturbance of colonies by picnickers, which apparently caused the adults to leave their eggs exposed to sufficient solar radiation to addle the eggs. The survival of chicks was lower on islands distant from sources of edible refuse (outer islands) than on islands close to sources of waste (inner islands), regardless of visits by picnickers. The nutrition and growth rates of chicks on inner and outer islands were similar. The attendance of parents on the territories was found to be less on an outer island than on an inner island. It is concluded that differences in parental behavior associated with greater foraging effort were responsible for a higher loss of chicks to predation on the outer islands.

INTRODUCTION

Populations of several species of gulls (*Larus* spp.) in different parts of the world have increased greatly during the twentieth century (Fordham 1967, 1970, Kadlec & Drury 1968, Harris 1970, Spaans 1970). These increases have been attributed to a combination of two factors: 1) passage of laws that limit hunting and egg collecting; and 2) increased food resources in the form of edible wastes supplied by a prosperous and expanding human population.

Several studies have sought to demonstrate a relationship between the availability of edible refuse and increases in the gull populations (Spärk 1950, Drury 1963*a* and *b*, Harris 1965, Ingolfson 1967, Spaans 1970). These authors have shown that gulls gather a large percentage of their food from man throughout the year. However, without data on the carrying-capacity of the natural feeding areas, it is difficult to show that the use of man's waste is required for either the support of the large gull populations or their present rate of increase.

The early work of Drury (pers. com.) and of Kadlec and Drury (1968) suggested that the influence of edible refuse on the reproductive success of Herring Gulls, *Larus argentatus,* could be demonstrated by comparing the productivity of colonies located at various distances from sources of waste. In this study I have examined this relationship by comparing four breeding colonies of Herring Gulls in Maine. Data were gathered on the productivity of the colonies, the foods brought to the chicks, the growth rates of the young and the parental care given by the adults.

STUDY AREA

The study was conducted in Penobscot Bay, Knox County, Maine (Fig. 1) during the summers of 1968, 1969, and 1970. The area contained a small number of localized sources of man's waste and a number of gull colonies on islands.

Three species of gulls nested in the area. The Herring Gull, *Larus argentatus,* was the commonest species and comprised 85–90% of the gull population. The Great Black-backed Gull, *L. marinus,* made up about 8–13%. The Laughing Gull, *L. atricilla,* once common, represented less than two per cent of the gulls in the area at the time of my study.

Colonies of Herring Gulls were studied on Goose Rock, Little Green Island, Flat Island and Sloop Island (which was not available for study in 1968). Examination of these colonies provided information about two of the possible factors affecting the reproductive success of gulls, disturbance and distance from foraging areas. Disturbance was measured subjectively on the basis of the number of old fireplaces, beer cans and picnic groups I encountered. Flat Island was a favorite picnicking area for local people, and several groups were encountered during my visits to the island. Sloop was also used by picnickers, but less frequently than Flat. Goose Rock and Little Green Island were not suitable picnic areas and neither island was visited by picnickers during my study. The distances to sources of man's waste were greatest from Sloop Island and Little Green Island (outer islands), while Flat Island and Goose Rock (inner islands) were relatively close to prime foraging areas (Table 1). Short descriptions of the islands are presented in Hunt (1970).

Natural foraging areas were abundant throughout the study area. Dumps in Camden and Belfast, fish processing plants in Rockland, and chicken processing plants in Belfast (Fig. 1) were important sources of food because large quantities of refuse were consistently available to the gulls. Lobster fishing also provided food for the gulls, particularly those nesting

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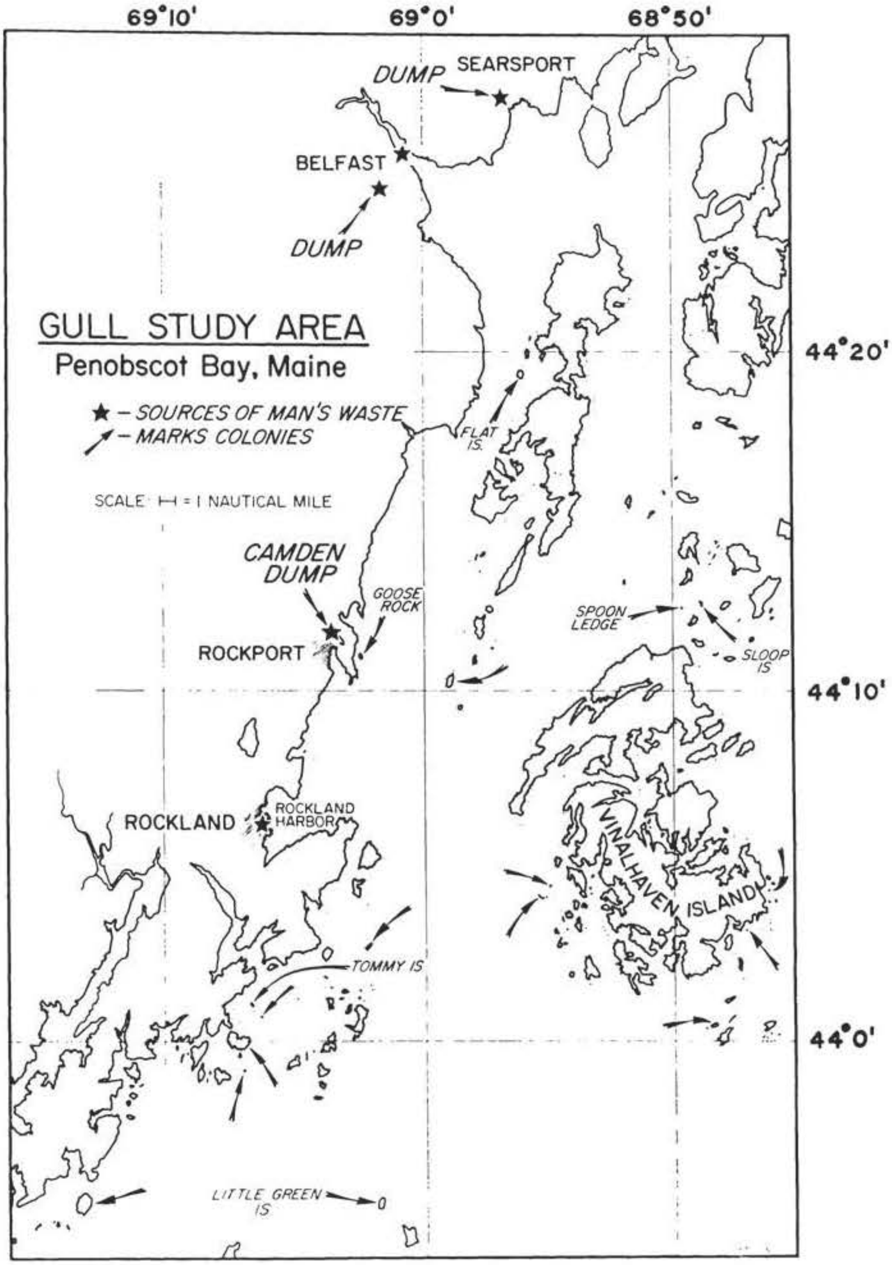

FIG. 1. Study area.

on the outer islands. Whenever traps were hauled, the old bait was thrown overboard.

Throughout this paper the terms "refuse" and "waste" are used interchangeably. They refer to all foods derived from man, including garbage, sewage and all fish made available to gulls by man's activities.

METHODS

Productivity

Nests in each colony studied were marked with a numbered stake. The eggs present in each nest were counted after the clutches were complete. Newly hatched chicks were banded, weighed, and their nest of origin recorded. A chick was banded if it was found on an unnumbered nest and the number of eggs and siblings on the nest was recorded. In these cases the nest was assigned a number and was included in the general statistics of the study.

After the initial banding, chicks were recaptured at intervals of two days to more than a week, depending on weather conditions governing travel to the islands and on my success in finding the birds. On each oc-

TABLE 1. Distances from colonies to major sources of man's waste (in kilometers)

	Goose Rock	Flat Island	Little Green	Sloop Island
Rockland harbor	10.1	27.8	20.1	26.4
Camden dump	4.0	16.3	30.9	20.6
Belfast harbor	27.9	14.2	56.5	29.6
Belfast dump	24.9	12.4	54.1	28.0
Searsport dump	31.9	15.8	60.4	29.9

casion the chick was weighed before and after the removal of any food in the foregut. This procedure was repeated until the chicks could no longer be captured.

The number of young surviving per nest was used as a measure of relative reproductive success, hereafter called "productivity." Since my disturbance of the colonies probably caused a lowering of productivity, my measures only provide estimates of the relative breeding success on the islands studied.

Because the exact age of many chicks was not known, survivorship curves and productivity were calculated on the basis of the birds living to a given weight. Herring Gull chicks, which weigh approximately 60–70 g at hatching, were considered to have survived the chick stage when they attained a weight of 500 g. In my experience, weight is a better indicator than age of a chick's physical condition and ability to defend itself.

It was not practical to follow the survivorship of chicks weighing more than 500 g. Chicks of 600 grams or more wander widely from their nests and become difficult to find. In addition, in two of the three years it was impossible to visit several of the islands late enough in the season to capture all birds attaining a greater weight.

Foods

Two methods were used to determine the food resources utilized by the different colonies. The first involved marking adult gulls with identifying colors at their nests and then making periodic surveys of feeding areas (see Weaver and Kadlec 1970, and Hunt 1970, for methods of trapping and marking).

The second method was an analysis of the foods brought to the chicks. Stomach contents of young gulls were obtained in a manner which allowed repeated sampling of the same chick. By inserting my index finger down the throat of the chick and hooking it behind the contents of the proventriculus, it was possible to remove all the food in the gull's foregut. Voluntary regurgitations appeared to give a biased sample. Not all the birds regurgitated when handled, often only part of the crop contents were released when regurgitation occurred, and certain soft items such as fish or earthworms were given up more readily than others.

The identification of most food items was straightforward. Whether fish in a sample had been obtained from man or from natural foraging areas was surmised by its size, species and condition. Fish of a species and size taken by commercial fishermen which were cut up, decomposed or lacking scales, were judged to have originated from man (see Hunt 1970, for details).

Food usage was determined by gravimetric and numeric measures of samples collected at different times of day and heights of tide. Both measures were affected by the presence of long-lasting hard parts which may have been obtained long before the sample was collected. These create a bias in the numeric analysis. Hard parts pose less of a problem to the gravimetric determination as they usually represented only trace amounts.

The nutritive value of the foods was investigated to determine whether the diets on the different islands were equivalent. In order to compare the caloric values of the diets in the different colonies, the average number of calories per 100 grams of food was calculated. This comparison is crude at best, but it is based on the known caloric values of 78–96% of the chicks' diets on the different islands. A comparison of the relative protein content of the diets was made by a similar method. The caloric and protein values were obtained from the Handbook of Biological Data (Spector 1956), the Agricultural Handbook (Watt and Merrill 1950), and through analysis of samples obtained in the field, performed by Herbert V. Schuster, Inc., of Boston, Massachusetts, using the methods of the Association of Official Agricultural Chemists (1965).

Growth rates

Data for the comparison of growth rates were gathered in 1968 and 1969 by weighing chicks after all food in the upper digestive tract had been removed. Growth rates were computed using all chicks of known age from which at least two weights between 125 and 600 g had been obtained. When possible the age of a chick was determined from the observation of hatching. In some cases where hatching was not observed, it was necessary to assume that a chick weighing less than or equal to 70 g was in its first day after hatching. Age was computed from the date of this initial weighing. In order to facilitate statistical comparison of the growth rates, the slope of the straight-line portion of the growth curve between age 5 days and age 25 days (Spaans, 1970) was determined by using a simple linear regression program.

Parental care

In 1969 I observed nest attendance by adult gulls on Little Green Island and Goose Rock. On each island about fifteen nests were selected which were visible from a suitable observation point. One adult at each nest was trapped and color-marked with a five per cent solution of silver nitrate. This color-marking made it easy to distinguish between members of a pair, and therefore a relatively simple matter to record attendance of each at the territory. Observation periods ranged from two to thirteen hours per day on 17 days. Data for comparison of parental care on the two islands were taken at 15 minute intervals, when each bird in a pair was scored as either present or absent. Times of arrival or departure, fights, and the feeding of chicks were recorded when observed between the fixed periods of observation. The length and number of absences of a foraging parent, the percentage of time that a nest or territory had no parent guarding it, and the percentage of time that both parents were present were compiled from these data.

Results

Productivity

In 1970 field studies were stopped by 17 July. Although all living chicks on Sloop and all but one on Flat Island had attained a weight of 500 g by my last visit, 21 of 60 living chicks on Little Green and 15 of 62 chicks on Goose Rock weighed less than 500 g. While the existence of the underweight chicks on Goose Rock creates bias against the hypothesis that proximity of refuse dumps increases reproductive success, those on Little Green Island bias the results in favor of this hypothesis. In order to eliminate bias in favor of this hypothesis, I have assumed, in all calculations involving chick survival and productivity for 1970, that chicks weighing 400 or more g on Little Green Island during my last visit survived to a weight of 500 g. In order to avoid any chance of biasing the results in favor of the above hypothesis, the criterion for survival remained at 500 g for chicks on Goose Rock.

In all three years Herring Gulls nesting on Goose Rock raised significantly (χ^2 test; $p < .05$) more chicks per pair than those on the other islands (Table 2). However, there were no statistically significant differences in productivity between the other three islands.

Throughout the study Herring Gulls nesting on Goose Rock and Little Green Island enjoyed a significantly greater hatching success (χ^2 test; $p \leq .05$) than those on either Flat Island or Sloop Island (Table 2). The data indicate that hatching success was consistently greater on Goose Rock than on Little Green Island, but only in 1968 was this difference statistically significant (χ^2 test; $p < .05$). Similarly, in one of the two years in which Sloop Island was studied, birds there showed a significantly greater hatching success than on Flat Island ($\chi^2 = 8.06$; $p < .01$).

TABLE 2. Herring Gull productivity

Year	Island	Total marked nests	Eggs per nest	Chicks hatched per egg	Chicks to 500 g per nest	Chicks to 500 g per chicks hatched
1968	Goose Rock	44[a]	2.7	.69	1.14	.53
	Flat Island	50[a]	2.6	.33	.65	.58
	Little Green	38[a]	2.8	.49	.74	.45
1969	Goose Rock	68[a]	2.5	.44	.68	.60
	Flat Island	94	2.3	.19	.25	.53
	Little Green	83	2.7	.40	.29	.27
	Sloop Island	51	2.5	.19	.16	.33
1970	Goose Rock	81	2.5	.54	.58	.43
	Flat Island	143	2.4	.22	.22	.42
	Little Green	169	2.6	.41	.21	.14
	Sloop Island	37	2.5	.36	.16	.18

[a]Eggs counted in 26, 45, 28 and 66 nests respectively. In all other cases eggs were counted in all marked nests.

When the data are grouped according to distance from food resources, there is no clear pattern in the percentage of eggs hatched:

	Inner	Outer	Significance
1969	30%	32%	$.70 > p > .50$
1970	34%	50%	$p < .001$

However, when the data are grouped according to colony disturbance by picnickers, it is clear that hatching success was much greater in the undisturbed colonies regardless of their distance from food resources:

	Disturbed	Undisturbed	Significance
1969	19%	43%	$p < .001$
1970	25%	54%	$p < .001$

Although the differences between colonies in the ability of parents to raise chicks (Table 2 and Figure 2) were not always statistically significant within each year, the differences between inner and outer colonies were consistent over the three years they were studied ($p < .001$, by Sign Test, Siegel 1956). This pattern is repeated when the data are grouped according to distance from food resources:

	Inner	Outer	Significance
1969	57%	28%	$p < .001$
1970	43%	20%	$p < .001$

When the data are grouped according to colony disturbance there are no significant differences in chick raising success:

	Disturbed	Undisturbed	Significance
1969	46%	42%	$p > .70$
1970	35%	29%	$p > .20$

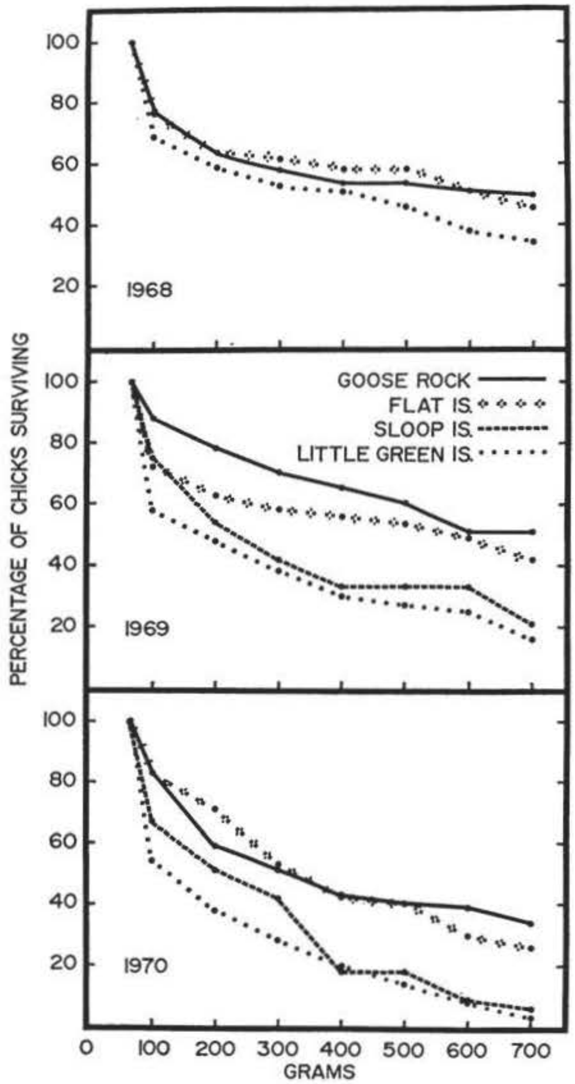

FIG. 2. Survivorship curves calculated on the basis of percentage of chicks surviving to a given weight. Note the very high mortality of small chicks.

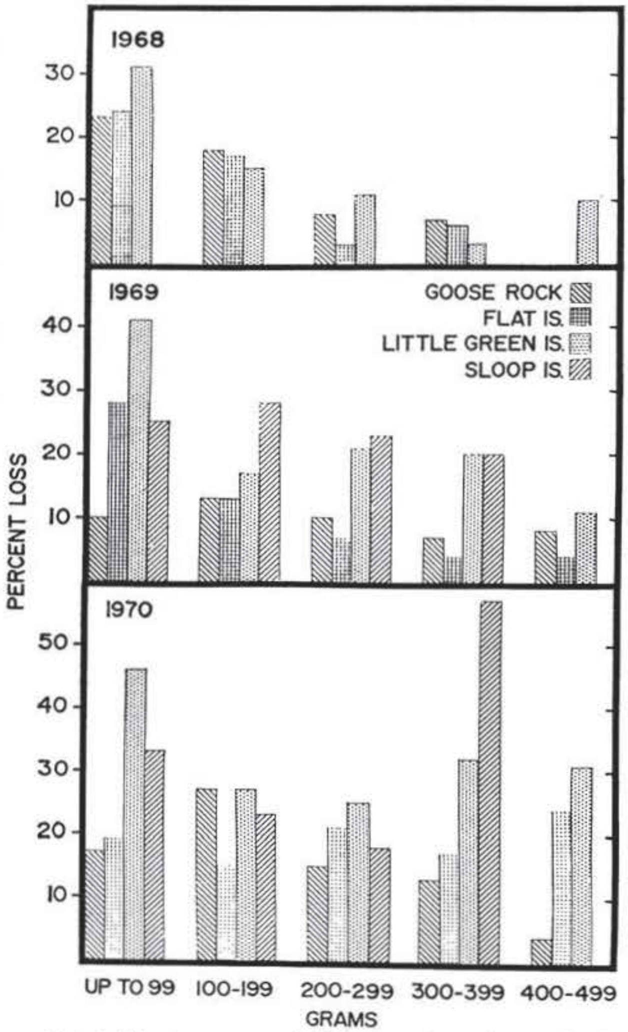

FIG. 3. The percentage of chicks entering a given weight class that failed to survive to the next weight class. (Sloop Island was not studied in 1968.)

The differences in rates of mortality between chicks on inner and outer islands were distributed over the entire growth period in all years (Fig. 3). These were statistically significant in 1969 and 1970 (using the Wilcoxin Matched-Pairs test, Siegel, 1956; $p > .05$, 1968; $p < .005$, 1969; $p < .005$, 1970). Chick mortality was greatest on all islands during the first few days after hatching (Figs. 2 and 3). This initial mortality was consistently greater on the outer islands.

Foods

The distribution of color-marked gulls, compiled from public reports and my own observations, showed that gulls from all colonies used refuse and that they generally restricted their foraging activities to sources of waste closest to their colonies (Table 1). Birds from Goose Rock fed primarily at the Camden dump, those from Flat Island at the Belfast dump and chicken processing plants, and those from little Green in Rockland harbor. Very few colored gulls from Sloop Island were seen foraging, although observations suggest that they used the same sources of refuse as the gulls on the other colonies. Although birds from several islands used the Camden dump and Rockland harbor, in general the birds from different colonies appeared not to overlap greatly in the foraging areas they used.

Foods sampled from Herring Gull chicks are summarized in Fig. 4. Table 3 shows that there were no clear-cut differences in the total amounts of refuse fed to chicks on inner and outer islands, although the kinds of waste used on the islands differed (Fig. 4).

TABLE 3. Percentage of food originating from man brought to Herring Gull chicks

Year	Island	% by weight	% by occurrence
1968	Goose Rock	44	35
	Flat Island	50	34
	Little Green	42	24
1969	Goose Rock	46	40
	Flat Island	48	36
	Little Green	56	37
	Sloop Island	61	47

No consistent variation in food types taken with change in date was apparent. This was true for individual colonies as well as for the study area as a whole.

Qualitative aspects of the diets of chicks in each of the colonies are presented in Tables 4 and 5. The nutritive value of the diets was similar on all islands.

Indices of the quantity of food provided to the chicks were obtained from the percentage of times that sampled chicks were found empty and the average weight of the samples obtained relative to the weight of the chicks sampled (Table 6). Within any given year there was no indication that chicks on outer islands were either consistently empty more often, or produced lighter food samples than chicks on the inner islands.

Growth rates

When the growth rates of surviving and non-surviving chicks were considered together, the only significant difference between colonies occurred in 1969 when chicks on Sloop Island showed lower growth rates than those on other islands (Table 7). Growth rates of surviving chicks were significantly greater than those of non-surviving chicks (Fig. 5) on all but Sloop Island where the difference between the two groups was not significant. Growth rates of surviving chicks on Goose Rock were significantly higher than those of surviving chicks on all other islands in 1968

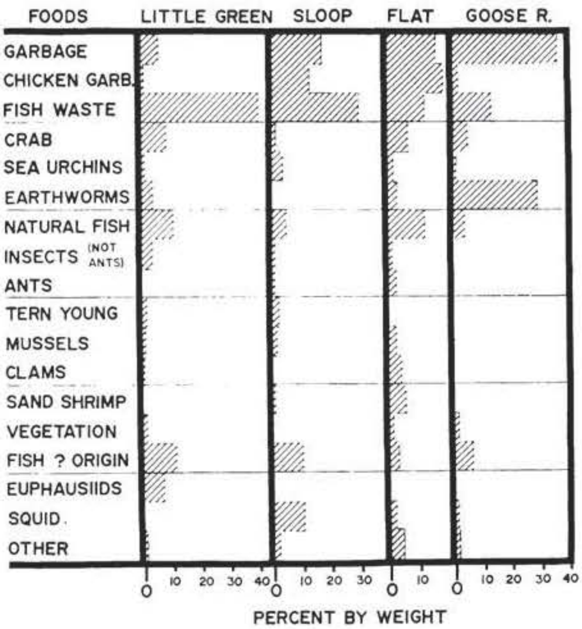

FIG. 4. Percentage by weight of foods represented in stomach contents obtained from young gulls on all islands in 1968 and 1969.

TABLE 4. Analysis of foods obtained in or commonly found in young Herring Gulls

Sample	Calories/ 100 gm.	Fat % by wt.	Protein % by wt.	Carbo-hydrate % by wt.	Crude fiber % by wt.	Ash % by wt.	Moisture % by wt.
Garbage "average mix"	154	7.9	18.8	1.7	0.3	4.0	67.2
Garbage – high fat	303	28.9	6.4	4.5	3.0	4.9	52.4
Garbage – lobster shells	153	12.1	10.9	0.0	3.8	4.6	70.6
Garbage – much paper	140	12.1	3.7	4.0	10.5	4.1	65.5
Herring direct from lobster trap	173	11.7	15.9	0.9	0.2	6.0	65.2
Rotten herring	131	7.0	17.1	0.0	0.6	3.0	72.6
Fresh herring & mackerel from gull	189	12.6	18.9	0.0	0.2	2.3	67.0
Redfish & freshwater fishes	117	5.1	17.8	0.0	0.2	3.0	74.7
Earthworms	71	1.2	12.3	2.7	0.6	5.7	77.5
Crab with eggs	99	5.1	1.3	11.9	2.6	10.8	68.3
Euphausiid shrimp	78	2.4	1.4	12.5	1.0	2.6	80.0
Starfish, crab & urchin mixed, no eggs	63	1.8	9.8	1.9	2.2	15.2	69.2
Atlantic herring[a]	191	12.5	18.3	0.0	0.0	1.3	67.2
Mackerel[a]	188	12.0	18.7	0.0	0.0	1.2	68.1
Crab sp.? (edible portion)[a]	86	1.6	16.1	0.6	—	2.1	80.0
Clam sp.?[a]	81	1.4	12.8	3.4	—	2.1	80.3
Butter[a]	716	81.0	0.6	0.4	0.0	2.5	15.5
French fries[b]	393	19.1	5.4	52.0	1.0	3.9	19.6
Blueberry[a]	61	0.6	0.6	11.0	2.1	3.4	83.0

[a]From Spector, 1956
[b]Watt and Merrill, 1950
Others from Hubert V. Schuster, Inc.
For methods see Association of Official Agricultural Chemists (1965).

TABLE 5. Qualitative measures of chicks' diets

	Goose Rock	Flat Island	Little Green	Sloop Island
Calories/100 g of food	121	116	123	117
Grams protein/100 g of food	19	16	14	18
Percent of total food on which calculations are based	96	81	90	78

TABLE 6. Percentage of empty chicks and sizes of food samples obtained

Year	Island	Chicks examined[a]	Percent empty chicks	Sample weight as % weight of chick	Standard deviation
1968	Goose Rock	101	76	6.4	5.6
	Flat Island	57	65	6.6	4.5
	Little Green	77	70	9.8	8.9
1969	Goose Rock	180	69	4.5	3.8
	Flat Island	59	59	5.6	4.4
	Little Green	83	57	4.9	4.8
	Sloop Island	35	57	6.8	5.8
1970	Goose Rock	80	45	4.2	5.0
	Flat Island	42	36	5.2	3.4
	Little Green	78	55	5.8	4.2
	Sloop Island	17	35	5.0	4.4

[a]Between the weights of 150 and 500 g

TABLE 7. Growth rates of chicks (surviving and non-surviving combined)

Year	Island	Number of chicks	Grams per day	Standard deviation
1968	Goose Rock	22	30.73	1.37
	Flat Island	22	30.03	1.35
	Little Green	19	29.62	2.90
1969	Goose Rock	33	31.41	1.17
	Flat Island	15	30.64	2.75
	Little Green	19	28.86	1.81
	Sloop Island	6	26.72	1.58

and the outer islands in 1969. For non-surviving chicks, there were no significant differences in growth rates between colonies.

Parental care

Parents on Little Green Island left their mates on the territory alone for longer periods than did birds on Goose Rock during both the egg and chick stages. The percentage distribution of absences of a given minimum length is shown in Table 8. The differences between absences on Little Green Island and Goose Rock are significant ($p < .01$, using the Kolmogorov-Smirnov two-sample test, Siegel 1956, p. 127).

Absences of a foraging parent were longer for

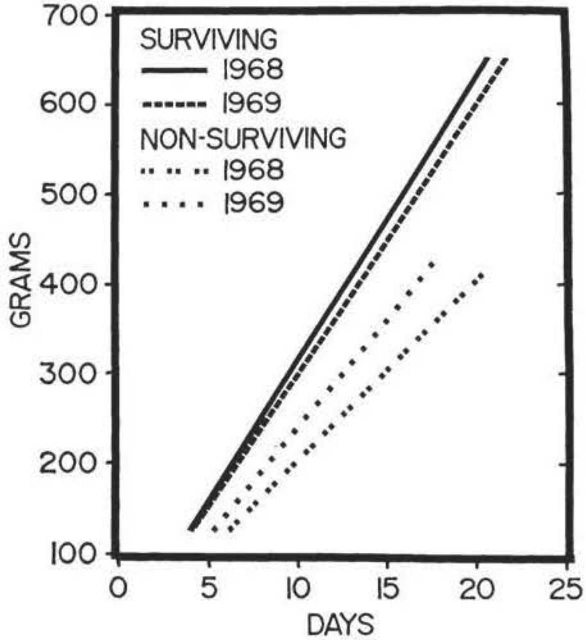

FIG. 5. Plots of the growth rates of surviving and non-surviving chicks from all colonies.

gulls which were incubating eggs than for parents with chicks (Table 8). It appeared that the length of absence during the incubation phase was less critical than it was during the period after the chicks had hatched. Even on Little Green Island, where absences of the foraging mate were longest, seldom did the incubating parent leave the nest completely unattended (Table 9). Absences of the guarding partner would result in the eggs or the chicks being undefended. The percentage of time in which eggs were left undefended was small on both islands and the differences between the behavior of the parents during the incubation period on the two islands is not significant ($0.5 > p > 0.25$). However, the difference in behavior between birds with chicks is significant (using a 2×2 contingency test, $\chi^2 = 56.36$, $p < .0025$).

The longer absences of the foraging parents with chicks on Little Green as contrasted with those on Goose Rock were important. As the length of absence increased, the adult left to guard the young became restless. Frequent solicitation of food by the young appeared to exhaust the guarding parent's supply. Further begging of food appeared to annoy the parent and it would often seek to avoid the chick. During prolonged absences, the guarding parent often left the territory, thereby leaving the chicks undefended. As can be seen from Figure 6, this became increasingly common on Little Green Island as the chicks grew larger, while the percentage of time that chicks were unguarded on Goose Rock remained more or less constant. On Goose Rock, I was not able to see where the guarding parents which left

TABLE 8. Length of absences of individual parent Herring Gulls from territory, 1969 (cumulative percentage)

Island	Nest	Absences of <1 Hour	<2 Hours	<3 Hours	<4 Hours	<5 Hours	Average absence (hours)	Number of absences in sample
Goose Rock	With eggs	57.6	82.9	92.4	94.9	98.7	.96	158
Little Green	With eggs	29.4	49.0	66.6	68.6	83.3	2.04	102
Goose Rock	With chicks	64.2	93.9	97.8	99.6	99.9	.73	330
Little Green	With chicks	35.1	65.6	77.9	90.2	96.0	1.85	154

TABLE 9. Percentage of time territory left unattended by both parents, 1969

	Goose Rock		Little Green	
	Nest with eggs	Nest with chicks	Nest with eggs	Nest with chicks
Percentage of time territory unattended	0.8	2.0	0.3	17.8
Nest-hours of observation	359.40	373.25	310.00	276.25

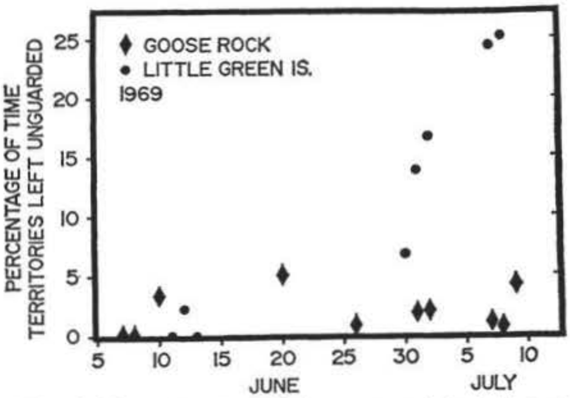

FIG. 6. The percentage of time parents left their territories unguarded on Goose Rock and Little Green Island.

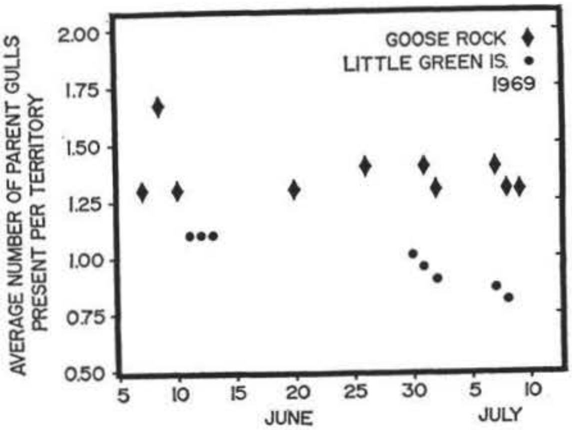

FIG. 7. The average number of parents present on territory on Goose Rock and Little Green Island.

their territories went; on Little Green Island parents flew down to the shoreline in search of food.

Another measure of parental attendance is the average number of parents present on the territory at any one time. During incubation the average number of parents present was greater on Goose Rock (1.44) than on Little Green Island (1.18). This difference held throughout the period when chicks were present (1.33 vs. 0.91). Using a 2×2 contingency test the difference in the average numbers of parents present was found to be statistically significant ($p < .01$). Figure 7 shows that as the season progressed, the average number of parents guarding their chicks declined to less than one on Little Green while remaining relatively constant on Goose Rock.

On several occasions the presence of the second parent seemed to be important. I once observed a chick taken from its territory by an intruding adult gull while the chick's parent was defending a second chick elsewhere in the territory. On several occasions I observed one parent defending the young while its mate was fighting with another gull.

DISCUSSION

When a colony is disturbed, the adults leave the eggs unprotected. Gull eggs are sensitive to overheating (Drent 1967) and even in the relatively cool Maine spring, incident radiation from the sun is capable of overheating them. Furthermore, the eggs are exposed to predation by other gulls flying in the vicinity.

Hatching success was greatly affected by disturbance of the colony, while it was unaffected by the distance of the colony from major sources of food. Thus, studies attempting to relate reproductive success of gulls to the availability of food must take into account the effect of disturbance on hatching success.

The higher survival rates of chicks on the inner islands does not appear to be related to such features as nest-spacing, vegetation and cover, or the roughness of the terrain, which have been studied by others (Patterson 1965; Tinbergen et al. 1967; Brown 1967; I. Nisbet, pers. comm.). Coulson et al. (1969) and Parsons (1970, 1971) have identified egg size as an important factor in chick survival. No measures of egg size were made in the present study, and while it is unlikely that egg size varied between inner and outer islands, this requires further investigation.

Likewise, differential exposure to harsh weather is not an adequate explanation for the difference in chick survival. Within the geographic distances with which I was working, exposure of chicks to occasional severe storms was determined more by the cover available in the colony than by the location of the island. On Goose Rock, with its lack of either vegetation or a drift zone, chicks were more exposed to rain and harsh weather than on the outer islands. Furthermore, severe storms were too infrequent to account for the higher mortality (Figure 3) on the outer islands throughout the growth period in 1969 and 1970.

The date of egg laying or chick hatching has been found useful in several studies in predicting the survival of young gulls (Paynter 1949, Brown 1967, Harris 1969*a*, Parsons 1971. Perrins 1970 gave a general discussion). In the present study the timing of reproductive effort was not an important variable. Chicks hatched within any given time interval on the outer islands had lower survival rates than those on the inner islands.

The concentration of foraging activity by gulls in the vicinity of their own colony was clear not only from the sightings of color-marked gulls, but also on the basis of the types of waste fed to their chicks. This result agrees with that of Drury and Nisbet (in press) who found that the foraging areas of Herring Gull colonies in Massachusetts were segregated on the basis of the proximity of a resource to a colony.

On the average, food samples containing waste were heavier than those containing natural foods (compare per cent waste by weight with per cent waste by occurrence, Table 3). This relationship was particularly evident on Little Green Island where the major sources of refuse were the fish processing plants in Rockland. In order to bring back larger amounts of food to their chicks, it was apparently more efficient for gulls to fly greater distances to sources of waste than it was to forage in natural areas closer to the colony.

There were no consistent changes in the use of man's waste as the summer progressed. This result contrasts with that of Spaans (1970), who found in Holland that as Herring Gull chicks grew larger and demanded greater quantities of food, the adults depended more heavily on sources of refuse for feeding their young.

The similarity in the quality of the diets and the quantity of food provided on the various islands suggests that nutrition was not responsible for the differences in survival rates between colonies (Tables 5 and 6). Since the diet of the chicks on each of the islands was varied and contained a number of different natural foods as well as waste (Figure 4), it is doubtful that any of the young birds were lacking an important vitamin or mineral.

The comparison of the combined growth rates of all chicks in each colony reflected the similar nutrition of chicks on all islands. Although surviving chicks on Goose Rock grew more rapidly than chicks on other islands, there was no correlation between growth rates in a colony and the percentage of chicks on that island which survived.

The difference in growth rates between chicks which survived and those which did not most likely reflects an increased vulnerability of underweight chicks to disease, predation or chilling (Kadlec et al. 1969).

The length of absence of a foraging parent appeared to be more important as a factor exposing the chicks to predation than as a factor affecting the nutrition of the young. Although it might be implied from the longer absences and less frequent returns of foraging parents from Little Green Island (Table 8) that those gulls brought food to their chicks less often than parents on Goose Rock, young gulls on Little Green were just as well fed as Goose Rock chicks (Table 6). This appears to be a paradox unless one assumes that not all of the periods of absence of parent gulls from Goose Rock were devoted to foraging, and that their chicks were fed no more often than those on Little Green Island. The fact that chicks on Goose Rock occasionally exhausted the food available from a parent suggests that parents may not have done as good a job of feeding their young as might have been expected from their many brief absences from the colony.

The parent gulls must provide not only sufficient food, but also adequate protection for their young, both from bad weather (Vermeer 1963, Harris 1964, Harris and Plumb 1965) and from predation. There is a trade-off between the amount of time adults remain at the colony guarding their chicks and the time they spend foraging (see Perrins, cited in Brown 1967). The time difference between the average lengths of absence of parent gulls on Little Green and Goose Rock was about one hour (Table 8), which approximates the commuting time expected of a gull flying at 40 km per hour (Pennycuick, 1969) over the additional distance that gulls from Little Green must cover to reach mainland food sources.

The minor differences in nest attendance on the two islands during the incubation period were not important since hatching success was similar on both islands in 1969 (Table 2). However, the effectiveness of parental protection as measured by attendance on the territory was very different on the two islands once the chicks had hatched.

Predation in the colonies I studied appeared to be an important source of chick mortality. Although a few very small chicks were found dead in or next to their nests, indicating a failure of their parents to make proper behavioral adjustments, many chicks disappeared without a trace after a few days of growth and are presumed to have been eaten by adult gulls in the colony (see also Harris 1964, Brown 1967, Kadlec et al. 1969). These findings agree with those of Paynter (1949), Fordham (1964), Kadlec and Drury (1968), and Parsons (1971). During this period of maximum vulnerability the presence of only one parent guarding the small chicks left broods on Little Green Island more exposed to predation than if two parents had been present.

It was observed on Little Green that parents whose food reserves had been depleted by the begging of their growing chicks would leave their territories to forage in the intertidal zone. Casual inspection of the littoral zone of Little Green Island revealed that few food items remained in areas exposed to foraging gulls. This suggests that chicks there were more exposed to predation not only because parents may have guarded them less well, but also because there were more adults seeking food on or near the island. Although I have only once observed a successful attempt at cannibalism, on many occasions I have observed chicks attacked by other gulls. Vermeer (1963), Harris (1964), Brown (1967) and Parsons (1971) have all concluded that predation and cannibalism are major causes of chick mortality. Lack (1968) has suggested that the inshore feeding seabirds will have many small colonies so as to minimize the distance between nest site and feeding area. The mechanism whereby this becomes important is clear from the results of this study. However, it is less clear why the Herring Gulls remain colonial when island nest sites are plentiful and the only predators of consequence appear to be the gulls in the colony.

Although it has been shown that the reproductive success of many species of seabirds is limited by the amount of food parents are able to provide their young (Murphy 1936, Ashmole 1963, Harris 1969*b*), gulls appear to be an exception. Studies of gull productivity in single colonies (Paynter 1949, Vermeer 1963, Harris 1964, Harris and Plumb 1965, Brown 1967), and Spaans (1970) provided no evidence for food limitation of reproductive success. Furthermore, both Vermeer (1963) and Harris and Plumb (1965) have demonstrated that two species of gulls were capable of raising broods of more than three chicks.

The differences in the survival of chicks on inner and outer islands, and the year to year fluctuations in reproductive success found by Fordham (1970), demonstrate that the availability of refuse may affect the reproductive output of gulls. The evidence that reproductive success is sensitive to the availability of food, and the conclusion that gull reproduction is not currently limited by the ability of the adults to provide their young with sufficient food, are not necessarily mutually exclusive. If predation and the lack of parental care were the proximate cause of the differential mortality between colonies on inner and outer islands, then the availability of food must be seen as the ultimate cause of this difference in chick survival. When the parents have to spend large amounts of time seeking food, their ability to provide protection to their young is reduced.

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