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# PARENTAL BEHAVIOR OF THE HERRING GULL (*LARUS ARGENTATUS SMITHSONIANUS*) AND ITS EFFECT ON REPRODUCTIVE SUCCESS

by

David Kerr Weaver

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
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Doctoral Committee:

Associate Professor George S. Hunt, Chairman
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ABSTRACT

PARENTAL BEHAVIOR OF THE HERRING GULL
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ITS EFFECT ON REPRODUCTIVE SUCCESS

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David Kerr Weaver

Chairman: George S. Hunt

The parental behavior of banded breeding adult Herring Gulls (Larus argentatus smithsonianus) was observed during the breeding seasons of 1968 and 1969 on Milk Island, Cape Ann, Massachusetts. In particular, the efficiency with which banded pairs reared young was studied in an attempt to determine if pairs varied significantly in reproductive competence.

The reproductive success of birds within study areas of varying substrate was followed. Behavioral observations were made from two blinds over a period of 316.5 hours. Particular behavior observed was brooding intensity, frequency of feeding, and territorial attentiveness. Other factors noted were weather conditions, time of day, whether or not a Herring Gull territory was adjacent to that of a Great Black-backed Gull (L. marinus), the cover in a territory available to chicks, and the number of chicks within each territory during a given observation period. Chicks of known Herring Gull pairs were weighed and these data were correlated with frequency of feeding data.

It was found that Herring Gulls did not always return to the same territory from year to year and that pair fidelity was incomplete. The data suggest that prolonged mating of a pair resulted in increased reproductive success. Pairs mated for at least two years (1968) and then three years (1969) produced 1.27 chicks per nest, while birds (age unknown) mated for the first time successfully reared 0.48 chicks per nest.

The incubation period for three-egg clutches was an average of 26.9 days from a sample of 60 Herring Gull nests. Brooding of the young rarely continued past six days of age.

Data concerning the frequency of feeding and the cover available to chicks were highly significant in their relation to the number of chicks produced by any given pair of gulls. Broods fed most frequently gained weight most rapidly.

Great Black-backed Gulls had a marked effect on the reproductive success of Herring Gulls if the Herring Gull chicks did not have adequate cover in an alarm situation; e.g., when humans were in the vicinity. The chicks left those territories in which there was poor cover, presumably in search for better cover, and in many instances did not return because they were lost and/or were preyed upon by Black-backs.

The question, "Are there good gull parents and poor gull parents?" was not answered definitively. There were differences in behavior between known pairs of gulls; but, the inconstancy of some of these differences during two

breeding seasons of observations did not permit an unequivocal answer.

The behavioral and physical variables that were considered were those thought to be the most important in the reproductive success of a pair of Herring Gulls. Further study on the effects of environmental variables, particularly nest site location, would be valuable.

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# INTRODUCTION

## Scope and Purpose of Study

Many studies have contributed a wealth of data on the biology of the Herring Gull (*Larus argentatus* Pont.),[1] however, little has been done concerning the parental behavior of this species and its effect on reproductive success.

The Herring Gull is a bird with a very low mortality rate and an essentially fixed clutch size (Kadlec and Drury, 1968: 652, 672). One of the critical factors regulating population numbers is the apparent inability of some breeding adults to raise young efficiently to the fledging stage. A previous study (Weaver, 1967) indicated that individual pairs of Herring Gulls (*L. a. smithsonianus* Coues) vary in their ability to rear young. As a sequel to that study, the purpose of the present research was to follow the breeding success of known pairs and to determine whether or not pairs of Herring Gulls were incompetent as parents, and, if so, did they continue to be incompetent in ensuing years. In other words, were there "good" and "poor" gull parents?

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[1] Birds' scientific names are in accordance with *Check-list of North American Birds*, 5th edition, published by AOU 1957.

This behavioral study was dependent upon the fact that the monogamous Herring Gull generally returns to the same nesting territory year after year and pairs with the same mate for extended periods of time (Tinbergen, 1961: 82, 97). A banded population of breeding adult Herring Gulls was required to identify individual birds. Having recognizable individuals permitted me to determine to what extent these birds did return to the same territory year after year and to what degree Herring Gulls do mate for at least extended periods of time.

More concrete data were sought on the length of the incubation period of Herring Gulls in the New England coastal areas (variations in the Herring Gull are shown in the literature to be geographically linked). A method for determining the sex of adult Herring Gulls in the field was also refined.

## Parental Behavior

Beer (1966: 190) defined parental behavior as that behavior of adult birds concerned with the covering and rearing of young.

### Incubation, Hatching, and Brooding of the Young

In the Laridae, the two parents share equally, for the most part, in nest-building, incubation of the eggs,

and caring for the young. Tinbergen (1961: 129) observed that while both members of a Herring Gull pair collect nesting material, the male collects more than the female. He also noted that prior to egg-laying, a mated pair will rarely, if ever, be separated, flying to the feeding grounds and returning to the colony together.

Partial incubation begins with the laying of the first egg. After the clutch has been completed, normally three eggs, full-time incubation begins. Usually, the nest and its eggs, thenceforth, are never unattended, one mate or the other always being present. Tinbergen (1961: 134) observed that the female was on the average slightly more attentive to the eggs than the male, although there was considerable variation, and the male sometimes assumed the greater share of the incubation.

Samorodov and Ryabov (1969) in their study of Great Black-headed Gulls (L. ichthyaetus Pall.) in the Kustanai region of Russia noted that the females did most of the nest-building, incubating, and brooding of the young. Females' incubation periods ranged from four to seven hours per sitting and the males' from one to four hours. In the smaller Black-billed Gull (L. bulleri) endemic to New Zealand, "one of the parents sits uninterruptedly throughout the night, but during the day the two relieve one another every two hours or so" (Beer, 1965: 3).

Bent (1921: 106) stated that the period of incubation of the Herring Gull varies from 24 to 28 days, the average

being 26 days. According to Tinbergen (1961: 160), the incubation period lasts about four weeks, averaging 30.5 days between laying and hatching, with extremes of 28 and 33 days. It is possible that this difference is geographically related, since Bent's data came from North American birds and Tinbergen's from European. Otherwise, I would presume that Bent's incubation period covered from the day the last egg was laid to the day the last egg hatched, and that Tinbergen counted from the day the first egg was laid to the day the last egg hatched. Kadlec and Drury (pers. comm.) maintained that the period of incubation along the New England coast was as little as 21 to 23 days from "full clutch" until hatching of the last egg.

The transition from the incubation of eggs to the brooding of young is a critical period in the reproductive cycles of any one pair of gulls. Since partial incubation begins with the laying of the first egg, the entire clutch does not hatch simultaneously, but usually one at a time over a span of three to four days in a 3-egg clutch. The appearance of the first chick represents a new stimulus to the adult bird and elicits a new response, that of brooding behavior. Thus begins the switch from incubation to brooding (parental) behavior (Beer, 1966). As a result, the number-two and number-three eggs in the nest receive decreasing amounts of attention. Proportionately less incubation is afforded the third egg as the number-two chick emerges, and, as a result, oftentimes does not hatch.

Beer (1966) in his study of Black-headed Gull (L. ridibundus) behavior described this change from incubation to parental behavior. Under natural, "undisturbed" conditions and experiments he determined whether this change is internally or externally controlled. He presented the problem this way (p. 190):

> As in the case of incubation behaviour the question can be asked: to what extent is the onset of brooding or parental behaviour a response to new external stimuli, and to what extent the result of internal processes more or less independent of the immediate external situation? . . . breaking it into three: can the switch from incubation to parental behaviour be effected before hatching would normally occur? can incubation behaviour be prolonged beyond the time when hatching would normally occur? can parental behaviour be switched back to incubation behaviour after hatching has occurred?

Beer concluded that the timing of the transition from incubation behavior to parental behavior is governed primarily by external stimuli. He based his conclusion on the fact that the normal period of incubation behavior was exceeded if the eggs failed to hatch and, conversely, if chicks were prematurely introduced into the nests of incubating gulls, incubation behavior ceased and parental behavior began. Beer also showed that as a gull gains experience with chicks, that gull's responsiveness towards eggs changes, and "less and less incubation-type behaviour is shown towards a nest with eggs as the post-hatching period advances" (p. 211).

Emlen and Miller (1969) in their work with the "pace-setting mechanisms of the nesting cycle in the Ring-billed Gull" (L. delawarensis) concluded similarly, that the change from incubation behavior to parental behavior is quantitatively uniform and is elicited by non-specific stimuli associated with the young. They further suggested that these "pace-setting mechanisms of the breeding cycle switch from internal (hormonal) to external (embryo and chick development) regulators early in the incubation phase of the cycle" (p. 260).

For about the first three to five days of a Herring Gull chick's life, it is brooded almost continuously with both parents sharing the duty (Tinbergen, 1961: 177). The "off-duty" adult will often bring food to the nest for the chicks. Following this initial period of brooding, the chicks are sheltered by their parents only occasionally until the chicks are about 10 to 12 days old.

Both Herring Gull parents feed the young (Tinbergen, 1961: 178). It is only a few hours following hatching when a chick is first fed, although, as Fordham (1964b) pointed out from his study of the Southern Black-backed Gull (L. dominicanus), the food may not be accepted simply because the chick is too weak to respond.

## Defense of the Young

The defensiveness of the adult gulls reaches a plateau as the eggs hatch, where it remains until the chicks are several weeks old (Tinbergen, 1961: 164). The adults become very aggressive toward humans and toward other Herring Gulls. Through display postures, calls, and associated movements, most hostile physical contact is avoided with other gulls (Tinbergen, 1961: 53-61).

Kadlec, Drury, and Onion (1969: 231) related that, "the evidence for heavy predation by adult gulls on chicks remains largely circumstantial." This conclusion arose from the fact that much of the chick mortality in their studies fell under the category "disappeared without any trace," as it did in Brown's (1967) study of Herring Gulls (L. a. argentatus) and Lesser Black-backed Gulls (L. fuscus) and as reported in my Master's study (Weaver, 1967: 28). Brown and I both hypothesized that gulls other than the parents were the chief cause for this mortality.

Harris (1964, 1965), Paludan (1951), and Paynter (1949) all attributed most of the chick and egg mortality in their studies to predation by Herring Gulls and Great Black-backed Gulls (L. marinus). Goethe (in Pettingill, 1939) observed egg-destruction by Herring Gulls and believed that those individuals involved were unpaired birds and certain breeding birds whom the unmated birds "introduced" to this practice.

Patterson (1965: 455) stated that many of the egg losses he had recorded as egg mortality should actually be losses of newly hatched chicks, since gull predators were often seen to take chicks while still wet. Similar to the above, as with egg losses, most of the young that Patterson classed as "dead" simply disappeared. In contrast to these observations, Emlen (1956) found that the juvenile mortality in a Ring-billed Gull colony in northern Lake Michigan was attributable primarily to attacks by adults when chicks wandered out of their territories. Similarly, Vermeer (1963) concluded that one of the major factors contributing to chick mortality in the Glaucous-winged Gull (L. glaucescens) "was the habit of the adults to attack strange chicks . . .", i.e., chicks outside their territories.

Bergman (1939) from his earlier studies on islands west of Helsinki, Finland, considered predation by Black-backs (Great Black-backed Gulls) largely an individual matter. More recently (1965), he observed that only a few Herring Gulls specialized in this practice, and did so on a large scale. Bergman also reported in his 1939 paper that the Black-back did not rob nests on its own breeding island but did so in other colonies. He made no reference to this in his 1965 paper, merely noting that the Black-back did prey upon the Herring Gull. Kadlec and Drury (1968: 656) suggested that "an adaptation inhibiting the feeding of a

gull on its breeding island might decrease the predation by Great Black-backed Gulls on their own island."

## Post-fledging Period

There is some information in the literature concerning the post-fledging relationship between the young and their parents. Although my field study did not include this aspect of parental behavior, it is mentioned here to illustrate that parental behavior does carry over into the post-fledging period. According to Drury and Smith (1968), adult Herring Gulls along the coasts of Maine and Long Island, New York, defend shoreline feeding areas in which they have been seen to feed fledged young-of-the-year believed to be their own. Drury (Drury and Smith, 1968: 198) also followed the movements of marked chicks in the vicinity of Gloucester, Massachusetts, and "found that they roosted on their colony and were fed by their parents on the colony a month after fledging."

Brown (1945) and Lloyd (1945) in England reported adults feeding young in January and in March, respectively. Similarly, Lack (pers. comm. in Ashmole and Tovar S., 1968) saw Herring Gull young-of-the-year begging for food from their (presumed) parents in Cornwall, England, at the end of October. On Maine garbage dumps from August into October, Schreiber (pers. comm. in Ashmole and Tovar S., 1968) regularly observed young Herring Gulls being fed by

adults, again presumably their parents. Some of the gulls involved in this latter case were banded in colonies several hundred miles away. In partial contrast to the above, Fordham (1964b: 115) observed that the tie between Southern Black-back chicks and their parents waned enough that even though the chicks remained in the adults' company and begged food from them "for some time after" fledging, rarely were they fed.

## DESCRIPTION OF THE STUDY ISLAND

The study areas were located on Milk Island, a low, flat island about 24 acres in size situated off of Cape Ann, Massachusetts (42° 37' 40" N. 070° 35' 21" W.; Figs. 1 and 2). Milk Island is state-owned and is officially known as the "Knight Wildlife Reservation." The primary wildlife species using the island during the study (1967, 1968, and 1969), was the Herring Gull which numbered about 3000 pairs during the breeding season. The Herring Gull was followed in abundance by the Great Black-backed Gull which numbered about 500 breeding pairs. Two to three pairs of Red-winged Blackbirds (Agelaius phoeniceus) made up the balance of the breeding species on the island.

A flock of about 150 Atlantic Brant (Branta bernicla) overwintered on Milk Island and two adjacent islands, Thacher and Straitsmouth Islands. Due to the brants' presence until mid-May, the grasses and a Polygonum sp. were closely cropped when the gulls began nesting. Other species of birds overwintering on and in the vicinity of Milk Island included the Mallard (Anas platyrhynchos) and the Black Duck (A. rubripes). The island served as a stop-over spot for migrating birds of many species -- warblers, sparrows, and shorebirds, in particular.

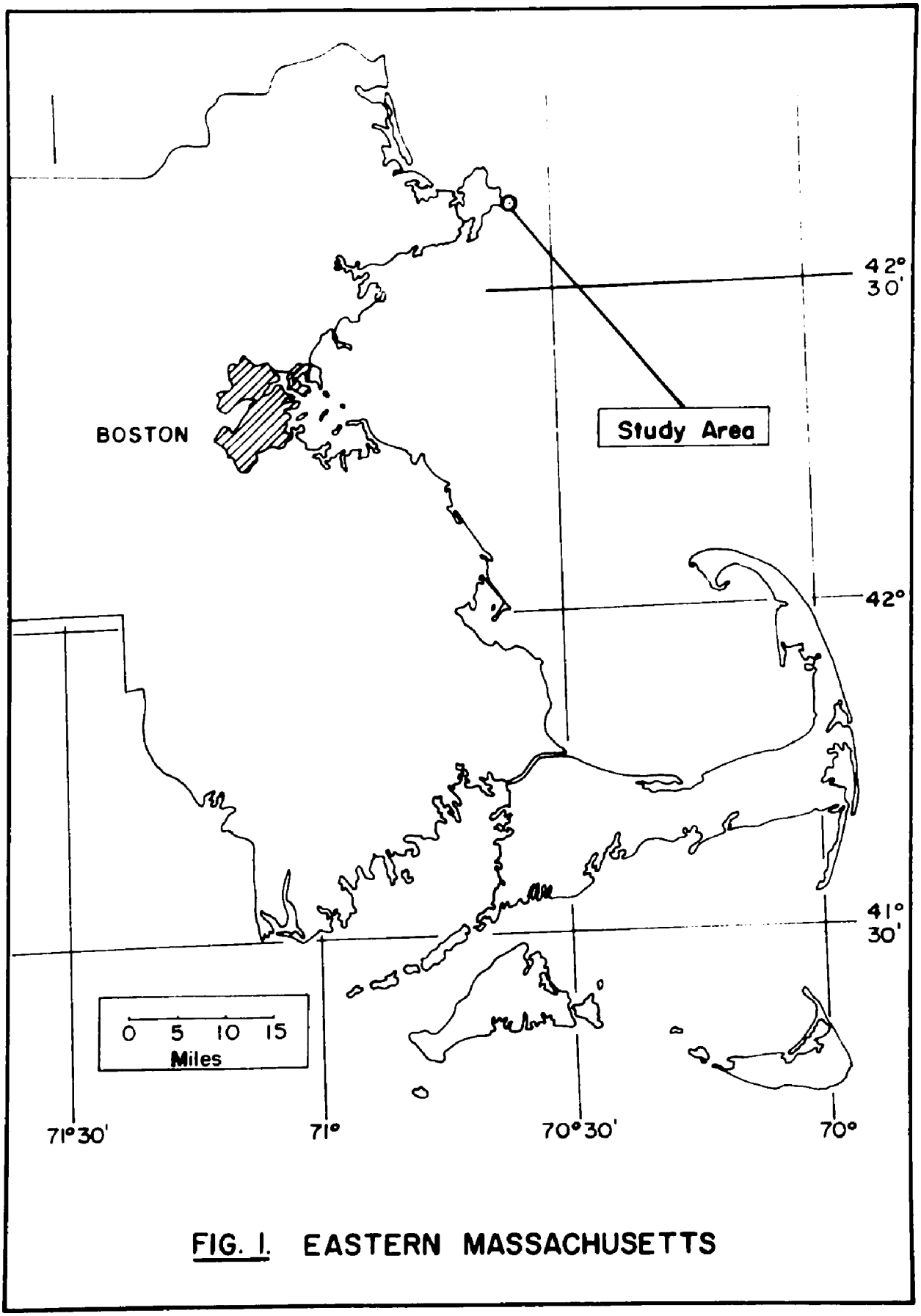



FIG. 1. EASTERN MASSACHUSETTS

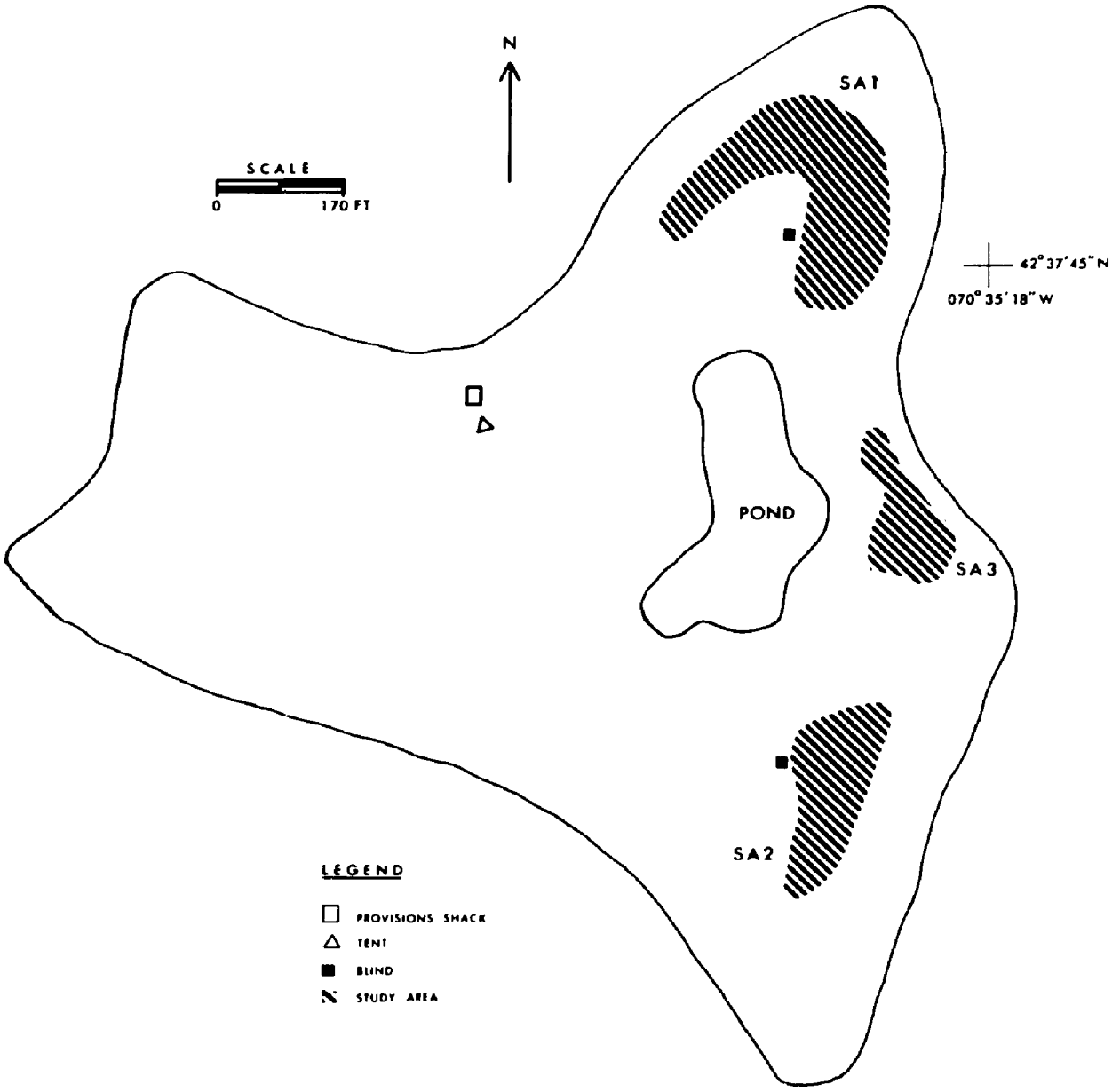



FIG. 2. MILK ISLAND

About 42 per cent of the island was covered by herbaceous vegetation, woody vegetation made up about two per cent of the area, 51 per cent was rock (ranging from pebbles to boulders to rock outcrop), and a pond on the east side of the island accounted for five per cent of the island's surface area (Reichle, 1969: 53). In the course of a dry summer, the pond dried up.

Milk Island acquired its name from the fact that cows and sheep were once pastured there. Upon their removal (the exact chain of events is uncertain), terns colonized the island. The terns were presumably Common Terns (Sterna hirundo). In 1957, Barnett (1958) reported that there were 55 to 60 pairs of Double-crested Cormorants (Phalacrocorax auritus) nesting on the north side of the island. As recently as 1967, there were about 10 cormorant nests. When these nests were destroyed by a northeast storm there was no attempt to renest and there were no cormorants seen during 1968 and 1969. Barnett also related that there were 51 Black-crowned Night Heron (Nycticorax nycticorax) nests on Milk Island during her 1957 visit. After gulls colonized the island and eventually occupied the entire area, the terns, night herons, and, more recently, the cormorants were displaced.

The east side of Milk Island was utilized for the study because it was located farthest away from the most accessible part of the island and would presumably be less

susceptible to human disturbance (Fig. 2). This area was chosen also because nesting density was highest there and more nests could be watched effectively from a single blind.

Three study areas were delineated by a painted red line: Study Area 1 (SA1), Study Area 2 (SA2), and Study Area 3 (SA3). SA1 was located on the northeast end of the island; SA3 on the east side; and SA2 on the southeast corner (Fig. 2). Both SA1 and SA3 had a substrate of 90 per cent rock with greater than 50 per cent boulder size (256 mm), and SA2 had a substrate of 90 per cent rock with greater than 50 per cent cobble size (64 to 256 mm) (Reichle, 1969: 54). SA1 was 0.31 acres in size; SA2 0.23 acres; and SA3 0.13 acres.

# METHODS AND PROCEDURES

## Trapping

It was necessary to band a number of breeding adult Herring Gulls on their territories, since the prime purpose of this study was to observe parental behavior of individual gulls. To do this required a trapping method that was selective and caused as little disturbance as possible to the nesting birds.

Several methods of trapping were considered, including cannon-netting (Dill and Thornsberry, 1950; Thompson and DeLong, 1967), the use of padded muskrat traps and clap-net traps at the nest (Kadlec and Drury, 1969), and the use of soporific drugs (Smith, 1967; Kadlec and Drury, 1969). Cannon-netting and muskrat and clap-net traps could not be used because of their high disturbance effect. A soporific that rendered a gull immobile at its nest without any preliminary flopping (which would alarm adjacent gulls), had no risk of mortality, and had a short recovery time, had not been developed at the time of this study.

The method of trapping finally used was developed by John C. Coulson of the University of Durham, Durham, England (Weaver and Kadlec, 1970). It was utilized because of its comparatively low disturbance effect, and because it allowed

banding of birds at their nests. Time was sacrificed to keep disturbance at a relative minimum. The trap was made of 1-inch mesh chicken wire and employed the funnel-entrance principle. The only requirement for this method of trapping was that a trap had to be placed on a nest in which eggs were being incubated.

## Banding and Marking

Two bands were placed on each unbanded bird trapped, the U. S. Fish and Wildlife Service's standard aluminum band and an experimental band of Incoloy or titanium. This was part of a program to evaluate the retentive capabilities of each band over a period of time. The Incoloy and titanium bands were wider than the aluminum ones and thereby accommodated larger numerals, allowing easier identification with a spotting scope. Band reading was the primary way to identify individual gulls. Some birds could be recognized through small plumage differences or other anatomical differences, such as iris color or bill shape.

Herring Gull chicks were web-tagged with a numbered fingerling fish tag soon after hatching to associate them with a given territory, and therefore, with a given pair of adults (Weaver, 1967: 7-9). The method for web-tagging is described by Grice and Rogers (1965: 8-11). Later in the breeding season the chicks were banded with either the standard aluminum band or one of the experimental bands and

their web-tag numbers recorded. The number of chicks banded gave a measure of production.

## Sex Determination

A male and a female of a known pair could, for the most part, be easily distinguished through the difference in the size of their heads, the male being the larger of the two. There were a couple of cases in which this difference was not very great, making sex identification difficult unless the two birds were on territory together. According to Tinbergen (1961: 104), "An interesting feature . . . has been pointed out by Goethe (1937) and fully confirmed by us. While there is considerable overlapping in size between males and females, exceptionally large females being larger than exceptionally small males, in every pair the male is larger than the female. Pairs in which the female is larger than the male have never been observed." This has been generally confirmed by my observations of the larger members of pairs mounting the smaller birds in copulation.

In addition to banding the Herring Gulls that were trapped, the distance from the back of the skull to the tip of the bill on each bird was measured with calipers to determine if the sexes could thus be differentiated in the field.

## Locating Nests and Young

Once a study area was delineated, each active nest within the area was located on a map using a tape and compass. Two five-foot iron pipes were driven into the ground within each of the Study Areas 1 and 2, a known distance apart and at a known azimuth from each other. These pipes were then used as base points in locating the nests. Each nest within a study area was marked by spray painting a red number on an adjacent rock. Every effort was made to locate the number so that it could be seen easily from the blind.

During the summer of 1968, the first year for concentrated behavioral observations, the nests in SA1 and SA2 were checked every other day when time and weather allowed. As chicks became older they would leave their territories at our approach in an apparent effort to find better hiding places. This action meant more time spent in searching for young and the disturbance from our presence increased accordingly. In an effort to cut down on the disturbance factor during the 1969 breeding season, once a chick was web-tagged and accounted for, it was not sought in subsequent nest checks. This procedure greatly decreased the time spent in a study area for a nest check. Chicks were later accounted for, if still alive and in the area, when they were banded. SA3, serving as a control area for chick production figures, was visited less frequently, at most once a week.

## Weighing of Chicks

Some chicks were weighed in an effort to correlate survival with average weight gained per day, and, therefore, with the parents' ability to provide their chicks with enough food. It was originally intended to weigh all those chicks associated with numbered nests in the "blind study areas" (that part of the study area readily observed from within the blind). However, the increased amount of time this operation required dictated against including so many chicks. Keeping the disturbance to a minimum was considered more important. Therefore, only chicks of banded adult Herring Gull pairs were weighed as a part of this study. To supplement these data, in 1969 a string of 60 nests outside of the study areas was utilized. These nests were spread out on the perimeter of the island to keep disturbance to any one nest at a low level.

The study area chicks were weighed every other day and those in the supplementary nests every day, as the weather allowed in either case. In 1968, chicks were weighed to the nearest gram on a triple beam balance. In 1969, some accuracy was sacrificed to expedite matters when a spring balance was used. A chick "survived" if it reached the arbitrary weight of 700 grams, or if it was alive, in apparent good health, and showing an average daily weight gain of more than 20 grams at the end of the study.

The 60 supplementary nests were initially divided evenly into 3-egg, 2-egg, and 1-egg nests. The purpose of this was to determine if there was any difference between the average daily weight gained by the number-one chick in each of the three categories.

## Behavioral Observations

Observations of behavior were made from semi-permanent blinds located in SA1 and SA2. Each blind was 4 ft. x 6 ft., constructed of canvas stapled to a wooden frame. Plywood roofs 5 ft. x 8 ft. slanted from a six-foot height in front to 5 feet in the rear. About 25 nests could be watched effectively for behavior from each blind. The balance of the nests within each of these two study areas was utilized for measuring production of young.

Alternate days were spent in each blind as the work schedule allowed. Prior to the peak of hatching, behavior was noted by pencil and paper because of the low level of activity during the incubation period. When the young began to hatch out, activity increased to the point where it became necessary to record observations with the aid of a portable cassette tape recorder. This permitted me to keep my eyes on the study area the entire period. Other equipment used within the blind included a 10 x 40 binocular, a spotting scope with a 20x and a 40x lens, and a 35 mm single lens reflex camera with an 85 mm and a 400 mm lens.

One of my co-workers accompanied me to a blind and then departed the area after I entered. "Satisfied" that nobody remained, the gulls would immediately return to their territories. The few times I had to go into a blind alone, it was 15 to 20 minutes before the gulls settled down.

At first, almost all behavior was recorded, since it was not known with what to be primarily concerned regarding parental behavior. By the second season of observations more particular behavior was observed. In order to watch a nest or nests continuously, watch periods of an hour were set up. Two to five nests which were close to one another would be watched for every detail during one of these watch periods. A visual sweep was taken of the other nests within the blind observation area every 15 minutes within a given watch period. For the next hour, two to five other nests would have a concentrated watch period. If any abnormal activity was noticed elsewhere within the blind area, my attention would momentarily be directed to that activity to note its nature, location, and participants.

In a typical observation period, the following were noted: the time of day; the weather conditions; the adult birds' activities, whether loafing, incubating the eggs, brooding, feeding, or defending the young; the number of chicks present within a territory; and the cover available to the chicks for hiding places.

## Analysis of Behavior and Other Factors

All data were coded for computer analysis. The time of day was divided into four periods: 1 = 0500-0900, 2 = 0900-1300, 3 = 1300-1700, 4 = 1700-2100. Weather data were recorded in three categories, cloud cover, precipitation, and temperature. These in turn were subdivided for coding:

| Cloud Cover | Precipitation | Temperature |
|---|---|---|
| 1 = clear | 1 = none | 1 = 60°-70° F. |
| 2 = partly cloudy | 2 = fog | 2 = 70°-80° |
| 3 = overcast | 3 = rain | 3 = 80°-90° + |

"Brooding-incubating" intensity (for that transitional period when there are both egg(s) and chick(s) in the nest), and brooding intensity of the young were quantifiable as a percentage of the total time of the observation period. As an example, on 20 June 1969, Herring Gull pair 1319 brooded their young for a total of 171 minutes out of the 370-minute observation period, or 46.2 per cent of the time.

Feeding of the young was quantified as the number of feedings per hour during a given observation period; e.g., on 23 June 1969, pair 1585 fed their young five times in a 4.5 hour period, or 1.11 feedings per hour. Food quantity and food quality were noted when possible, but oftentimes were unobservable. Food quantity was recorded as follows: 1 = no feed, 2 = minimum, 3 = moderate, 4 = maximum. Food quality was similarly divided: 1 = no feed, 2 = poor,

3 = fair, 4 = good. The "no feed" category was recorded when an adult gull regurgitated food and then reconsumed it prior to any ingestion by a chick.

Defense of the young was noted as defenses per hour during a given observation period in 1969; this behavior was not recorded in 1968. The cover of a territory was classified as excellent (=4), good (=3), fair (=2), poor (=1), or none (=0). Due to growth of vegetation or the growth of a chick, this classification could change during the period of parental care. The number of days from hatching of the number-two chick in a 3-chick and a 2-chick nest was utilized as "chick-age."

Analyses of these data were carried out with the aid of two UCLA Biomed computer programs, Correlation Matrix with Item Deletion (BMD3D) and Step-wise Multiple Regression (BMD2R). The following variables were used in the correlation matrix: 1) number of chicks (in any given observation period), 2) chick age, 3) brooding-incubating intensity, 4) brooding intensity, 5) defense, 6) feeding frequency, 7) food quantity, 8) food quality, 9) cloud cover, 10) precipitation, 11) air temperature, 12) time of day, 13) territory attentiveness (whether or not an adult was on territory 100 per cent of the time), 14) cover, and 15) territory adjacent to a Great Black-backed Gull territory (yes or no).

In the first stepwise multiple regression run the number of chicks was the dependent variable. Subsequent runs of this analysis omitted the variables defense, food quantity, and food quality, leaving one dependent variable (number of chicks) and 11 independent variables. In all analyses, each study area was treated separately and then in combination with the other.

# RESULTS

## Trapping

In 1967, a total of 1958 breeding adult Herring Gulls were trapped and banded. Of the 1958 birds there were 159 taken within SA1 and 108 within SA2. As a result of trapping, productivity, though not specifically measured, appeared to be much lower than the 1.06 young per nest observed by Kadlec and Drury along the New England Coast over 61 "colony years" (1968: 656).

Trapped gulls vigorously attempted to escape at our approach. Consequently, many eggs were broken. No known adult mortality occurred related to this trapping method; however, minor injuries were often sustained. Minor injuries of three types were observed: skin at the base of the upper mandible was peeled back by repeated thrusting of the bill through the wire mesh; wrists were skinned and bloodied by attempts to fly; and an occasional toe nail was caught in the wire mesh and torn. This method of trapping was also used successfully on Great Black-backed Gulls in May of 1968 and 1969.

## Pair Formation and Establishment of Territory

In 1969, when I first viewed Milk Island from the mainland on 6 March, both Herring Gulls and Black-backs were on-territory. On 24 March, an estimated two-thirds of the breeding population (about 4500 gulls) were present and on-territory. By mid-April, the remainder of the breeding birds had returned.

Two pair formations were witnessed, both of which were in SA1. In both cases, the male was already on-territory and the female presented herself to him. Over a period of five days, Herring Gull male 1505 was courted by at least three different females. On 2 May 1969, he accepted the female which had been banded on territory 1869 the year before, 22 feet south of 1505. On the next day, 3 May, the female 1869 continued to be very solicitous; she was head-tossing and courtship begging very intently.

The second pair formation was under what surely must be termed odd circumstances. The female at territory 1858 laid a single egg and then failed to return. Soon thereafter, the male 1858 accepted another female. She added a single egg of her own to the first egg, neither of which hatched.

Observations concerning the establishment of a territory by a Herring Gull breeding for the first time were not recorded.

## Territory and Mate Fidelity

There were 69 gulls within the blind study area out of the 159 trapped and banded in SA1. In SA2, 34 of the 108 total banded were within the blind study area. Table 1 illustrates the changes that took place between 1967 and 1969 as far as presence and absence of marked birds and their movements within the blind study areas.

The data set forth in Table 1 indicate that not all gulls returned to the same nesting territory year after year. The nine movements noted in 1968 in SA1 ranged from a minimum of 5 feet to a maximum of 58 feet, the average being about 15 feet. The seven moves in 1969 ranged from 9 to 40 feet, averaging 18 feet. In SA2, there were 10 territorial moves in 1968 of 5 to 14 feet, with an average of 10.5 feet; in 1969, the distances ranged from 8 to 19 feet in four moves averaging 11.5 feet. Nine of the 10 changes in SA2 in 1968 involved territories with a grassy substrate.

These changes in territory were all that were noted. It is possible that there were others. Some of the birds not seen at all after the 1967 season, or seen and not associated with a territory, could have moved to a new nesting territory outside of the study area and not been noted. There were several instances of birds moving their nest site a distance of less than 5 feet. These movements were not considered territorial moves.

TABLE 1. Territory fidelity of known banded Herring Gulls within the blind study areas.

| Study Area | Total Birds Banded in 1967 | Birds Return | Birds Return to Terr. | Birds Move to New Terr. | Birds Seen on Terr. in 1968 Back on Terr. in 1969 | Not Seen in 1969 | Move to New Terr. | Birds on Terr. Not Seen in 1968 |
|---|---|---|---|---|---|---|---|---|
| SA1 | 69 | | | | | | | |
| 1968 | | [a]42 | 28 | 9 | -- | -- | -- | -- |
| 1969 | | [a]49 | 38 | 7 | 18/28 | 6/28 | [b]3/28 | 10 |
| SA2 | 34 | | | | | | | |
| 1968 | | 31 | 21 | 10 | -- | -- | -- | -- |
| 1969 | | [a]28 | 21 | 4 | 9/21 | 6/21 | [b]4/21 | 2 |

a. (Birds Move to New Terr.) + (Birds Return to Terr.) ≠ (Birds Return), because balance are banded birds seen in the study area but not associated with a territory.

b. (Move to New Terr.) + (Not Seen in 1969) + (Back on Terr. in 1969) ≠ (Birds Return to Terr. in 1968), because balance are banded birds seen in the study area but not associated with a territory.

In moves involving members of known pairs in both blind study areas, only two moves out of 17 included both mates (i.e., they both moved to the same new territory), while the other 15 moves involved a single member of the pair. Therefore, the latter moves all meant a change of mate. Only three of the other pair members (out of the 15) were seen in the area, and none of these were known to be on-territory.

Gulls that had been mated for at least two and then three years (i.e., they were banded as a pair in 1967 and continued to be paired in 1968 and 1969) had a higher overall reproductive success than did newly mated birds (Tables 2 and 3). In SA1, there were 17 changes in mates out of 28 marked pairs in the 1968 and 1969 breeding seasons; there were eight changes out of 11 marked pairs in SA2. The 17 positive new pairings in SA1 yielded eight young, or 0.47 chicks per nest. In SA2, six new pairings produced three young, or 0.50 chicks per nest. Combining the two study areas, there was a production of 0.48 chicks per nest as compared to an overall production of 0.84 chicks per nest (i.e., combining SA's 1 and 2 for 1968 and 1969, Table 4).

During the 1969 breeding season, in SA2 there were two pairs of gulls that defended a territory but did not build a nest. The female was not banded originally in either pair, so the respective mates' fidelity is uncertain. One pair, 1915, had nested the year before, but was

TABLE 2. Reproductive success (chicks per nest) of Herring Gull pairs known to have been paired in 1967, 1968, and 1969 as compared to newly formed pairs. (Sample sizes are in parentheses.)

| Study Area | Long Term Pairs 1968 | 1969 | New Pairs |
|---|---|---|---|
| SA1 | (8) 1.63 | 1.63 | (17) 0.47 |
| SA2 | (3) 0.33 | 0.33 | (6) 0.50 |
| SA1+2 | (11) 1.27 | 1.27 | (23) 0.48 |

TABLE 3. Reproductive success of long term Herring Gull pairs known to have been paired in 1967, 1968, and 1969.

| Study Area | Banded Pair # | Eggs Laid 1968 | 1969 | Eggs Hatched 1968 | 1969 | Chicks at Final Count 1968 | 1969 |
|---|---|---|---|---|---|---|---|
| SA1 | 1500 | 3 | 3 | 3 | 3 | 2 | 0[a] |
| | 1548 | 3 | 3 | 3 | 3 | 2 | 2 |
| | 1550 | 3 | 3 | 3 | 3 | 1 | 1 |
| | 1585 | 3 | 3 | 3 | 3 | 2 | 3 |
| | 1632 | 3 | 3 | 2 | 3 | 2 | 1 |
| | 1706 | 3 | 3 | 3 | 3 | 2 | 0 |
| | 1855 | 2 | 3 | 2 | 3 | 1 | 3[a] |
| | 1885 | 3 | 3 | 3 | 3 | 1 | 3 |
| SA2 | 1052 | 3 | 2 | 3 | 2 | 0 | 0 |
| | 1133 | 3 | 3 | 3 | 3[b] | 0 | 1 |
| | 1927 | 3 | 3 | 3 | 0 | 1 | - |

a. Number-one chick of pair 1500 at 12 days of age (6-27-69) moved to pair 1855; this chick plus three 1855 chicks were cared for by 1855 adults through at least 7-2-79. On 7-19-69, #1-1500 chick and #2-1855 chick were banded at 1855.

b. Nest destroyed by Great Black-backed Gull; 1927 pair newly paired in 1968.

unsuccessful because of Black-backed Gull predation. The other pair, 1122, was not seen in 1968 and presumably did not breed. Territory 1915 was occupied as early as 9 April 1969, but the 1122 male was not seen until 21 April. The behavior displayed on these two territories gave every indication of a normal breeding sequence. There was the usual courtship behavior culminating in copulation many times. There was an occasional effort made toward nest-building, but nothing past a scrape was formed.

Table 1 illustrates the indication that there are a number of non-breeding adult gulls each year. Thirty birds out of the 103 banded in 1967 did not return in 1968. In 1969, 17 of those gulls returned: 12 on their 1967 territories (one of which did not nest, but did defend its territory), two nesting on new territories, and three with no nests or territories.

## Reproductive Success

Records of the reproductive success of each study area were kept. Although it was intended to gain a more "natural" reproduction through less disturbance in 1969 by checking the study areas less frequently and over a shorter period of time than in 1968, there is no evidence that variations in technique affected mortality. According to the 1969 figures, SA2 is the only study area which improved in chick production over 1968; SA's 1 and 3 declined (Table 4).

TABLE 4. Herring Gull chick production in Milk Island study areas.

| | SA1 | | SA2 | | SA3 | |
|---|---|---|---|---|---|---|
| | 1968 | 1969 | 1968 | 1969 | 1968 | 1969 |
| Nests | 146 | 115 | 93 | 69 | 62 | 68 |
| Eggs Laid | 407 | 319 | 258 | 193 | 169 | 192 |
| Eggs per Nest | 2.79 | 2.77 | 2.77 | 2.80 | 2.71 | 2.82 |
| Eggs Hatched | 321 | 252 | 184 | 142 | 126 | 155 |
| Eggs Hatched per Nest | 2.20 | 2.19 | 1.98 | 2.06 | 2.02 | 2.18 |
| % Egg Loss[a] | 21.2 | 21.0 | 28.5 | 26.4 | 25.5 | 19.3 |
| Chicks Reaching 10 Days | 189 | -- | 101 | -- | 83 | -- |
| Chicks per Nest | 1.30 | -- | 1.09 | -- | 1.34 | -- |
| % Mortality[b] | 41.1 | -- | 45.1 | -- | 34.1 | -- |
| Chicks at Final Count | 146 | 109 | 48 | 51 | 63 | 61 |
| Chicks per Nest | 1.00 | 0.95 | 0.52 | 0.74 | 1.02 | 0.90 |
| % Overall Mortality[c] | 54.5 | 56.7 | 73.9 | 64.1 | 50.0 | 60.6 |

a. % Egg Loss = (Eggs Laid - Eggs Hatched) / Eggs Laid.

b. % Mortality = (Eggs Hatched - Chicks Reaching 10 Days) / Eggs Hatched.

c. % Overall Mortality = (Eggs Hatched - Chicks at Final Count) / Eggs Hatched.

In 1968, the majority of chick mortality occurred in the first 10 days following hatching (Table 4). Comparable data were not obtainable during the 1969 breeding season due to the method of checking nests.

## Incubation of the Eggs and Brooding of the Young

The incubation period, counting from the day that the third egg was laid to the day that the third egg hatched, was an average of 26.9 days from a sample of 60 nests. In 1968, 20 of the 60 nests averaged 27.2 days, ranging from 25 to 29 days. In 40 nests in 1969, there were again extremes of 25 and 29 days, but a mean of 26.8 days.

As Tinbergen (1961) noted, it was found that near the end of the incubation period, the gulls became more defensive of their nest and were aggressive toward intruders. These aggressive tendencies reached a plateau shortly before the young hatched out and persisted until they were several weeks old. Individual gulls varied markedly in their aggressiveness toward humans, some offering what appeared to be token aggression, and others being boldly hostile to the point of actually striking a person on the head with the bill or feet as they dove past. The territory defense variable was omitted in the final analysis due to a small sample size and the fact that measures for this variable were not refined enough to be of value.

Following hatching, the chicks were brooded intensely for the first two days of life. Brooding ceased, on the average, in SA1 after the chicks were four days of age and in SA2 after six days of age. There was a reduction in brooding intensity in both study areas as the chicks became older (Table 5). Although the sample size in SA2 was smaller than that in SA1, it appears that the brooding intensity in SA2 did not diminish with chick age as rapidly as it did in SA1.

Older chicks were rarely brooded, even in the heaviest rains, or on the hottest or coldest days. The parent of two chicks, 12 and 13 days old, attempted to brood them in a hard rain, but was ineffective due to the chicks' size. The oldest chick observed to be brooded effectively was nine days of age.

Until a chick has grown some of its contour feathers, which occurs during the third and fourth weeks of life (Kadlec et al., 1969), it is highly subject to over-exposure during periods of inclement weather. Unless there was adequate cover within a territory, whether the cover was a rock, a log, or some form of vegetation, chicks sometimes died from the heat or the wet (Drury, pers. comm.). Chicks of broodable size often sought shelter under a parent only to have the adult walk away. There was one instance in which two chicks that were almost fully feathered died from over-exposure to a prolonged period of heavy rain.

TABLE 5. The mean brooding intensity (percentage of observation period) of adult Herring Gulls as related to chick age. (Fractions in parentheses: numerator = no. of pairs brooding; denominator = total no. of pairs having chicks of that particular age.)

| Chick Age | SA1 Brooding Intensity | | SA1 Range | SA2 Brooding Intensity | | SA2 Range |
|---|---|---|---|---|---|---|
| 1 da. | 87.4% | (14/14) | 40.0-100.0 | 98.1% | (9/9) | 94.0-100.0 |
| 2 da. | 54.9% | (4/4) | 46.0- 69.0 | 81.8% | (2/3) | 66.0- 97.5 |
| 3 da. | 37.9% | (5/6) | 12.3- 83.5 | 90.5% | (2/2) | 89.0- 92.0 |
| 4 da. | 28.8% | (5/8) | 05.0- 42.0 | 38.3% | (4/4) | 03.0- 75.0 |
| 5 da. | 21.8% | (2/9) | 11.0- 32.5 | 35.8% | (5/5) | 09.0- 81.0 |
| 6 da. | 6.2% | (3/9) | 04.0- 09.0 | 41.7% | (3/4) | 30.0- 54.0 |

## Feeding of the Young

A behavioral trait was observed in 1968 that was to assist in deciding whether a bird was a "good" or "poor" parent. This characteristic was the ease with which a bird regurgitated food for its young. During the first season of observations it very definitely appeared as though some adults regurgitated with a great deal more ease than others. With what were termed "difficult feeders," it seemed that chicks had to expend a greater amount of energy in begging for food before they were finally fed. In contrast, there were some parents that fed their young with comparatively little begging on the chicks' part. It appeared as though the ease with which an adult regurgitated food was dependent upon the type of food consumed, a loose offal coming up somewhat more easily than a large whole fish.

Observations in 1969 erased all that was hypothesized from the previous year. The same adult gulls that had been "difficult feeders" in 1968, had very little difficulty regurgitating food, with the exception of large, flat fish. The important observation here is that, for the most part, the adult birds in 1969 were actually actively soliciting the chicks and many times were seen to regurgitate without any begging from the young. In 1968, many parents seemed to be actually avoiding a chick's begging.

The data for the food quantity and food quality variables were difficult to gather objectively. Although

it may have been obvious that an adult gull was feeding its chicks, the quantity and type of food being fed were oftentimes hidden from my view behind a rock or some vegetation. Therefore, due to a small sample size and the highly subjective nature of these variables, in the final analysis they were discarded.

Feeding frequency data (number of feedings per hour) were somewhat easier to record. Figure 3 is a scatter diagram of the feeding frequency variable plotted against the number of chicks by observation period. A positive correlation is suggested.

The feedings for the first couple of days following hatching normally consisted of small bits of food which were easily managed by a chick. The food was held in the parent's bill while the chicks pecked at it or else it was regurgitated onto the ground. After the "small bits and pieces" phase, which lasted two or three days, anything from a whole fish to offal was regurgitated. Some adults picked apart the larger pieces of food for their chicks, while others would leave an entire fish on the ground which the chicks pecked at futilely.

Table 6 summarizes the feeding frequencies of pairs of adult Herring Gulls located in the blind study areas. The table also offers a compilation of the absolute and mean number of chicks produced by these pairs, as well as the cover found in each pair's territory. Table 7 is a tabulation

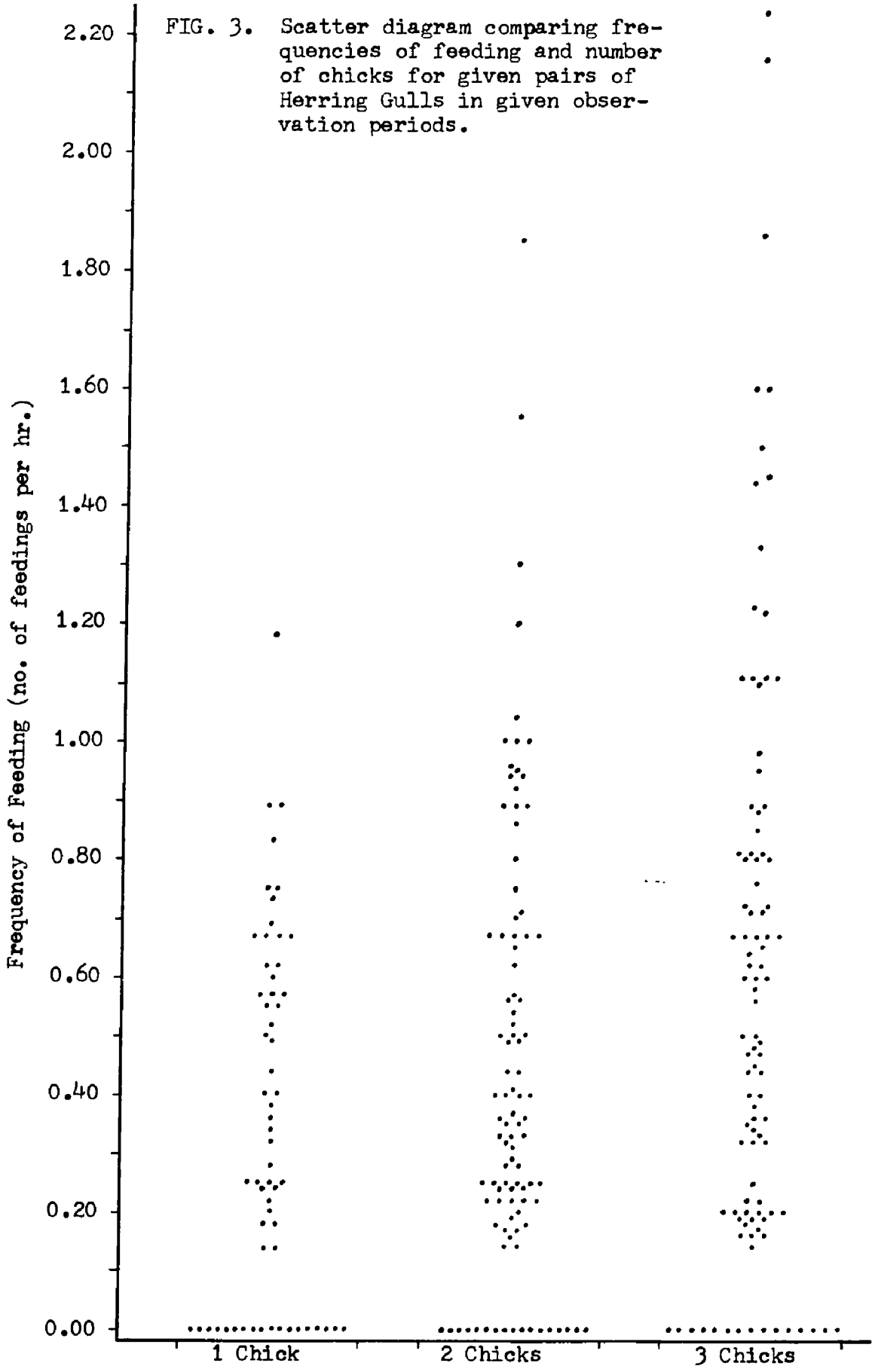



FIG. 3. Scatter diagram comparing frequencies of feeding and number of chicks for given pairs of Herring Gulls in given observation periods.

TABLE 6. Summary of chicks produced, feeding frequencies, and cover in territories of blind study areas.

| Study Area | Pair # | 1968 Chicks at Final Blind Observation | 1968 n[a] | 1968 $\bar{x}$ Chicks | 1968 $\bar{x}$ Feed. Freq.[b] | 1968 $\bar{x}$ Cover[c] | 1969 Chicks at Final Blind Observation | 1969 n | 1969 $\bar{x}$ Chicks | 1969 $\bar{x}$ Feed. Freq. | 1969 $\bar{x}$ Cover |
|---|---|---|---|---|---|---|---|---|---|---|---|
| SA1 | 1344[f] | 3 | 6 | 3.0 | 0.20 | 3.0 | 2 | 5 | 2.6 | 0.25 | 3.0 |
| | 1500[f] | 1 | 8 | 2.1 | 0.48 | 1.0 | 0[d] | 3 | 3.0 | 1.18 | 1.0 |
| | 1505[g] | 1 | 4 | 1.0 | 0.52 | 2.3 | 1 | 4 | 1.3 | 0.31 | 2.5 |
| | 1542 | 1 | 5 | 1.0 | 0.21 | 2.4 | 2 | 6 | 2.0 | 0.25 | 2.5 |
| | 1548[f] | 2 | 9 | 2.1 | 0.31 | 3.0 | 2 | 6 | 2.7 | 0.41 | 3.0 |
| | 1585[f] | 2 | 9 | 2.2 | 0.51 | 3.4 | 3 | 9 | 3.0 | 0.56 | 3.6 |
| | 1632[f] | 2 | 9 | 2.0 | 0.45 | 3.0 | 2 | 10 | 2.4 | 0.80 | 3.0 |
| | 1825[g] | 1 | 8 | 2.0 | 0.38 | 1.8 | 1 | 8 | 1.6 | 0.67 | 1.9 |
| | 1855[f] | 1 | 7 | 1.4 | 0.15 | 2.1 | 3[d] | 8 | 2.9 | 0.56 | 1.9 |
| | 1857 | 2 | 9 | 2.0 | 0.47 | 2.3 | 2 | 9 | 2.1 | 0.64 | 2.6 |
| | 1870 | 1 | 5 | 1.0 | 0.25 | 2.4 | 2 | 6 | 2.8 | 0.29 | 2.5 |
| | 1885[f] | 1 | 8 | 2.3 | 0.27 | 3.0 | 3 | 8 | 2.9 | 0.49 | 3.0 |
| | 1319 | - | - | - | - | - | 3 | 8 | 3.0 | 0.48 | 2.3 |
| SA2 | 958 | 0 | 3 | 2.7 | 0.38 | 1.3 | 1 | 5 | 2.0 | 0.24 | 1.2 |
| | 1046 | 2 | 8 | 2.1 | 0.44 | 0.3 | 0[e] | 4 | 1.7 | 0.66 | 0.3 |
| | 1052[f] | 2 | 8 | 2.5 | 0.48 | 2.5 | 0 | 3 | 1.7 | 0.27 | 1.3 |
| | 1133[f] | 1 | 7 | 2.1 | 0.26 | 0.3 | 1 | 7 | 1.7 | 0.49 | 0.6 |
| | 1364[g] | 1 | 10 | 1.8 | 0.60 | 1.5 | 1 | 9 | 1.6 | 0.56 | 1.6 |
| | 216 | - | - | - | - | - | 2 | 10 | 2.9 | 1.02 | 0.3 |
| | 665 | - | - | - | - | - | 2 | 8 | 2.0 | 0.60 | 2.5 |
| | 1591[g] | - | - | - | - | - | 1 | 4 | 1.0 | 0.36 | 2.5 |

a. n represents the number of observation periods used in gaining chick, feed. freq., and cover means.
b. Feed. Freq. = number of feedings per hour.
c. Cover: 0 = none, 1 = poor, 2 = fair, 3 = good, 4 = excellent.
d. #1 chick of pair 1500 at 12 da. of age (6-27-69) moved to pair 1855; this chick plus three 1855 chicks were cared for by 1855 adults thru at least 7-2-69. On 7-19-69, #1-1500 chick was banded at 1855.
e. Two chicks wandered from 1046 territory; one was seen in adjacent territory for one observation period.
f. Banded pairs comprising the same birds in 1968 and1969.
g. Pairs comprised of different birds in 1969 than in 1968.

TABLE 7. Range, mean, standard deviation, and 95% confidence interval of frequency of feeding and cover variables.

| | Feed. Freq.[a] | | | Cover[b] | |
|---|---|---|---|---|---|
| | SA1 | SA2 | SA1+2 | SA1 | SA2 |
| n | 171 | 90 | 261 | 171 | 90 |
| range | 0.00-2.24 | 0.00-2.16 | 0.00-2.24 | 1-4 | 0-3 |
| $\bar{x}$ | 0.44 | 0.50 | 0.46 | 2.5 | 1.2 |
| s | 0.393 | 0.457 | 0.416 | 0.76 | 1.02 |
| $s_{\bar{x}}$ | 0.030 | 0.048 | 0.026 | 0.058 | 0.107 |
| $t_{.05}s_{\bar{x}}$ | ±0.059 | ±0.095 | ±0.051 | ±0.114 | ±0.214 |
| 95% interval estimate of u | .381-.499 | .405-.595 | .409-.511 | 2.306-2.614 | 0.986-1.414 |

a. Feed. Freq. = number of feedings per hour.
b. Cover: 0 = none, 1 = poor, 2 = fair, 3 = good, 4 = excellent.

of the basic statistics concerning frequency of feeding and cover.

### Records of Chick Weights

Chick weight data for 1968 and 1969 are few for known adult gull pairs. However, when the average daily weight gained by the chicks is totaled for each brood and compared with the overall mean frequency of feeding recorded for each of the brood's parents, there is a positive correlation ($r = 0.922$) between the two (Table 8, Figure 4).

Table 9 reflects that there is little difference overall in the average daily weight gained by the number-one and number-two chicks in a three-chick and a two-chick nest, but that the number-three chick averages a bit lower in weight gained. Averaging the weights of chicks that survived in these different sized broods yields results that are close to the average daily increase in weight for all chicks that survived (study area plus supplemental nests), 29 grams per day (Table 10).

## The Effect of Great Black-backed Gulls on the Herring Gull

The gull colony on Milk Island had no mammalian predators of any consequence. Avian predators consisted of the gulls themselves (L. argentatus and L. marinus). During the 1968 and 1969 breeding seasons on Milk Island, predation

TABLE 8. Average daily increase in weight (grams) of Herring Gull chicks from known adult pairs compared with mean frequency of feeding (feedings per hour) of chicks by adults. (Number of days over which chicks were weighed in parentheses.)

| Adult Pair No. | 1968 #1 Chick | 1968 #2 Chick | 1968 #3 Chick | 1968 Feed. Freq. | 1969 #1 Chick | 1969 #2 Chick | 1969 #3 Chick | 1969 Feed. Freq. |
|---|---|---|---|---|---|---|---|---|
| 1500 | 31↑[a] (16) | 9↓[b] (4) | 26↑ (8) | 0.48 | 35↑[f] (10) | 23↓ (10) | 15↓ (6) | 1.18 |
| 1548 | 28↑ (21) | 31↑ (13) | ↓ | 0.31 | -- | -- | -- | -- |
| 1585 | ↓ | 27↑ (16) | 29↑ (21) | 0.51 | 31↑ (16) | 33↑ (16) | 30↑ (16) | 0.56 |
| 1632 | 29↑ (26) | 31↑ (16) | -- | 0.45 | -- | -- | -- | -- |
| 1855 | ↓ | 30↑ (17) | -- | 0.15 | 30↑[c] (10) | 28↑ (17) | 30↑ (17) | 0.56 |
| 1885 | 32↑ (21) | 26↓ (16) | ↓ | 0.27 | 35↑ (18) | 34↑ (18) | 25↑ (18) | 0.49 |
| 1052 | 30↑ (21) | 13↓ (11) | 29↑ (6) | 0.48 | 57↓ (3) | ↓ | -- | 0.27 |
| 1133[e] | 31↓ (6) | 33↓ (6) | 20↓ (6) | 0.26 | 26↓[d] (10) | 22↓ (2) | 22↑ (10) | 0.49 |

a. ↑ - "survived" -- alive and in good health through final weighing.
b. ↓ - died.
c. ↑ - fate questionable; probably survived.
d. ↓ - fate questionable; probably died.
e. In 1968, 1133 chicks ran from their territory due to human disturbance and never returned. #2 chick was later found dead.
f. #1-1500 chick cared for by 1855 adults following 6-27-69.

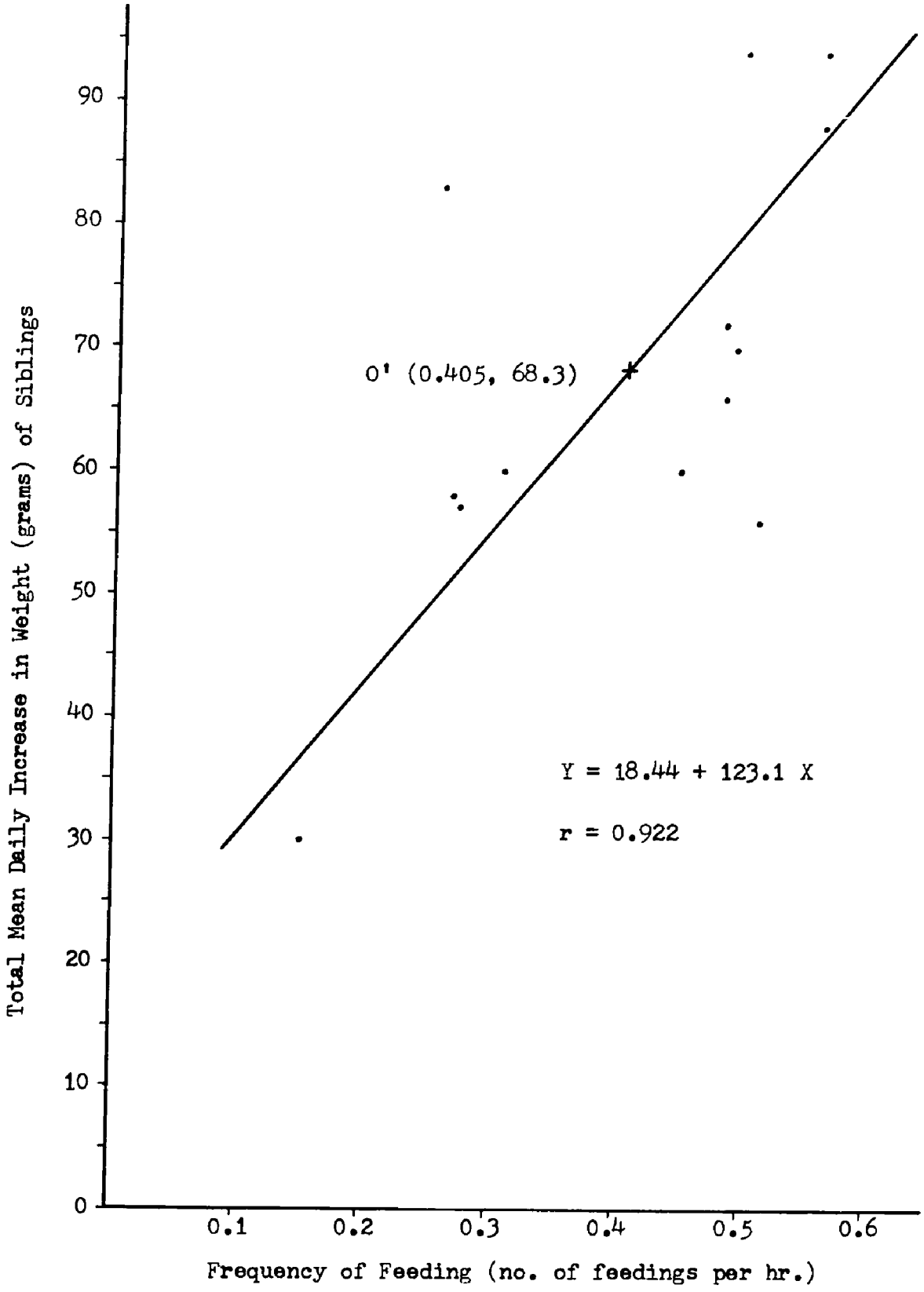



FIG. 4. Sample regression of total sibling mean daily increase in weight on frequency of feeding.

TABLE 9. Average daily increase in weight (grams) of Herring Gull chicks from 3-chick, 2-chick, and 1-chick nests. (Sample sizes are in parentheses.)

| | 3-Chick Nest | | | 2-Chick Nest | | 1-Chick Nest |
|---|---|---|---|---|---|---|
| | #1 Chick | #2 Chick | #3 Chick | #1 Chick | #2 Chick | #1 Chick |
| $\bar{x}$ [a] | 18(11) | 20(11) | 15(11) | 21(18) | 20(18) | 23(28) |
| $\bar{x}$ [b] | 31 (4) | 26 (5) | 27 (4) | 27 (9) | 31 (5) | 28(16) |

a. Average daily increase in weight of all chicks.
b. Average daily increase in weight of chicks that "survived."

TABLE 10. Average daily increase in weight (grams) of Herring Gull chicks that survived and that died. (Sample sizes are in parentheses.)

| Chicks Survived | Chicks Probably Survived | Chicks Died | Chicks Probably Died |
|---|---|---|---|
| 29(58) | 27(9) | 15(27) | 11(18) |

by both Herring Gulls and Great Black-backed Gulls on eggs and young was observed. Black-backs were seen to take Black-back chicks as well as Herring Gull chicks, whereas, Herring Gulls were only seen taking their own kind. The Black-back was much the more serious predator: 20 separate instances of chick predation plus evidence of more were seen, as compared to three instances of predation involving a Herring Gull.

Milk Island Black-backs preyed on Milk Island eggs and chicks. It was found, as Bergman suggested, that this predation was done largely by particular birds. During the 1968 season, in SA2, one male Black-back displaced 12 Herring Gull pairs from their territories. This involved an irregular area of approximately 20 feet by 50 feet.

This male Black-back ("BB1591") was paired and successfully hatched one or two chicks (records of Black-back reproduction were not kept). Sometime early in the season, BB1591 pair lost their chicks. Following this, BB1591 was circumstantially accountable for taking 13 Herring Gull chicks and 16 eggs; he was actually seen taking two chicks. One of these chicks was actively sought out in its hiding place, removed therefrom, and then consumed (Figure 5). A male Black-back in SA1 was seen preying on Herring Gull chicks in the same manner. In an hour's time, this Black-back took three chicks from a single territory; this despite the fact that the chicks



a b c d

FIG. 5. Great Black-backed Gull predation on Herring Gull chick.

were in what I considered to be good hiding places (i.e., concealed from casual sight). During none of these observations was the mate of either male Black-back seen to partake in the activities in any way other than through Long-Calling (note in Figure 5c). The SA1 Black-back, in contrast to BB1591, had two chicks of its own and was observed to regurgitate one of the ingested Herring Gull chicks for them.

The parents' defense of their young in these situations was varied but futile against the larger and stronger Black-back. The defending Herring Gull (sex unknown) in SA1 was noticeably more aggressive than the one in SA2. The SA1 bird flew into the air, and calling the Charge Call (calls after Tinbergen, 1961: 9-12) attacked the intruding Black-back by flying low attempting to hit him with lowered legs or bill. When the Black-back had picked up the third chick, the Herring Gull on one of its low flying runs hit the Black-back with enough force to knock him over causing him to drop the chick. However, the Black-back retook that chick shortly thereafter.

In contrast to the SA1 Herring Gull's defense, the SA2 Herring Gull (a female) was somewhat less aggressive. As BB1591 approached, the defending Herring Gull vigorously went through the usual defensive postures and displays (Tinbergen, 1961: 53-57). When this behavior failed to stop the Black-back's approach, she went into the air and

began low-flying runs as did the SA1 bird. However, the SA2 Herring Gull was less intensive in its Charge Calls which accompanied aborted low-flying runs. These actions did not deter BB1591. As soon as the Black-back had taken the chick and left the Herring Gull's territory, the female Herring Gull was back down preening with her mate (who had just returned) standing by as if nothing had happened.

The only records of Herring Gulls being successful in their attacks on Black-backs relate to the instances when the Black-back involved was a stranger; i.e., the Black-back was not a territory-holder within the immediate vicinity. These Black-backs departed immediately when challenged by a territorial Herring Gull. However, those nesting adjacent to Herring Gulls, such as BB1591, were never dominated by the Herring Gulls.

Although unbanded, it is almost certain that BB1591 returned to his expanded territory in 1969. He and his mate raised two chicks. In the process, they retained the territory they had established the year before, except for a slight infringement by another pair of Black-backs. One Herring Gull male, which had been displaced by BB1591 in 1968, attempted to nest with a new mate in 1969 a short distance from his old nest site. Once again, this Herring Gull was unsuccessful because BB1591 took its eggs. There were four other pairs of Herring Gulls which attempted to establish a territory within BB1591's territory, but to no avail.

Herring Gull pair 1911 in SA2 was unsuccessful in hatching their eggs in both 1968 and 1969 due to the presence of Black-backs. 1968 conclusions were purely circumstantial, but in 1969 male "BB13" was seen chasing the incubating female "HG1911" off her nest, and then pulling the nest material apart, and breaking and beginning to eat one of the eggs. At this point, male HG1911 returned and drove off BB13. He then proceeded to share the remainder of the egg with his mate. BB13's behavior was elicited by one of its chicks wandering too closely to the HG1911 nest. The Black-back was defending its young in the presence of HG1911. This meant driving HG1911 off her nest. The next observation period yielded an empty nest at 1911. In both 1968 and 1969, after their reproductive efforts had been disrupted, the 1911 adults behaved as if they were going to renest; i.e., they collected nest material and carried out normal courtship behavior short of copulation. However, there was no renest either year.

Black-backs also preyed upon Black-back chicks. A male Black-back was seen taking a total of four Black-back chicks that had strayed out of their territories. These chicks ranged from one to four weeks in age. There was further evidence of Black-back chick predation in the form of carcasses that had been stripped and the skin left inside out, which is how an adult Black-back leaves a larger chick that it has preyed upon. My observations indicated

that Black-back young have a tendency to wander more than do Herring Gull young. If a Black-back chick went outside of its territory, the attending parent effectively defended that chick if its movements were through a Herring Gull's territory. If the chick entered another Black-back's territory, the chick, if unable to fend for itself, often became a prey of opportunity. This was because the parent bird was ineffective in its defense against another adult Black-back in that bird's territory.

Raleigh A. Blouch, who assisted me in the field in 1969, conducted an independent study on Milk Island concerning the probable effects of Great Black-backed Gulls on Herring Gull productivity. Following the productivity of Herring Gulls nesting adjacently to Black-back territories, Blouch classified each nest according to one of four substrate types. Eleven nests in the forb substrate produced 0.09 chicks per nest; 17 nests in tall grass, 0.24 chicks per nest; 20 nests in short grass, 0.70 chicks per nest; and 24 nests with a rocky substrate, 0.75 chicks per nest. Overall, the 72 nests produced 0.51 chicks per nest.

A second phase of Blouch's study involved measuring the distance between the Herring Gull nests and the adjacent Black-back nests in the short grass and rock substrates to see if there was a positive correlation between distance and Herring Gull productivity. Although the samples were small, there was a trend toward a positive correlation; i.e., as the distance between a Herring Gull nest and a Black-back

nest increased, the chances of the Herring Gull chicks surviving increased.

## The Effect of Human Disturbance

Black-back chicks, as mentioned above, moved about noticeably more than did Herring Gull chicks. A Herring Gull chick was seldom seen going outside of its territory under "normal" circumstances. When there were human beings in the vicinity, there was a great deal of movement by Herring Gull and Black-back chicks alike. This movement became more accentuated as the chicks became older. At my approach the chicks in SA2 moved more than did the chicks in SA1. Once I was in the SA2 blind and my escort had departed, the chicks would begin returning to their respective territories, being pecked by adult birds in the process. There were several instances in which chicks, presumably lost or killed, did not return to their territories.

In SA1, most chicks stayed within their territories. Whether or not a chick did remain in-territory appeared to be a direct function of the hiding places available to it within its territory. Rocks in SA1 were much larger on the average than in SA2, providing more hiding places for chicks. As a result, there was more hiding and less running in SA1. In SA2, chicks had to go about 20 to 40 feet east-southeast and out of the area before they reached hiding places in terrain comparable to that of SA1. The differences in the

terrain of the study areas are reflected in the number of chicks produced per nest (Table 4). SA3 had terrain much like that of SA1.

## Regression Analysis of Behavior and Other Factors

The quantified behavior data and the physical factors which were treated individually and, in some cases, in pairs earlier in this section, were analyzed together with the other variables using a correlation matrix and a stepwise multiple regression. This was done in an effort to establish which variables were related to the number of young produced by a pair of Herring Gulls.

With the aid of the UCLA Biomed BMD3D computer program (Correlation Matrix with Item Deletion), each of the variables was treated separately and correlated with each other in turn. Appendix I is a partial reproduction of the matrices from the computer print-out for SA1 and SA2 individually, and then combined. Table 11 illustrates to what degree the number of chicks is correlated with each of the other variables. Frequency of feeding (Figure 3, Tables 6 and 7) is the only variable of any consequence which is significant at the 0.01 level for all three cases in Table 11. The correlation coefficient for cover (Tables 6 and 7) is highly significant in SA1 and SA1+2, but is not significant in SA2 (Table 11).

TABLE 11. Coefficients resulting from correlation matrix showing the simple correlations between the number of chicks and other variables. (Sample sizes are in parentheses.)

| Variable | Number of Chicks | | |
|---|---|---|---|
| | SA1 | SA2 | SA1+2 |
| Chick Age | **-0.203 (180) | *-0.229 (92) | **-0.210 (272) |
| Brooding-incubating Intensity | -0.072 (180) | *-0.222 (92) | *-0.151 (272) |
| Brooding Intensity | * 0.146 (180) | ** 0.348 (92) | ** 0.220 (272) |
| Frequency of Feeding | ** 0.195 (179) | ** 0.367 (92) | ** 0.256 (271) |
| Cloud Cover | **-0.201 (180) | -0.115 (92) | **-0.178 (272) |
| Precipitation | 0.047 (180) | 0.015 (92) | 0.012 (272) |
| Air Temperature | -0.077 (172) | *-0.268 (91) | *-0.156 (263) |
| Time of Day | -0.001 (180) | -0.075 (92) | 0.009 (272) |
| Territory Attentiveness | *-0.169 (180) | -0.159 (92) | **-0.163 (272) |
| Cover | ** 0.241 (180) | 0.155 (92) | ** 0.233 (272) |
| Adjacent Black-back | 0.061 (180) | 0.075 (92) | 0.030 (272) |

* = $0.05 \geq P > 0.01$
** = $P < 0.01$

Similarly, brooding intensity (Table 5) is highly significant ($P < 0.01$) in both SA2 and SA1+2 (Table 11), the significance for the latter resulting from the high correlation in SA2. In SA1, brooding intensity and number of chicks are less significantly correlated ($P < 0.05$). In SA2, brooding intensity is also highly correlated with precipitation, which is not shown in Table 11 (See Appendix I).

The analysis completed with the UCLA Biomed BMD2R computer program (Stepwise Multiple Regression) afforded a comparison of the relative contributions of each independent variable to the dependent variable, the number of chicks produced. Table 12 presents the significant variables from this regression analysis. The variables frequency of feeding and cover are the most significant inputs to the variability of the number of chicks produced. Analysis of the combined data of the study areas (SA1+2) reflects at the 0.01 level of significance that approximately six per cent of the variability in the number of chicks produced is related to frequency of feeding and that almost 12 per cent of the variability is associated with a combination of frequency of feeding and cover. These percentages were extracted from the "RSQ" column in Table 12, the coefficient of determination. The variables were significant at the 0.01 level through the sixth variable entered into the analysis. According to the results, these six variables

TABLE 12. The most significant variables in the order entered in a stepwise multiple regression with the dependent variable, number of chicks. (Taken from Appendix II; sample sizes are in parentheses.)

| Area | Variable Entered | R | RSQ | F |
|---|---|---|---|---|
| SA1 | Cover | 0.2529 | 0.0639 | **11.5456 |
| (171) | Frequency of Feeding | 0.3262 | 0.1064 | ** 7.9853 |
| | Territory Attentiveness | 0.3630 | 0.1318 | * 4.8742 |
| | Chick Age | 0.3985 | 0.1588 | ** * 5.3314 |
| | Brooding-incubating Intensity | 0.4280 | 0.1832 | ** * 4.9294 |
| | Cloud Cover | 0.4433 | 0.1965 | ** 2.7155 |
| | Air Temperature | 0.4783 | 0.2288 | ** 6.8259 |
| SA2 | Brooding Intensity | 0.3557 | 0.1265 | **12.7499 |
| (90) | Frequency of Feeding | 0.4853 | 0.2355 | **12.4030 |
| SA1+2 | Frequency of Feeding | 0.2493 | 0.0621 | **17.1627 |
| (261) | Cover | 0.3394 | 0.1152 | **15.4680 |
| | Brooding Intensity | 0.3843 | 0.1477 | ** 9.8036 |
| | Brooding-incubating Intensity | 0.4192 | 0.1757 | ** 8.7009 |
| | Cloud Cover | 0.4451 | 0.1981 | ** 7.1130 |
| | Air Temperature | 0.4884 | 0.2385 | ** 13.4930 |

R = multiple correlation coefficient  * = $0.05 \geq P > 0.01$
RSQ = coefficient of determination  ** = $P < 0.01$

SA1: $Y = 3.508 - 0.007803\ X_2 - 0.007192\ X_3 + 0.2442\ X_5 - 0.3218\ X_6 - 0.2678\ X_8 - 0.4375\ X_{10} + 0.2556\ X_{11}$

SA2: $Y = 1.555 + 0.01160\ X_4 + 0.6265\ X_5$

SA1+2: $Y = 2.628 - 0.006926\ X_3 + 0.006536\ X_4 + 0.3707\ X_5 - 0.2847\ X_6 - 0.2501\ X_8 + 0.1603\ X_{11}$

accounted for about 24 per cent of the variability in the number of chicks produced.

The F values for SA1+2 in Table 12 decrease from frequency of feeding through cloud cover and then the F value for air temperature shows a marked increase over that of cloud cover. The apparent reason for this is that cloud cover and air temperature when correlated separately with the dependent variable are insignificant, but when placed into a multiple regression combine to become significant at the 0.01 level, air temperature bolstering the effect of cloud cover. The same phenomenon occurred with the data in SA1.

Table 12 does not portray whether the variables affected the dependent variable positively or negatively, but illustrates which variables together had the greatest effect on the variability of the number of chicks produced. Appendix III is a partial reproduction of the correlation matrices resulting from the stepwise multiple regression, showing whether a variable was negatively or positively correlated with the dependent variable.

# DISCUSSION AND CONCLUSIONS

## Insignificant Variables

There were several physical factors and some behavioral ones which were apparently insignificant in the final analysis. Among these were the variables brooding-incubating intensity, territorial attentiveness, adjacent Black-backs, time of day, and chick age.

Brooding-incubating intensity is shown as being significantly related to the variability in the number of chicks produced (Table 12); however, it is also shown to be negatively correlated with the number of chicks (Appendix III). The latter makes no sense whatsoever. This would mean that with less brooding-incubating there would be more chicks; or, conversely, the more brooding-incubating, the fewer chicks produced. This is not to say that brooding-incubating intensity is unimportant. It is probably very important, but was difficult to observe significantly as a continuum during the brief time that it was a factor for any one pair of gulls; i.e., that period of time between hatching of the first and last egg. Consequently, the data entered into the analysis were perhaps misleading.

Similarly, the territory attentiveness variable is shown as being significant at the 0.05 level in SA1 (Table 12), but is negatively correlated with the number of chicks produced (Appendix III). This indicates that there were greater chick numbers with less territory attentiveness (i.e., neither parent on-territory), which is illogical.

The variable for Black-backed Gulls nesting adjacently to Herring Gulls was irrelevant in the statistical analyses used. Apparently the reason for this is the fact that those Herring Gulls which were affected by neighboring Black-backs were not included in the parental care observations. This was simply because these Herring Gull pairs never had any chicks to begin with or only had chicks for a very short time.

The only meaningful correlation for the time of day variable was with frequency of feeding in SA1 (Appendix I). This was a negative correlation significant at the 0.05 level, which indicates that there was a higher rate of feeding earlier in the day than there was during the later hours.

Chick age was utilized primarily to attain a time reference between the Herring Gull pairs. This variable turned out to have a highly significant negative correlation with brooding intensity (Appendix I), which supports the data put forth in Table 5.

The weather factors as they were used in this analysis were, generally speaking, not very important. Since the effect of one observation period's weather would not be evident until the next observation period (even then, absolute confirmation of its effects would be doubtful), the variables for cloud cover, precipitation, and air temperature are probably meaningless in their present context. One exception to this would be the positive correlation noted between precipitation and brooding intensity in SA2. The absence of any severe weather or prolonged wet or hot periods is conceivably reflected in the lack of correlation between the weather variables and the number of chicks produced.

## Establishment of Territory

Kadlec and Drury (pers. comm.) had thought earlier that perhaps the Black-backed Gulls returned to a breeding island in the spring before the Herring Gulls, and this was the reason why Black-backs had the "optimal" nesting territories. Unfortunately, I was unable to be on the island early enough in the year to determine which species returned first. It is more likely that the Great Black-backed Gulls occupy optimal territories simply because they nest two to three weeks earlier in the breeding season, and therefore form territories relatively earlier than the Herring Gulls.

The question remains as to how a gull selects its territory. Is it a random selection? Are there only certain areas in an established breeding colony where first-year breeders can find a territory? There are apparently territorial sites more optimal, more desirable, than others. Do the gulls themselves recognize these degrees of optimality?

Drost, Focke, and Freytag (1961) claimed that a considerable number of young Herring Gulls select their prospective breeding ground prior to sexual maturity. They went on to say that first-time breeders establish territories later in the season than the older birds and have a lower reproductive success.

Tinbergen (1961: 127-128) dealt with the selection of territory in nebulous terms. Fordham (1964a: 11, 18) was somewhat more explicit. He stated that it "seems likely" that the male Southern Black-backed Gull takes the initiative in choosing the actual nest site. Fordham then gave nest-site preferences by percentage of nests within a particular habitat.

The only other quantitative data found in the literature dealing with nest-site location of gulls is that of Reichle's (1969) study on the Great Black-backed Gull. He utilized four parameters in an attempt to establish what are preferential nest-site locations. These parameters were: distance from shore line (mean high water), height above sea

level, habitat type, and substrate. Reichle concluded, "Black-backs generally occupied a nest site well away from wave action and in a relatively high place that afforded good visibility . . . usually did not nest in woody vegetation . . . [nests] were not built on solid rock outcrops" (p. 79).

If the New England Black-back population continues to grow at its present rate of doubling every 12 to 15 years (Kadlec and Drury, 1968: 671), the Black-back will have to start compromising its nesting habitat preferences, as, no doubt, the now larger Herring Gull population had to do some time ago.

Klopfer and Hailman (1965: 295) in writing about habitat selection in gulls claimed that, "The development of the original perception which led to the selection of . . . possible sites from all other places in the colony remains obscure."

## Mate and Territory Fidelity

Mates and territories may change from one breeding season to the next. The reasons for these changes are probably many. A male Herring Gull may have paired with a different female in 1969 than he had in 1967 and 1968 only because the first mate died between the '68 and '69 breeding seasons. One mate or the other may have moved to a new territory and as a result, paired with the bird presenting

itself on that territory.

Coulson (1966) found in his study on the Kittiwake (Rissa tridactyla) that birds which changed their mates were, on the average, 13 per cent less successful in reproduction than those birds which retained their mate. The reason for this, he suggested, was "that birds in a newly formed pair are less well adjusted to each other, that they do not stimulate each other to as high a level of reproductive drive and that they cannot coordinate their incubation pattern as well as a long-established pair" (p. 275). Failure to hatch the eggs was practically the sole cause for this difference in breeding success. Coulson further showed that on the average, 0.39 fewer young were produced by birds which changed their mate since the previous breeding season than by those birds which retained the same pair. "It is suggested that there is a marked selective value in retaining the same mate . . . but that in incompatible pairs (which fail to hatch their eggs) there is more advantage in changing mates as by so doing they are more likely to breed successfully" (p. 279).

Since production was followed in Study Areas 1 and 2 for only 1968 and 1969, there is insufficient data to establish firmly what effect a new pairing had on breeding success in this study. Even though the sample size is small, my results for Herring Gulls (Table 2) tend to agree with Coulson's findings for the Kittiwake. The difference in reproductive success between newly paired birds and pairs which have been together for more than two years is best

illustrated from data collected in SA1 where the sample size was larger than that for SA2. SA2 is illustrative of an area in which there was a heavy concentration of Black-backed Gull nests. In this instance, it is possible that whether a Herring Gull pair was newly formed or long-established had little bearing on a pair's reproductive success.

Why gulls change territories can only be hypothesized. Observations would indicate that the increasing nesting density of the dominant Black-back causes Herring Gulls to shift their territories. An increasing Herring Gull population also makes the competition keen for territorial space.

Drost et al. (1961) showed that some mature adult Herring Gulls failed to breed for one or more breeding seasons. Kadlec and Drury (1968: 651-652) concluded that "in the Boston area, 15 to 30% of the adult [Herring Gull] population is not breeding. This may be due to 'taking a year off' . . . age (Drost et al. 1961, Coulson 1966), inadequate motivation, or exclusion from territories on the islands." A gull returning to its territory of two years ago following a year's absence will oftentimes find that territory occupied. The territory may be occupied by a second-year breeder or by a bird which had not been mated for a year -- in any case, by another bird which had occupied the territory during the returning gull's absence. If this should happen, one of three things may occur. The old territory holder will: move to a new territory (presumably there

should be territories available since other breeding birds take time off); dispossess the new occupant; or a stalemate will prevent either bird from breeding successfully.

Perhaps some gulls may be more fickle than others in their nest-site location. One bird had three different territories in three successive years for no obvious reasons. The nine changes in SA2 noted in 1968 that involved territories with a grassy substrate may be attributable to the fact that there are, to human eyes, less obvious lines of demarcation for territorial boundaries in grassy areas than rocky areas.

## Incubation

Hypothetically, it would appear from my observations that the female that lays her clutch of eggs in the shortest period of elapsed time has a better chance of higher reproductive success. The closer (in time) one egg is laid to its predecessor, the shorter the transition period will be from incubation to brooding behavior after the number-one egg is hatched, and the greater chance the number-two and -three eggs have of hatching. Also, the closer together the eggs hatch, the less time the number-one chick has to gain an edge on its siblings in size and mobility, especially on the number-three chick. The time required for laying may depend to some degree upon how well established the pair-bond

is and upon the breeding experience of any given pair (Coulson, 1966).

## Defense and Predation of the Young

What made defense of territory or young unquantifiable were the ramifications involved in leading up to a defensive act. There is no ready explanation for the differences shown by individual birds in their defensive capabilities. The defensive attitude of any one gull may be related to the aggressiveness of its neighbors, which in turn may be directly related to nesting density. If a particular bird's neighbors were relatively unaggressive, then that one gull's defensive abilities would never be elicited.

During the summer of 1968 Black-backed Gull predation was observed on Herring Gull chicks. Until then, predation by other gulls was considered to be minimal, presumably because of an abundant food supply made available by man's effluent (Bergman, 1965: 61-62, 64-65; Kadlec et al., 1969: 231).

The amount of chick predation for which there was evidence probably was a function of several things, one factor being nesting density and another being the intensity of my observations. It is logical to assume that as both the Herring and Black-backed Gull populations increase, so will the nesting density grow, with a resulting decrease in territory size. However, as Huxley (1934: 277) stated,

"Territories are . . . partially compressible, but their compressibility is not complete. They are like elastic discs, of which there is a lower as well as a higher number which can be placed together to cover a given area." This is what appears to be happening on Milk Island. The nesting density, at least among the Black-backs, has increased over the last couple of years, and the areas of the territories have been decreasing. As a result, there is a strong resistance building up to the point where the territory sizes will reach (have reached?) a certain size and stop. It appears that the Herring Gulls may have reached this equilibrium. Consequently, both the Herring Gulls and the Black-backs are experiencing a density pressure; the Black-backs more so since they normally have a larger territory than do the Herring Gulls. With more nests per unit area, there are more chicks wandering outside their smaller territories, and, subsequently, more chicks are lost to predation.

When parents attempt to protect young that wander out of their territory, conflicts arise with other adults. When the other territorial adult is a Great Black-backed Gull, the Herring Gull usually has difficulty defending its young owing to the disparity in size and strength. However, in a previous study, the unmolested transit of a Herring Gull chick through a Black-back's territory was seen (pers. obs.). The chick's successful crossing was due only to the

highly aggressive and protective attitude of its parent. This was an unusual case.

Fordham (1964b: 113-114) in his Southern Black-backed Gull study found a positive correlation between egg losses and nesting density. Egg losses were caused primarily by predation of neighboring gulls whose effect was accentuated when nests were close together. It would appear that this correlation applies to chick loss also.

Blouch's study on the effect of Great Black-backed Gulls nesting adjacently to Herring Gulls suggested a positive correlation between chicks produced and distance between nests. The production figures of 0.70 and 0.75 chicks per nest in the short grass and rocks are close to the production figures of SA2, 0.52 and 0.74 chicks per nest (Table 4), in which there was a large population of Black-backs. His work lends support to my conclusion that Black-backs do reduce the reproductive success of Herring Gulls.

## Significant Variables

Of the several variables considered, brooding intensity, frequency of feeding, and cover are the most significantly related to the variability in the number of chicks produced. It is evident from the analyses of the data presented that the frequency with which adults feed their young is positively correlated ($P < 0.01$) with the number of

chicks produced. The cover available to the chicks within their territories for hiding places clearly plays an important part in a particular area's production figures. Brooding intensity is related to almost 13 per cent of the variability in chick numbers in SA2, but is insignificant in SA1 where cover is most important (Table 12). This indicates, looking at the production figures in Table 4, that the cover variable is more significant than brooding intensity. The figures in Table 12 for SA1+2 support this premise.

The fact that brooding intensity and the number of chicks produced are less significantly correlated in SA1 than in SA2 is attributable to the greater amount of brooding that was seen in SA2. Better cover available in SA1 precluded any extended brooding of chicks.

The correlation coefficient for the cover variable was highly significant in SA1 due to the number of good hiding places for chicks. However, in SA2, cover showed no correlation with chick production due to the lack of cover; i.e., there was little, if any, contribution (positively or negatively) to the number of chicks produced.

One variable not included in any of the statistical analyses and one which was important as an indirect chick mortality factor, is that of human disturbance. This variable may be related to that of cover. A human's

presence will cause chicks in insecure hiding places to run from their territories into areas with more adequate hiding places. The intrusion of a human being or the close presence of a Black-back were the only stimuli which elicited alarm in the parents and subsequent hiding of the chicks. If there were sufficient hiding places, chicks would not leave their territories with the approach of a human. This would in turn decrease the amount of predation resulting from chicks straying into alien territories enroute back to their own after the alarm was over. Except for those Black-backs mentioned, which actively sought out chicks in their hiding places, most of the predation resulted from the chick being out of its home territory -- opportunistic predation. Therefore, Black-back predation of Herring Gull chicks and human disturbance are closely related.

Human presence in a gull colony must be considered a natural independent variable which contributes considerably to the variability in the number of chicks produced. To be able to quantify to what extent this variable does influence the number of chicks produced would be most difficult.

The final reproductive outcome, to a large degree, can be attributed to the selection of territory by the adult gulls. The territories with the best hiding places for chicks provide good conditions for high reproductive success.

Frequency of feeding, the most significant of the variables when the two study areas were combined, would

logically be an important factor in the successful reproduction of Herring Gull young. This becomes all the more evident when Figure 4 is taken into account. Although the sample size is small, the figure shows a preliminary indication of a highly significant positive correlation between frequency of feeding by known pairs of gulls and the totaled average daily weight gains of these pairs' respective broods. Since all these birds presumably have the same food sources available to them, a parent's ability to bring its young adequate food becomes an individual matter. There were some pairs which apparently fed their chicks more often than others with better results.

The behavioral and physical variables that have been considered were those thought to be the most important in the reproductive success of a pair of Herring Gulls. Further study on the effects of environmental variables, particularly nest site location, would be valuable.

The question, "Are there good gull parents and poor gull parents?" has not been answered with a definitive "Yes" or "No." There are differences in behavior between known pairs of gulls; but, the inconstancy of some of these differences over the 316.5 hours of observations does not permit an unequivocal answer.

## SUMMARY

The parental behavior of a number of banded breeding adult Herring Gulls was observed during the breeding seasons of 1968 and 1969 on Milk Island, Cape Ann, Massachusetts. Of particular interest was the behavior of banded breeding pairs, and whether or not these pairs were inefficient as parents. If so, did these pairs, if sustained over a period of years, continue to be inefficient in the ensuing years?

The reproductive success of birds within study areas of varying substrate was followed. Behavioral observations were made from two blinds over a period of 316.5 hours. Particular behavior observed was brooding intensity, frequency of feeding, and territory attentiveness. Other factors noted were weather conditions, time of day, whether or not a Herring Gull territory was adjacent to that of a Great Black-backed Gull, the cover in a territory available to chicks, and the number of chicks within each territory during a given observation period. Chicks of known Herring Gull pairs were weighed and these data were correlated with frequency of feeding data.

It was found that Herring Gulls did not always return to the same territory from year to year and that pair fidelity was incomplete. The data suggest that prolonged mating of a pair resulted in increased reproductive

success. Pairs mated for at least two years (1968) and then three years (1969) produced 1.27 chicks per nest, while birds (age unknown) mated for the first time successfully reared 0.48 chicks per nest.

The incubation period for three-egg clutches was an average of 26.9 days from a sample of 60 Herring Gull nests. Brooding of the young was rarely done past six days of age.

Data concerning the frequency of feeding and the cover available to chicks were highly significant in their relation to the number of chicks produced by any given pair of gulls. A sample regression of total sibling mean daily increase in weight on frequency of feeding yielded a sample correlation coefficient of 0.922.

Great Black-backed Gulls had a marked effect on the reproductive success of Herring Gulls if the Herring Gull chicks did not have adequate cover in an alarm situation; e.g., when humans were in the vicinity. The chicks left those territories in which there was poor cover, presumably in search for better cover, and in many instances did not return because they were lost and/or were preyed upon by Black-backs.

The question, "Are there good gull parents and poor gull parents?" was not answered definitively. There were differences in behavior between known pairs of gulls; but, the inconstancy of some of these differences during two breeding seasons of observations did not permit an unequivocal answer.

# APPENDICES

# APPENDIX I

## CORRELATION MATRIX WITH ITEM DELETION
(Sample sizes in parentheses)

**Variables**

| | | |
|---|---|---|
| 4-Number of chicks | 9-Feeding freq. | 14-Air temperature |
| 5-Chick age | 10-Food quan. | 15-Time of day |
| 6-Brooding-incubating inten. | 11-Food qual. | 16-Terr. attentiveness |
| 7-Brooding intensity | 12-Cloud cover | 17-Cover |
| 8-Defense | 13-Precipitation | 18-Adjacent Black-back |

STUDY AREA 1

| | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|
| 4 | 1.000 (180) | -0.203 (180) | -0.072 (180) | 0.146 (180) | 0.279 (84) | 0.195 (179) | 0.191 (142) | 0.303 (73) |
| 5 | | 1.000 (180) | -0.328 (180) | -0.445 (180) | -0.260 (84) | -0.220 (179) | -0.226 (142) | -0.379 (73) |
| 6 | | | 1.000 (180) | 0.056 (180) | -0.145 (84) | 0.030 (179) | 0.185 (142) | 0.256 (73) |
| 7 | | | | 1.000 (180) | 0.033 (84) | 0.198 (179) | 0.244 (142) | 0.408 (73) |
| 8 | | | | | 1.000 (84) | 0.227 (83) | 0.287 (82) | 0.316 (51) |
| 9 | | | | | | 1.000 (179) | 0.798 (141) | 0.753 (72) |
| 10 | | | | | | | 1.000 (142) | 0.878 (73) |
| 11 | | | | | | | | 1.000 (73) |

| | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|
| 4 | -0.201 (180) | 0.047 (180) | -0.077 (172) | -0.001 (180) | -0.169 (180) | 0.241 (180) | 0.061 (180) |
| 5 | 0.324 (180) | -0.080 (180) | 0.180 (172) | -0.348 (180) | -0.171 (180) | -0.040 (180) | -0.012 (180) |
| 6 | -0.142 (180) | -0.046 (180) | -0.020 (172) | -0.067 (180) | 0.080 (180) | 0.121 (180) | 0.084 (180) |
| 7 | -0.085 (180) | 0.109 (180) | -0.042 (172) | -0.047 (180) | 0.077 (180) | 0.104 (180) | 0.154 (180) |
| 8 | -0.132 (84) | 0.154 (84) | 0.101 (84) | 0.122 (84) | 0.051 (84) | 0.008 (84) | 0.230 (84) |
| 9 | -0.066 (179) | 0.192 (179) | -0.087 (171) | -0.152 (179) | -0.117 (179) | -0.012 (179) | 0.085 (179) |
| 10 | -0.007 (142) | 0.171 (142) | -0.095 (139) | -0.194 (142) | -0.130 (142) | 0.100 (142) | 0.088 (142) |
| 11 | -0.199 (73) | 0.285 (73) | 0.003 (73) | -0.168 (73) | -0.104 (73) | 0.156 (73) | 0.182 (73) |

(cont'd.)

APPENDIX I (cont'd.)

| | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|
| 12 | 1.000 (180) | 0.412 (180) | -0.633 (172) | -0.201 (180) | -0.024 (180) | -0.059 (180) | -0.077 (180) |
| 13 | | 1.000 (180) | -0.355 (172) | -0.115 (180) | -0.001 (180) | 0.020 (180) | 0.008 (180) |
| 14 | | | 1.000 (172) | -0.090 (172) | -0.043 (172) | 0.004 (172) | 0.076 (172) |
| 15 | | | | 1.000 (180) | 0.263 (180) | 0.068 (180) | -0.083 (180) |
| 16 | | | | | 1.000 (180) | -0.004 (180) | -0.292 (180) |
| 17 | | | | | | 1.000 (180) | 0.001 (180) |
| 18 | | | | | | | 1.000 (180) |

STUDY AREA 2

| | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|
| 4 | 1.000 (92) | -0.229 (92) | -0.222 (92) | 0.348 (92) | 0.261 (51) | 0.367 (92) | 0.198 (92) | 0.344 (40) |
| 5 | | 1.000 (92) | -0.413 (92) | -0.462 (92) | 0.399 (51) | -0.033 (92) | 0.045 (92) | -0.138 (40) |
| 6 | | | 1.000 (92) | -0.086 (92) | -0.307 (51) | -0.190 (92) | -0.206 (92) | -0.201 (40) |
| 7 | | | | 1.000 (92) | -0.296 (51) | 0.017 (92) | 0.009 (92) | 0.094 (40) |
| 8 | | | | | 1.000 (51) | 0.311 (51) | 0.312 (51) | 0.320 (51) |
| 9 | | | | | | 1.000 (92) | 0.819 (92) | 0.733 (40) |
| 10 | | | | | | | 1.000 (92) | 0.866 (40) |
| 11 | | | | | | | | 1.000 (40) |

| | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|
| 4 | -0.115 (92) | 0.015 (92) | -0.268 (91) | -0.075 (92) | -0.159 (92) | 0.155 (92) | 0.075 (92) |
| 5 | 0.026 (92) | -0.296 (92) | 0.262 (91) | 0.264 (92) | -0.011 (92) | -0.354 (92) | 0.105 (92) |
| 6 | 0.096 (92) | 0.138 (92) | -0.103 (91) | -0.177 (92) | -0.005 (92) | 0.350 (92) | -0.056 (92) |
| 7 | 0.207 (92) | 0.367 (92) | -0.268 (91) | -0.058 (92) | -0.007 (92) | 0.207 (92) | -0.042 (92) |
| 8 | -0.100 (51) | -0.054 (51) | 0.007 (51) | -0.045 (51) | -0.171 (51) | -0.278 (51) | 0.351 (51) |

(cont'd.)

APPENDIX I (cont'd.)

| | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|
| 9 | 0.005 (92) | 0.099 (92) | -0.230 (91) | -0.100 (92) | -0.106 (92) | -0.024 (92) | 0.229 (92) |
| 10 | 0.056 (92) | 0.114 (92) | -0.111 (91) | -0.014 (92) | -0.126 (92) | -0.035 (92) | 0.186 (92) |
| 11 | -0.060 (40) | 0.106 (40) | -0.245 (40) | -0.206 (40) | -0.138 (40) | -0.126 (40) | 0.195 (40) |
| 12 | 1.000 (92) | 0.637 (92) | -0.391 (91) | 0.044 (92) | -0.067 (92) | -0.009 (92) | -0.085 (92) |
| 13 | | 1.000 (92) | -0.468 (91) | -0.161 (92) | -0.115 (92) | 0.054 (92) | -0.091 (92) |
| 14 | | | 1.000 (91) | 0.336 (91) | 0.137 (91) | -0.141 (91) | 0.056 (91) |
| 15 | | | | 1.000 (92) | -0.071 (92) | -0.070 (92) | 0.006 (92) |
| 16 | | | | | 1.000 (92) | -0.058 (92) | -0.126 (92) |
| 17 | | | | | | 1.000 (92) | -0.091 (92) |
| 18 | | | | | | | 1.000 (92) |

STUDY AREAS 1 + 2

| | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|
| 4 | 1.000 (272) | -0.210 (272) | -0.151 (272) | 0.220 (272) | 0.145 (135) | 0.256 (271) | 0.171 (234) | 0.334 (113) |
| 5 | | 1.000 (272) | -0.360 (272) | -0.443 (272) | -0.010 (135) | -0.148 (271) | -0.109 (234) | -0.294 (113) |
| 6 | | | 1.000 (272) | -0.006 (272) | -0.187 (135) | -0.066 (271) | -0.009 (234) | 0.020 (113) |
| 7 | | | | 1.000 (272) | -0.106 (135) | 0.119 (271) | 0.125 (234) | 0.247 (113) |
| 8 | | | | | 1.000 (135) | 0.254 (134) | 0.307 (133) | 0.237 (81) |
| 9 | | | | | | 1.000 (271) | 0.807 (233) | 0.733 (112) |
| 10 | | | | | | | 1.000 (234) | 0.859 (113) |
| 11 | | | | | | | | 1.000 (113) |

(cont'd.)

APPENDIX I (cont'd.)

| | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|
| 4 | -0.178 | 0.012 | -0.156 | 0.009 | -0.163 | 0.233 | 0.030 |
| | (272) | (272) | (263) | (272) | (272) | (272) | (272) |
| 5 | 0.210 | -0.162 | 0.211 | -0.141 | -0.073 | -0.133 | 0.032 |
| | (272) | (272) | (263) | (272) | (272) | (272) | (272) |
| 6 | -0.022 | 0.056 | -0.055 | -0.130 | 0.034 | 0.135 | 0.040 |
| | (272) | (272) | (263) | (272) | (272) | (272) | (272) |
| 7 | 0.063 | 0.247 | -0.141 | -0.085 | 0.035 | 0.048 | 0.090 |
| | (272) | (272) | (263) | (272) | (272) | (272) | (272) |
| 8 | -0.020 | 0.099 | 0.045 | 0.023 | -0.040 | -0.257 | 0.318 |
| | (135) | (135) | (135) | (135) | (135) | (135) | (135) |
| 9 | -0.030 | 0.162 | -0.144 | -0.145 | -0.095 | -0.052 | 0.161 |
| | (271) | (271) | (262) | (271) | (271) | (271) | (271) |
| 10 | 0.037 | 0.161 | -0.104 | -0.144 | -0.104 | -0.048 | 0.162 |
| | (234) | (234) | (230) | (234) | (234) | (234) | (234) |
| 11 | -0.174 | 0.195 | -0.079 | -0.144 | -0.122 | 0.105 | 0.150 |
| | (113) | (113) | (111) | (113) | (113) | (113) | (113) |
| 12 | 1.000 | 0.510 | -0.533 | -0.145 | -0.033 | -0.096 | -0.045 |
| | (272) | (272) | (263) | (272) | (272) | (272) | (272) |
| 13 | | 1.000 | -0.392 | -0.172 | -0.045 | -0.073 | 0.014 |
| | | (272) | (263) | (272) | (272) | (272) | (272) |
| 14 | | | 1.000 | 0.047 | 0.061 | -0.060 | 0.070 |
| | | | (263) | (263) | (263) | (263) | (263) |
| 15 | | | | 1.000 | 0.041 | 0.176 | -0.123 |
| | | | | (272) | (272) | (272) | (272) |
| 16 | | | | | 1.000 | -0.092 | -0.141 |
| | | | | | (272) | (272) | (272) |
| 17 | | | | | | 1.000 | -0.195 |
| | | | | | | (272) | (272) |
| 18 | | | | | | | 1.000 |
| | | | | | | | (272) |

# APPENDIX II

## STEPWISE MULTIPLE REGRESSION

### Summary Tables

Variables

| | | |
|---|---|---|
| 1-Number of chicks (Y) | 5-Feeding freq. | 9-Time of day |
| 2-Chick age | 6-Cloud cover | 10-Terr. attentive. |
| 3-Brooding-incubating inten. | 7-Precipitation | 11-Cover |
| 4-Brooding intensity | 8-Air temperature | 12-Adj. Black-back |

STUDY AREA 1 (Sample size = 171)

| Step No. | Variable Entered | Multiple Correlation Coefficient | Coefficient of Determination | F Value |
|---|---|---|---|---|
| 1 | 11 | 0.2529 | 0.0639 | 11.5456 |
| 2 | 5 | 0.3262 | 0.1064 | 7.9853 |
| 3 | 10 | 0.3630 | 0.1318 | 4.8742 |
| 4 | 2 | 0.3985 | 0.1588 | 5.3314 |
| 5 | 3 | 0.4280 | 0.1832 | 4.9294 |
| 6 | 6 | 0.4433 | 0.1965 | 2.7155 |
| 7 | 8 | 0.4783 | 0.2288 | 6.8259 |
| 8 | 9 | 0.4914 | 0.2415 | 2.7054 |
| 9 | 7 | 0.4936 | 0.2436 | 0.4609 |
| 10 | 4 | 0.4937 | 0.2437 | 0.0256 |
| 11 | 12 | 0.4938 | 0.2438 | 0.0126 |

STUDY AREA 2 (Sample size = 90)

| Step No. | Variable Entered | Multiple Correlation Coefficient | Coefficient of Determination | F Value |
|---|---|---|---|---|
| 1 | 4 | 0.3557 | 0.1265 | 12.7499 |
| 2 | 5 | 0.4853 | 0.2355 | 12.4030 |
| 3 | 6 | 0.5216 | 0.2721 | 4.3152 |
| 4 | 8 | 0.5471 | 0.2993 | 3.3069 |
| 5 | 3 | 0.5665 | 0.3209 | 2.6656 |
| 6 | 10 | 0.5837 | 0.3407 | 2.4917 |
| 7 | 2 | 0.5961 | 0.3554 | 1.8682 |
| 8 | 7 | 0.6054 | 0.3666 | 1.4320 |
| 9 | 11 | 0.6091 | 0.3710 | 0.5672 |
| 10 | 12 | 0.6100 | 0.3721 | 0.1418 |
| 11 | 9 | 0.6103 | 0.3725 | 0.0475 |

(cont'd.)

APPENDIX II (cont'd.)

STUDY AREAS 1 + 2 (Sample size = 261)

| Step No. | Variable Entered | Multiple Correlation Coefficient | Coefficient of Determination | F Value |
|---|---|---|---|---|
| 1 | 5 | 0.2493 | 0.0621 | 17.1627 |
| 2 | 11 | 0.3394 | 0.1152 | 15.4680 |
| 3 | 4 | 0.3843 | 0.1477 | 9.8036 |
| 4 | 3 | 0.4192 | 0.1757 | 8.7009 |
| 5 | 6 | 0.4451 | 0.1981 | 7.1130 |
| 6 | 8 | 0.4884 | 0.2385 | 13.4930 |
| 7 | 10 | 0.4940 | 0.2441 | 1.8500 |
| 8 | 2 | 0.4964 | 0.2464 | 0.7891 |
| 9 | 9 | 0.5001 | 0.2501 | 1.2378 |
| 10 | 12 | 0.5010 | 0.2510 | 0.3061 |
| 11 | 7 | 0.5011 | 0.2511 | 0.0070 |

## APPENDIX III

### STEPWISE MULTIPLE REGRESSION

**Correlation Matrix for Study Area 1**
(Sample size = 171)

**Variables**

1 - Number of chicks (Y)
2 - Chick age
3 - Brooding-incubating intensity
4 - Brooding intensity
5 - Frequency of feeding
6 - Cloud cover
7 - Precipitation
8 - Air temperature
9 - Time of day
10 - Territorial attentiveness
11 - Cover
12 - Adjacent Black-back

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1.000 | -0.183 | -0.066 | 0.139 | 0.202 | -0.173 | 0.065 | -0.079 | -0.031 | -0.184 | 0.253 | 0.077 |
| 2 | | 1.000 | -0.347 | -0.454 | -0.226 | 0.289 | -0.107 | 0.180 | -0.321 | -0.160 | -0.036 | -0.033 |
| 3 | | | 1.000 | 0.058 | 0.032 | -0.162 | -0.053 | -0.019 | -0.057 | 0.085 | 0.125 | 0.079 |
| 4 | | | | 1.000 | 0.201 | -0.085 | 0.114 | -0.041 | -0.052 | 0.078 | 0.095 | 0.159 |
| 5 | | | | | 1.000 | -0.062 | 0.201 | -0.087 | -0.164 | -0.121 | -0.015 | 0.090 |
| 6 | | | | | | 1.000 | 0.397 | -0.634 | -0.155 | -0.003 | -0.059 | -0.108 |
| 7 | | | | | | | 1.000 | -0.355 | -0.093 | 0.009 | 0.022 | -0.004 |
| 8 | | | | | | | | 1.000 | -0.092 | -0.043 | 0.005 | 0.077 |
| 9 | | | | | | | | | 1.000 | 0.253 | 0.069 | -0.064 |
| 10 | | | | | | | | | | 1.000 | -0.005 | -0.286 |
| 11 | | | | | | | | | | | 1.000 | 0.002 |
| 12 | | | | | | | | | | | | 1.000 |

(cont'd.)

APPENDIX III (cont'd.)

STEPWISE MULTIPLE REGRESSION

Correlation Matrix for Study Area 2
(Sample size = 90)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1.000 | -0.223 | -0.235 | 0.356 | 0.338 | -0.107 | 0.005 | -0.243 | -0.118 | 0.210 | 0.111 | 0.042 |
| 2 | | 1.000 | -0.421 | -0.473 | -0.010 | 0.010 | -0.311 | 0.265 | 0.284 | -0.040 | -0.342 | 0.123 |
| 3 | | | 1.000 | -0.090 | -0.192 | 0.092 | 0.134 | -0.099 | -0.179 | 0.088 | 0.361 | -0.056 |
| 4 | | | | 1.000 | 0.021 | 0.203 | 0.362 | -0.264 | -0.059 | 0.127 | 0.215 | -0.040 |
| 5 | | | | | 1.000 | 0.030 | 0.109 | -0.217 | -0.136 | 0.003 | -0.076 | 0.203 |
| 6 | | | | | | 1.000 | 0.635 | -0.393 | 0.058 | -0.177 | 0.014 | -0.071 |
| 7 | | | | | | | 1.000 | -0.462 | -0.164 | -0.112 | 0.061 | -0.090 |
| 8 | | | | | | | | 1.000 | 0.357 | -0.004 | -0.126 | 0.069 |
| 9 | | | | | | | | | 1.000 | 0.088 | -0.106 | -0.017 |
| 10 | | | | | | | | | | 1.000 | 0.187 | -0.139 |
| 11 | | | | | | | | | | | 1.000 | -0.129 |
| 12 | | | | | | | | | | | | 1.000 |

(cont'd.)

APPENDIX III (cont'd.)

STEPWISE MULTIPLE REGRESSION

Correlation Matrix for Study Areas 1 + 2
(Sample size = 261)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1.000 | -0.194 | -0.151 | 0.221 | 0.249 | -0.154 | 0.023 | -0.144 | -0.031 | -0.064 | 0.212 | 0.032 |
| 2 | | 1.000 | -0.376 | -0.455 | -0.142 | 0.178 | -0.188 | 0.212 | -0.112 | -0.124 | -0.119 | 0.025 |
| 3 | | | 1.000 | -0.007 | -0.066 | -0.036 | 0.050 | -0.054 | -0.124 | 0.089 | 0.141 | 0.037 |
| 4 | | | | 1.000 | 0.122 | 0.062 | 0.248 | -0.139 | -0.087 | 0.101 | 0.043 | 0.092 |
| 5 | | | | | 1.000 | -0.018 | 0.171 | -0.139 | -0.164 | -0.074 | -0.072 | 0.152 |
| 6 | | | | | | 1.000 | 0.500 | -0.535 | -0.103 | -0.050 | -0.077 | -0.063 |
| 7 | | | | | | | 1.000 | -0.390 | -0.155 | -0.018 | -0.067 | 0.005 |
| 8 | | | | | | | | 1.000 | 0.054 | -0.030 | -0.049 | 0.074 |
| 9 | | | | | | | | | 1.000 | 0.182 | 0.155 | -0.111 |
| 10 | | | | | | | | | | 1.000 | 0.008 | -0.200 |
| 11 | | | | | | | | | | | 1.000 | -0.203 |
| 12 | | | | | | | | | | | | 1.000 |

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