THE UNIVERSITY OF MANITOBA

REPRODUCTIVE SUCCESS AND BEHAVIOUR IN HERRING GULLS BREEDING IN ADJACENT CLIFF AND FLAT HABITATS

by
BRIAN KNUDSEN

A thesis
submitted to the Faculty of Graduate Studies
in partial fulfillment of the requirements for the
degree of Doctor of Philosophy

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ABSTRACT

A study was conducted from 1977 to 1979 on herring gulls (Larus argentatus) nesting on cliffs and flatland at Kent Island, New Brunswick, Canada. Previous studies had indicated that nesting on cliffs required specialization.

Overall reproductive success was not significantly different between cliff and flat areas: in both areas 20% of the eggs laid survived to the end of the period of high chick mortality. Within and between habitats there was considerable spatial and temporal heterogenity in mortality of chicks and eggs. Infanticide and cannibalism appeared to be much more important than cliff-related causes of death in chicks. It was concluded that reproductive success in herring gull colonies is less dependent on the general type of habitat than on factors such as the ability of parents to protect their chicks from attack, the density of neighbouring nests, and the degree to which nesting territories expose chicks to attacks by gulls.

To measure the importance of vocal communication in chick survival, chicks were tested for their ability to respond selectively to their parents' vocalizations. Chicks were placed in cloth-covered cages and their responses noted to their parents' and strangers' "mew" calls, which usually precede the feeding of chicks. Significantly more chicks responded to their parents' calls than to strangers' calls, demonstrating an ability by the chicks to recognize their parents' calls.

Simulations of patterns of chick mortality were conducted under varying conditions of density and predation by neighbours. These simulations revealed that when nesting densities become high, and when feeding opportunities near the colony favour preying on chicks, survival rates of chicks become extremely variable. This variability is caused by the positive feedback nature of chain-reaction cannibalism in gull colonies. Flatland and cliff nests would not be affected differentially by this process.

Studies of breeding biology in gulls could benefit from early consideration of the potentially confounding effect of patchy mortality on results.

The robust reproductive strategy of herring gulls appears to centre on protecting chicks and controlling their movements, regardless of whether the greatest threats to survival of chicks are cliffs or predatory neighbours.

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Brad Johnson scrutinized the programming of the computer simulation, tested the adequacy of random number generators, speeded up some procedures, found an error of mine which would have been extremely embarassing, and generally set an example of how to do a careful job of programming. The importance of all this should be obvious.

Ken Lertzman was a good friend and valuable assistant in the summer of 1977. I appreciate his hard work and useful comments during field work.

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GENERAL INTRODUCTION

In the late nineteenth century, the herring gull (Larus argentatus) was a rare bird along the eastern coast of North America (Sturtevant pers. comm. in Kadlec and Drury 1968). Since that time, the herring gull population of this area has increased dramatically, doubling every 12 to 15 years between 1900 and 1970 (Kadlec and Drury 1968, 1969; Drury and Kadlec 1974; Kadlec 1976). The breeding component of the population increased from less than 10,000 to more than 100,000 in 65 years (Kadlec and Drury 1968).

The increase in abundance of herring gulls occurred in three ways. The range of the species expanded (Hailman 1963; Parnell and Soots 1975). Existing colonies became larger (Kadlec and Drury 1968; Drury and Kadlec 1974). New colonies became established within the old range of the species (Kadlec and Drury 1968; Bongiorno and Swinebrod 1969). Similar increases occurred in other locations (Andersson 1970; Harris 1970; Chabrzyk and Coulson 1976; Davis and Dunn 1976) suggesting that the increase in numbers during this century is representative of the entire species, rather than of one population.

These data indicate that the herring gull is a successful species. Doubtless many factors contributed to the species' success, including opportunistic and catholic tastes in food (Harris 1965; Ashmole 1971; Davis 1975b). Another is the ability to nest in large colonies (Paynter 1949; Brown 1967), in small colonies (Ingolfsson 1970; Burger 1977), and solitarily (Bent 1921; Godfrey 1966; Salt and Wilk 1966; Jehl and Smith 1970). Of special interest in this thesis, however, is the capacity of the species to nest in many habitats. The best-known breeding habitat for the herring gull is probably the one in which Tinbergen (1953) did so much work: partially vegetated coastal dunes. However, herring gulls also nest successfully in habitats such as mixed vegetation along coastlines and on islands (Noseworthy and Lien 1976; Burger 1977), salt marshes (Burger 1977), coastal cliffs (Macpherson 1961; McLannahan 1973; Andrle 1976), islands in the Great Lakes (Godfrey 1966), islands in prairie lakes (Thompson 1891), boulders in tundra ponds (Macpherson 1961; Godfrey 1966; Jehl and Smith 1970), islands in salt water (Paynter 1949; Davis 1975a; Noseworthy and Lien 1976), along flowing water in boreal forests (Erskine 1977), and even trees (Bent 1921). The use of these habitats can be measured in decades.

One aspect of this list of breeding habitats is inconsistent with available theories and data: nesting on cliffs. From 1957 to 1975 several investigators attempted to describe the morphological and behavioural adaptations of certain species to nesting on the ledges of cliffs (Cullen 1957, Emlen 1963, Hailman 1965, Snow and Snow 1967, Hailman 1968, McLannahan 1973, Hodges 1974, Burtt 1975). Cullen gave the impression that there was very little variation among birds in their behavioural adaptations to cliff-nesting. All of the black-legged kittiwakes (_Rissa_ _tridactyla_) she studied apparently chose small, relatively inaccessible ledges, recognized their own chicks late, if at all, handled their eggs carefully, and produced chicks that became mobile at an older age. Cullen wrote before it was commonplace to provide measures of variation in the frequency of occurrence of behavioural traits (_cf_. Chatfield and Lemon 1970; Altmann and Altmann 1977), so we have no direct measure of variation in her data. We can infer, from the lack of qualifying remarks in Cullen's paper, however, that the behaviour she observed was relatively stereotyped. The table in which she summarized differences between black-legged kittiwakes and ground-nesting gulls presents the two situations as contrasting almost perfectly.

In the light of this relative lack of variability, it appears that cliff-nesting, as practised by black-legged kittiwakes, is a precarious adaptive peak (Wright 1932). Implicitly, individuals that deviate from the optimal combination of behavioural and physiological characteristics are unlikely to reproduce successfully.

Other papers on the behaviour of cliff-nesting gulls (Hailman 1965, 1968; Maunder and Threlfall 1972; McLannahan 1973; Hodges 1974; Burtt 1975) qualitatively and quantitatively supported Cullen's thesis: nesting on cliffs requires a very particular collection of attributes, sharply defined for each species.

Could this set of cliff-nesting "skills" develop in some groups of cliff-nesting herring gulls through learning or colony-specific selection? Probably not, for although Emlen (1963) and McLannahan (1973) reported that herring gull chicks learned to avoid cliff edges, their experiments dealt with only one item in Cullen's long list of cliff-nesting adaptations. In order to develop genotypic specialization within colonies, gene flow between colonies would have to be restricted, and birds therefore would have to be extremely faithful in returning to their natal colonies to breed. There is, however, no evidence for strong fidelity to natal colonies. Ludwig (1963) found that 40% of the young surviving to fledging did not breed in their natal colonies. Chabrzyk and Coulson (1976) estimated that 65% of the surviving young did not return to their natal colony, and concluded that there "appears to be no liklihood that herring gull colonies consist of inbreeding groups; there is clearly too much interchange."

The above data create a paradox: the herring gull apparently has no barriers to gene flow, yet it successfully uses a wide range of breeding habitats, including cliffs, which are commonly associated with extreme specialization.

The objective of this thesis was to resolve this paradox, by studying the breeding ecology of herring gulls that nest on cliffs and flatland on Kent Island, New Brunswick. The first question I asked was whether herring gulls in fact are adapted to both habitats. In PART 1 of this thesis, I tested the null hypothesis that there were no differences in reproductive success between cliff and flatland nesting herring gulls on Kent Island.

During my study of survival patterns, questions arose regarding vocal communication between parents and chicks and how communication influenced the movements of chicks. It appeared that there would be a selective advantage associated with the early development of parent-young individual recognition. This had not been documented in herring gulls prior to this study, and its existence in this species has been questioned recently (Holley 1984). Examination of parent-young communication in general, and of individual recognition of vocalizations in particular, constitutes PART 2 of this thesis.

Another question which arose during the study of survival patterns of chicks was the importance of cannibalism and infanticide in herring gulls. Some studies (Davis and Dunn 1976, Burger 1984, Schoen and Morris 1984, this study) reported that these types of mortality occurred, occasionally creating large areas in which almost all chicks were killed. This mortality often occurred as a chain-reaction process, in which parents who lost all their chicks remained on territory and preyed on neighbouring chicks, creating more parents who had lost all their chicks, and more predation on chicks, and so on. I realized that these large patches of cannibalistic mortality, interesting in their own right, could be significant to this study if they were to affect cliff and flatland nesting herring gulls differentially. Because the patches were rare, it was difficult, if not impossible, to measure their effects directly in a statistically reliable manner. I therefore applied an indirect approach, using computer simulations to determine if the occurrence of these patches could be expected to influence significantly the overall reproductive success of herring gulls in either habitat. This simulation study is reported in PART 3 of this thesis.

PART 1: SURVIVAL PATTERNS OF HERRING GULL CHICKS ON CLIFFS AND FLATLAND

INTRODUCTION

As noted in the GENERAL INTRODUCTION, herring gulls have been reported to nest on cliffs and flatland, but no data have been published on relative reproductive success within these habitats in the same colony. I tested the null hypothesis that reproductive success is equal on cliffs and flatland. The paradigm existing before this study was that specialization was required for cliff-nesting. I therefore predicted the rejection of the null hypothesis, with greater reproductive success occurring on flatland. This prediction implies that gulls use both optimal and suboptimal habitat in the same region, an event already documented for several species (e.g. Krebs 1971; Robertson 1972), and linked with a number of aspects of biology, such as mating systems (e.g. Verner and Willson 1966).

To compare reproductive performance in cliff and flat areas, measuring only the contribution of the type of habitat, I required study areas that were significantly different in habitat but not significantly different regarding all other factors influencing reproductive success. The latter consideration is important because studies of the breeding biology of larids have shown that factors such as location within the colony (Coulson and Wooler 1976; Haymes and Blokpoel 1980; Pugesek 1983), timing of laying and hatching (Coulson and White 1961; Chardine and Morris 1983), number of eggs in the clutch (Harris 1964), and ages of breeding birds (Davis 1975a; Ryder 1975; Mills 1973), can cause differences in reproduction, survival, or both. In this chapter, I first tested to ensure that significant differences existed between study areas with respect to cliff and flat habitat characteristics. Then I ensured that no confounding significant differences occurred between habitats. Finally, I tested for equal reproductive success in these two habitats.

Supplementary to the analysis of reproductive success, I tested for differences in the nesting behaviour of gulls in both habitats, to determine whether herring gulls compensated for habitat differences by behaving differently at cliff and flatland nest sites.

METHODS

THE STUDY AREA

Location. Kent Island (44^{o} 35' N, 66^{o} 46' W), one of the three outermost islands in the Grand Manan Archipelago in Charlotte County, New Brunswick, is approximately 24 km west of the coast of Maine. The island is 2.82 km long, 0.17 - 0.80 km wide, and approximately 60 ha in area (McCain et al. 1973).

Different estimates of the number of pairs of herring gulls on the island have been reported: 15,000 pairs (Paynter 1949), 17,000 pairs (Pimlott 1952), 5,000 pairs (Cannell and Maddox 1983), and a series of unpublished aerial estimates, cited in Cannell and Maddox (1983), extending from 8,000 to 10,000 pairs. Although herring gulls nest almost everywhere on the island, at varying densities, most of the pairs are on the two hills, approximately 15 m high, on the southern end of the island. My study area was located on the southern exposure of one of these hills (Fig. 1).

I chose the study area because it included flatland (Figs. 2, 3) and cliffs (Fig. 4). Both were on the periphery of the colony. The study area had the additional advantage of being far from sources of disturbance which might seriously bias my data. The dock, and the buildings which housed about 10 people, were approximately 1.5 km north of the study area.

The flat area was relatively bare when the breeding season began (Fig. 2), but was covered by a dense growth of common

Fig. 1. Kent Island and vicinity.

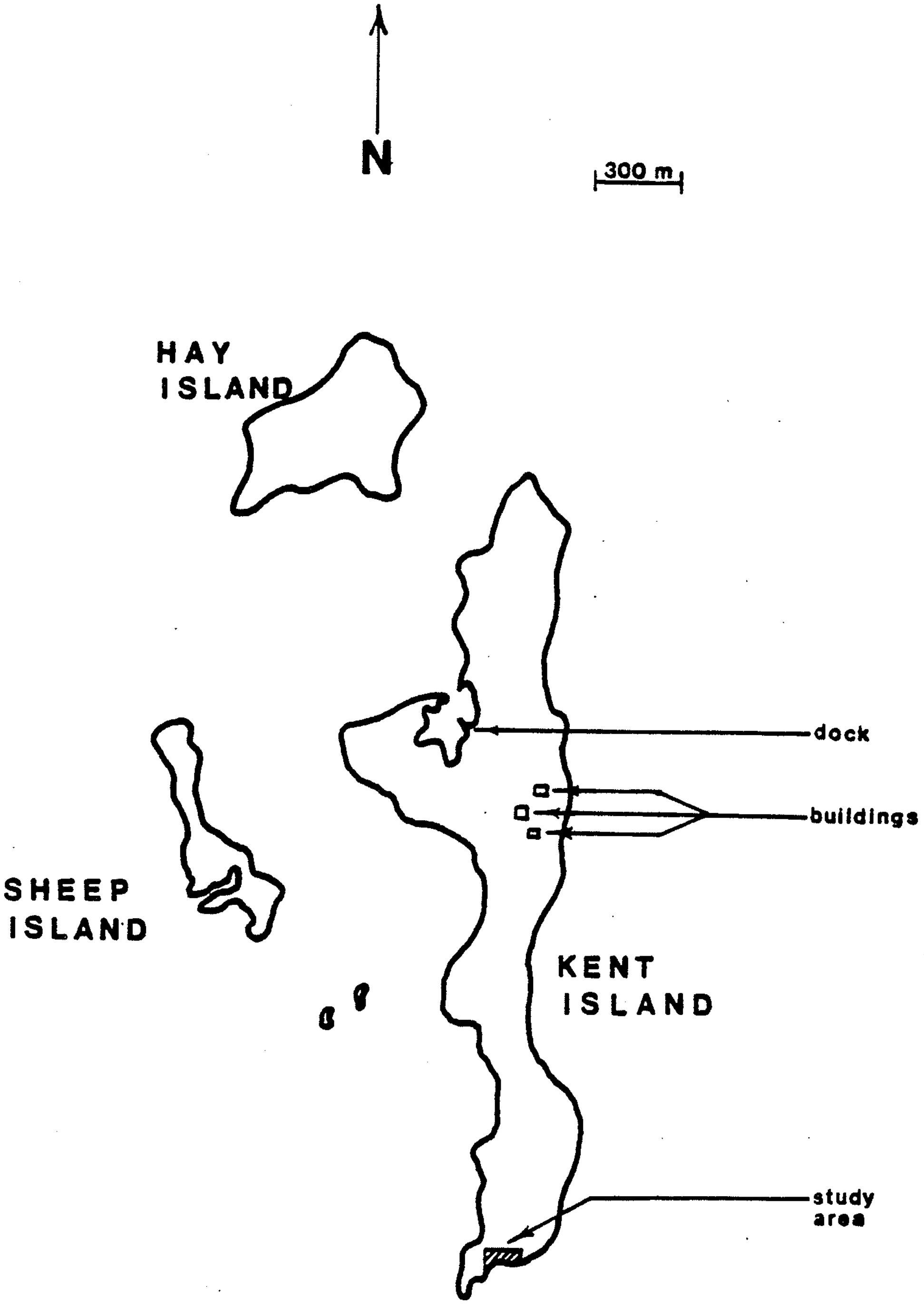
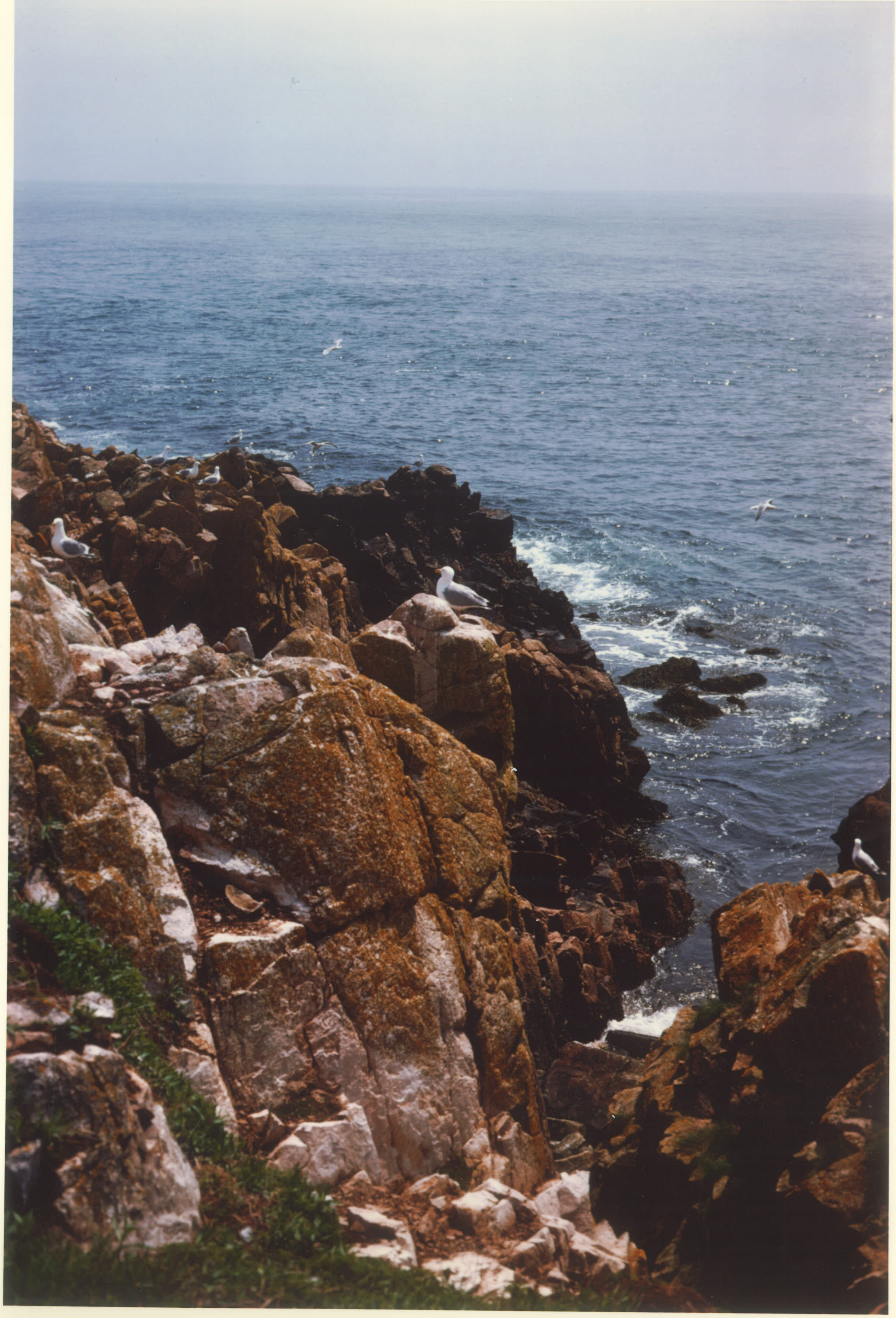

N
300 m
HAY ISLAND
SHEEP ISLAND
KENT ISLAND
dock
buildings
study area

Fig. 2. Part of the flatland study area at the time of nest initiation.

Fig. 3. Part of the flatland study area when chicks were present

Fig. 4. Part of the cliff study area.

13a



ragweed (*Ambrosia artemisiifolia*) by the time chicks were present (Fig. 3). In the cliff area vegetation was absent, but cracks and crevices were abundant.

Birds and Mammals. The herring gull is by far the most conspicuous animal on Kent Island. Leach's storm-petrel (*Oceanodroma leucorhoa*) is also extremely abundant, but seldom seen because it is nocturnal and nests in burrows. Other birds common on the island are common eider (*Somateria mollissima*), black guillemot (*Cepphus grylle*), great black-backed gull (*Larus marinus*), tree swallow (*Iridoprocne bicolor*), barn swallow (*Hirundo rustica*) and savannah sparrow (*Passerculus sandwichensis*). Only two of these species, the great black-backed gull and the common eider, interact with herring gulls to any significant degree. Approximately 50 pairs of great black-backed gulls nested on Kent Island, with approximately 10 pairs 100 - 200 m north of my study area. These gulls prey on herring gull chicks (Paynter 1949). Common eider ducklings are preyed upon by herring gulls. The only species of mammals on the island were the snowshoe hare (*Lepus americanus*) and the muskrat (*Ondatra zibethica*).

Flora. Only six families of plants occur on the southern hills (McCain 1975). On the rest of the island, which includes areas of forest, old fields, and freshwater and salt marshes, those six families account for only 48% of the species of plants. McCain attributes this lack of diversity and predominance of weed species on the southern hills to the constant disturbance created by thousands of gulls.

The physical differences in soil characteristics between the southern hills and the rest of the island are conspicuous. On the southern hills the water content of the soil is the highest on the island (69.0%) and the pH of the soil is the lowest (4.93) (McCain 1975). In 152 m of transects McCain found only eight herb species and one shrub species. For comparison, four 152 m transects in old fields averaged 26 herb species and three shrub species.

Blue aster (<u>Aster foliaceus</u>) was the most common herbaceous species on the southern hills. It had an importance value (I.V.) (Grieg-Smith 1983) of 64.62 (McCain 1975). Next in abundance was common ragweed (I.V.=58.02) (McCain 1975), followed by sorrel (<u>Rumex acetosella</u>) (I.V.=14.28) (McCain 1975). Red raspberry (<u>Rubus idaeus</u>) was the most common shrub, covering large areas higher on the hills. I did not study nests located in the pure red raspberry stands, primarily because of the virtual impossibility of following chicks as they wandered through the thick growth. Moreover, to visit a nest in the red raspberry patches, one trampled a number of stems around the nest. Each visit by an investigator therefore altered the cover afforded to the parents, eggs, and chicks. In vegetation that was a mixture of blue aster, common ragweed, and red raspberry, one could visit nests often, check the eggs, and search for chicks without appreciably altering the surroundings of the nest.

DATES AND DURATION OF FIELD WORK

My field seasons on Kent Island in 1977 and 1978, the years when I collected data on survival patterns, lasted from mid-May to the end of July.

GENERAL CONDUCT IN THE COLONY

It has been shown that for several species of gulls, the behaviour of adults and the survivorship of eggs and chicks can be altered by the activities of biologists seeking to study these quantities (Hunt 1972, Burger 1974, Gillett et al. 1975, Robert and Ralph 1975, Fetterolf 1983). Fetterolf's data are particularly relevant. He found a direct relationship between the degree of disturbance of a colony and the number of adoptions, disappearances of chicks, and deaths caused by pecking. In response to these findings, and following the advice of Duffy (1979), I am providing more detail regarding my activities in the gull colony than was required previously in methods sections.

Within my study area, there was virtually no disturbance from other investigators. In 1977 another investigator moved through the sea edge of the area to check black guillemot nests once a week. He made every effort to avoid gull nests and his effect on the colony appeared to be negligible. None of the other biologists working on the island conducted any work within the study area or regularly passed through it. In 1977 an assistant and I worked in the study area. In 1978 and 1979 I was alone.

Observations were carried out from several blinds, usually made of wood. One, in 1977, was cloth. The cloth blind was not used in later years because it moved in strong winds and showed the shadow of the inhabitant under some lighting conditions. In spite of the liabilities of the cloth blind, it did not seem to disturb birds more than momentarily. One nest, located less than 1 m from the door, went through normal incubation of eggs and caring for chicks.

We placed blinds on or near an edge of the study area. During our use of the blinds, we saw no indication that disturbance from our presence consisted of anything more than brief periods of alarm while we arrived or left. Most birds stood, stepped off the nest momentarily, and resumed incubation. Many birds in the area overlooked by the blind did not even get off their nests. We did not observe any losses of chicks or eggs while we entered or left blinds. While we were in the blinds, gulls occasionally saw a face at a viewing hole and stared at the blind. If we remained quiet and motionless for a few moments the alerted gull always adopted a more relaxed posture (head not extended, gaze not fixed on the blind). These incidents rarely elicited alarm calls from the alerted birds.

Some of our activities caused eggs and chicks to be lost to neighbouring gulls. Walking through the colony occasionally disturbed a parent and allowed another gull to rob the nest. This type of incident became less common as the breeding season progressed, probably because of increased attentiveness and habituation to our presence.

Our most disruptive activity was visiting nests to measure characteristics of the site, locations of chicks, and survival of eggs or chicks. This usually displaced both parents from the territory. The time until parents returned to the immediate vicinity of the nest to stand guard varied considerably. We often saw intruders land near a nest as we walked away from it. Usually one of the resident birds drove off the intruder before any damage could be done, but chicks and eggs sometimes were attacked. We knew of only two chicks killed because of our disturbance. On extremely hot days, or on cold, wet days, the checking of nests was either postponed until the next day, or was conducted during the mildest part of the day. For example, on sunny, calm days, the nests were not disturbed from 1100 h to 1600 h.

Because of the "noise" introduced into the data by the above disturbances, visits to nests subsequent to completion of laying were kept to the minimum number (approximately every fourth day) that would provide a description of survival patterns.

During hatching, when it was critical to identify the A, B, and C chicks (hatching from the eggs laid first, second, and third, respectively), nests were sometimes visited more often than every fourth day.. These visits were made as quickly as possible. This frequency of visiting nests falls between Fetterholf's "moderately disturbed" (1 visit of 8 min every 2 days) and "least disturbed" (1 visit). The number of adoptions observed in this study (e.g. in 1978, only 1 out of 142 chicks in 68 nests) suggests that the disturbance of birds was as low as is possible when data on survival over time are needed. This rate of adoption is lower than published rates (16 out of 119 nests) for some undisturbed colonies (Holley 1984).

Every fourth day, when chicks were handled to weigh them and note their locations, there was a risk of causing the brood to be split up or a chick to be killed by another gull (Fetterolf 1983; this study). To minimize this possibility, each chick was first placed individually in a dark container, usually a large tin can, as soon as it was seen. Chicks almost always remained quiet and motionless once inside the can. After the chick's location and weight were recorded, the chick was returned to the can. After a few moments, the can was lifted from each chick as it sat on the ground. This procedure usually left all the chicks in the brood exactly as they were before the nest was visited.

CAPTURING AND MARKING

In 1977, all chicks were marked with felt pens (blue, green, and yellow) on different parts of their bodies. Each chick was distinct from all others in the same portion of the study area. In 1978, each chick was marked with a unique masking tape leg band on the first nest check after it hatched.

To allow the recognition of some adult gulls, required by all three parts of this thesis, some were captured in the study area either by by immobilizing them with lights shined into their eyes at night (jacklighting) or by capturing them during the day in traps on the nest. Nests were selected to make the capturing as efficient as possible and to minimize disturbance to neighbouring nests. Jacklighting was inefficient, because one could misidentify a bird and could frighten birds enough to disrupt their courting and territorial behaviour. Consequently only four birds were captured and marked using this technique.

Funnel-type traps were used to capture 22 incubating birds. The traps were made from either chicken wire or hardware cloth as described in Weaver and Kadlec (1970). Early versions were made without a floor. After one egg was cracked by a parent and one egg was eaten by a gull during the parent's absence, all traps were made with floors. No further eggs were lost.

To facilitate handling, weighing, and marking by one person, and to reduce the possibility of injuring a struggling bird, trapped birds were restrained with a board and straps.

Each adult was marked with a standard U.S. Fish and Wildlife Service monel band. For some purposes, gulls also had to be marked in a way that identified them at the nest. Coloured leg bands were inadequate because they were not visible when a bird was incubating and because the vegetation in the study area obscured leg bands even when a gull was standing. I chose a modified version of the nasal saddle or disc (Lee 1958; Lindmeier and Johnson 1958; Erskine 1962; Sherwood 1966; Sugden and Poston 1968).

The nasal marker consisted of four parts: two acrylic washers, a stainless steel machine screw, approximately 2 mm by 20 mm, and a stainless steel nut. The threads of the central 12 mm of the screw were filed off to prevent abrasion of the nares. The washers, approximately 10 mm in diameter and 2 mm thick, were made in three shapes (square, circle, triangle) and four colours (red, yellow, blue, black). When observing resting gulls, I found that it was usually easy to observe both sides of the bill, so I used different markers on the left and right sides. This gave a total of 144 individual combinations of markers.

When the markers were applied, the nut was tightened until approximately 1 mm was left on each side of the bill. This allowed air and hypertonic secretions of the salt glands to flow freely between the washers and the bill. The nut was locked in place with an adhesive, usually an epoxy glue. When the marker was in place, the washers did not interfere with the cutting edges of the upper mandible.

COMPARISON OF CLIFF AND FLAT HABITATS

In 1977, preliminary criteria were drawn up for classification of nests in cliff and flat categories. The 1977 criteria were modified, on the basis of their satisfactory and unsatisfactory aspects during subsequent analysis, to generate 1978 criteria. These were used for classification of nests during the collection of data for detailed comparison of survival and growth of chicks.

In 1977, I measured the distance from the rim of each nest cup to the closest cliff. I also measured the heights of the nearest cliff and the tallest within 3 m. In making these measurements, I defined a cliff as any vertical or near-vertical surface that would prevent a chick from returning to its nest after it had fallen.

This is not a common definition of a cliff, but is appropriate in a functional sense. If a chick cannot return to its nest, it is likely to be poorly fed and sheltered (if at all) and probably be killed by a neighbouring gull (Davis and Dunn 1976; Hunt and Hunt 1975). Thus a fall over a cliff which is 2 m high can be just as likely to be lethal as one which is over a cliff 100 m high.

To compare nesting hazards in the two habitats, I conducted a discriminant function analysis (DFA) of nests in cliff and flat areas in 1978, using five variables which could be measured at each nest. Three of these variables measured the pattern and density of neighbouring nests, under the assumption that close neighbours can be more dangerous to the young (Hunt and Hunt 1975; Davis and Dunn 1976; Hunt and Hunt 1976). These variables were: the distance to the nearest neighbour (also measured in 1977), and the number of nests within 2.5 m and within 5.0 m (convenient metric approximations of Parsons' (1976) radii of 7.5 ft and 15.0 ft. These measures were made with a steel tape, from rim to rim of nest cups. I created two other variables, the number of dangerous quadrants and the number of safe quadrants around the nest, to measure the inherent danger or safety of the immediate nest site in terms which were not unique to one habitat type.

To count dangerous and safe quadrants, I divided the area around the nest cup into four quadrants of a circle with a radius of 1.5 m. The quadrants were bounded by the circumference and the east-west and north-south lines running through the nest cup. If a quadrant in either habitat contained an open area large enough to expose a chick located there to a predator flying over the nest it was classified as dangerous. The minimum diameter of an open area was set at about 50 cm, a size found to be large enough to completely expose a herring gull chick located therein. In the cliff area, a quadrant was also classified as dangerous if it contained a cliff which would prevent a fallen chick from returning to its nest. The sum of all the dangerous quadrants was recorded for each nest. Likewise, if a quadrant contained a cave or a patch of vegetation dense enough to provide a chick with a hiding place, it was classified as safe. The sum of the safe quadrants for each nest was also recorded. Note that a quadrant could conceivably be classified as both safe and dangerous if it contained a large open area and a patch of dense cover or a cave. Thus the sum of the dangerous and safe quadrants for each nest does not necessarily equal four. The two measures are therefore statistically independent.

The DFA was conducted by using SPSS Version M, Release 7.2, implemented on OS/360. All variables were included in the discriminant function.

Data on nest density for two years were examined by univariate methods.

To document the dates of laying, nests were marked in 1977 and 1978 with stakes during routine searches for nests as described above. Staked nests were visited daily to check for newly laid eggs. In 1978 eggs were marked A, B, or C, and classified as known status or estimated status. Eggs were only classified as known status if they were found in sequence during the laying of a 3-egg clutch. In smaller clutches, I could not be certain that the first egg found was the first egg laid, because an egg could have been laid and stolen before I visited the nest.

Hatch dates were recorded during routine checking of nests (usually every fourth day, as previously described). Indicators such as pipping dates and wet chicks usually allowed me to know the exact day of hatching. When the exact day was not known, the date was almost always known to within one day. Checking nests during laying allowed determination of clutch size for each nest. As with any study of this type, it was not possible to state with certainty that two-egg clutches were not three-egg clutches in which an egg was stolen immediately upon being laid.

COMPARISON OF REPRODUCTIVE SUCCESS IN CLIFF AND FLAT HABITATS

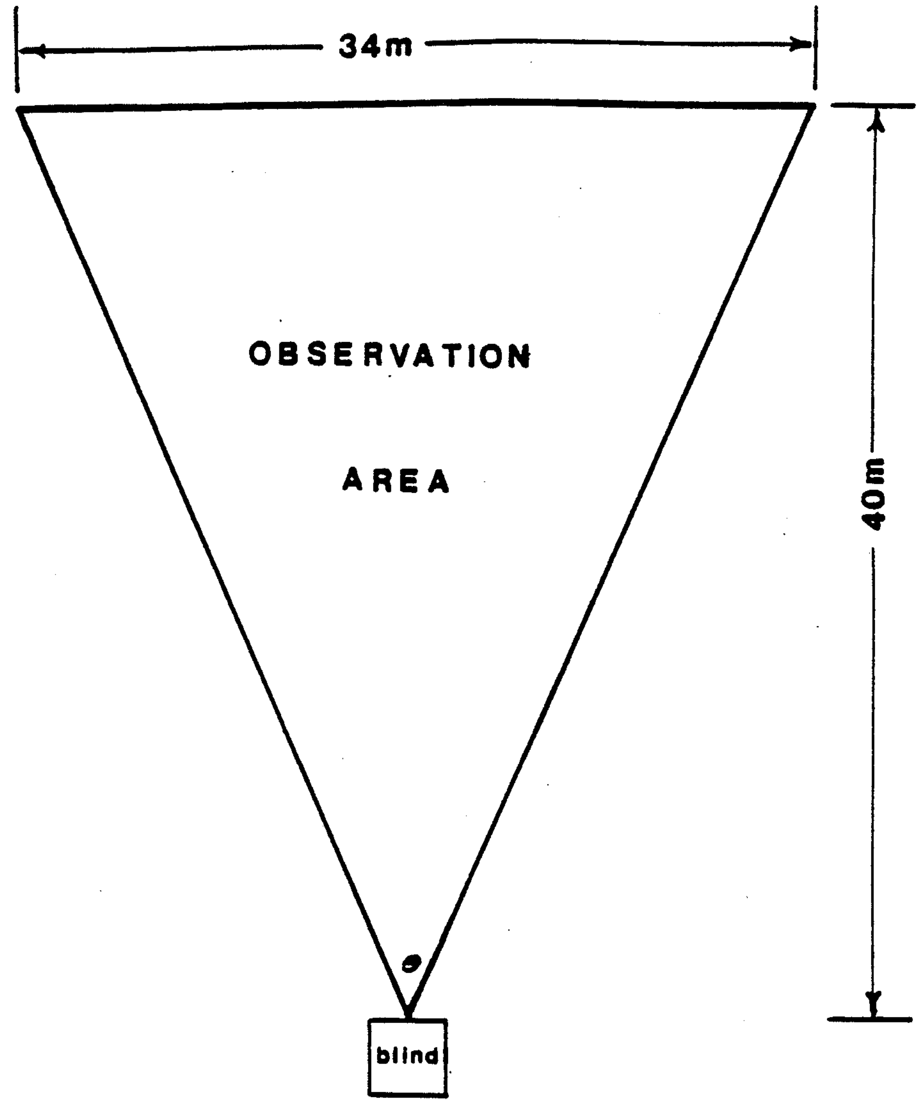
I used both indirect and direct measures of reproductive success. Indirect methods consisted of measuring the number of nests initiated in each type of habitat. If cliffs were a suboptimal nesting habitat, with lower reproductive success, one would predict that during the initial period of establishing breeding territories the better habitat (flat) would be crowded with birds attempting to establish and hold territories, and that cliff habitat would be used only by birds which had not gained or held territories on flatland. To determine whether this situation occurred, I tested the the null hypothesis that there are no differences between cliff and flat areas in the number of nest initiations during the period of territorial establishment.

To compare the number of nest initiations during the period of territorial establishment, portions of the cliff and flat study areas were selected for observation from 19 - 26 May 1977, when most territories on Kent Island were being defended and nests were being built. The areas were selected on the basis of ease of locating and entering blinds. The boundaries of the cliff area could not be staked because of the rock substrate, so the areas of observation were triangular (Fig. 5). The height of the triangle was paced. The included angle at the blind was measured by looking through the viewfinder of a 35 mm single-lens reflex camera with a 50 mm lens. When the left-hand border of the frame was placed at a predetermined landmark, the area visible in the frame was exactly as given in Fig. 5. When the observer needed to determine if a bird was inside the observation area, a glance through the viewfinder as above would objectively include or exclude the bird.

Observations were made simultaneously by two observers in flat and cliff areas. Each bout of observation lasted 1 h. Observers were assigned randomly to the two areas. Twelve pairs of bouts were conducted, covering the period from 0800 h to 1900 h. When more than one bout was conducted on one day, the data from the bouts were averaged to produce a single data point for the day. After entering the blind, each observer waited 15 min before beginning observation.

We considered that a pair was initiating nesting, or attempting to do so, if one or more of the following criteria were met (following Tinbergen 1953, 1959; Moynihan 1958; Stout et al. 1969; Stout 1975): (1) a bird defended a territory, either by fighting, using the upright threat posture, or by threatening with raised wings; (2) a pair gave simultaneous long calls (Appendix 2) at the same site more than once during

Fig. 5. The shape and size of the area used in tests for suboptimal habitat. The angle in the vertex at the blind (θ) is 46°.


34m
40m
OBSERVATION
AREA
θ
blind

the bout; (3) a pair performed mutual choking (Appendix 2) more than once in a bout; (4) a bird engaged in grass-pulling with another bird; (5) nest construction occurred; or (6) incubation or sitting on a nest occurred.

Significance of differences in nesting density between habitats was tested with the normal approximation of the Mann-Whitney U-test.

A direct measure of reproductive success in the two habitats was based on differential survival of the young. One cannot rigorously prove equality in reproductive success without following offspring through to reproductive maturity. However, large differences in survival of chicks between two areas, if present, would argue strongly for a difference in reproductive success between the birds in the two areas, because of the relatively low mortality of birds between fledging and maturity. I therefore tested the null hypothesis that there is no difference between cliff and flat areas in the number of chicks per nest surviving the early, high-risk, weeks of life. (See Appendix I for justification of the choice of this period.)

In 1977 the criterion for surviving the dangerous early weeks was living until 25 July (the median date for chicks reaching the age of three weeks). In 1978, when I focused on the success of individual nests, rather than of areas, survival for a chick was considered to be achieving a weight of 500 g. Both these criteria are consistent with the various criteria which have been used in other studies to define survival of chicks. Parsons (1976) used survival to the age of 10 days, if not found dead thereafter. Davis and Dunn (1976) used survival to the age of 22 days. Hunt and Hunt (1976) used survival to the weight of 500 g. Kadlec et al. (1969) found that mortality from the fourth to the seventh week of life was minor.

In 1977, chicks were considered dead if they were not found on two consecutive censuses. Only one chick out of 124 was found alive after being classified as dead by this criterion. In 1978, I continued to search for missing chicks until the end of the field season or until there was no sign of parents or chicks on the territory. Only 19 out of 143 chicks were missed and found again. These were typically small but mobile chicks that discovered a good hiding place before I did. Chicks that weighed nearly 500 g were usually conspicuous, so it is unlikely that estimates of mortality included chicks which were alive but never found.

COMPARISON OF NESTING BEHAVIOUR BETWEEN HABITATS

To examine the possibility that herring gulls compensate for differences in habitat by behaving differently in the two areas, I examined four behaviours that I thought could be related to cliff-nesting hazards: attendance of parents, use of parental "mew" calls (Appendix 2), positioning of parents and young during feedings, and mobility of the young. For each behaviour, I tested the null hypothesis that there was no difference between the two habitats.

To measure attendance of parents, data were gathered at the end of 20 min bouts of feeding observations. At the end of each bout, all the nests which could be seen from the blind were classified as having zero, one, or two parents at the nest. Data were collected on eight days between 9 and 28 July 1977. On each day data were taken from both cliff and flat areas.

To measure use of parental mew calls during chick feeding bouts, equal numbers (24 in each area) of 20 min observation bouts were conducted in cliff and flat areas. Chicks being observed were less than three weeks old. Feedings were classified as follows: (1) feedings in which mew calls were used before food was regurgitated; (2) feedings in which other calls were used; (3) feedings in which no call was used; or (4) feedings in which I could not determine whether a call was used.

The positioning of parents and chicks during feeding was measured during the same bouts in which I measured the use of mew calls during feedings. Only the behaviour immediately preceding a feeding was recorded. Movements related to feedings were classified as follows: (1) parent moves toward chick; (2) chick moves toward parent; (3) parent and chick both move toward one another; (4) neither moves toward the other; or (5) not classified.

The mobility of chicks when we disturbed them was measured during regular nest visits. The area around each nest was searched and the distance from each chick to its nest cup was measured and recorded.

RESULTS

CONSEQUENCES OF CAPTURING AND MARKING

Twenty-four gulls were fitted with nasal markers. After being released, the birds responded overtly to the presence of the nasal marker for only a few minutes. They scratched at the marker with their feet, shook their heads, splashed their heads in water, and scraped the sides of their bills against the ground. These actions only occurred within 15 min of the bird's release. All birds captured on the nest returned to incubation immediately after being marked.

In 1977, five birds with nasal markers nested in areas where I was conducting extensive observations. During approximately 100 h of observation in these areas, the territories of these five birds were always visible. I observed no scratching at the marker and no debris hanging from it. All five birds returned to approximately the same territories in 1978, with nasal markers intact. No enlargement of the nares was visible through a spotting scope at very close range. All appeared to be in good health, and courted, incubated, and fed chicks in a normal way. The acrylic retained both shape and colour well, even after two years.

COMPARISON OF CLIFF AND FLAT HABITATS

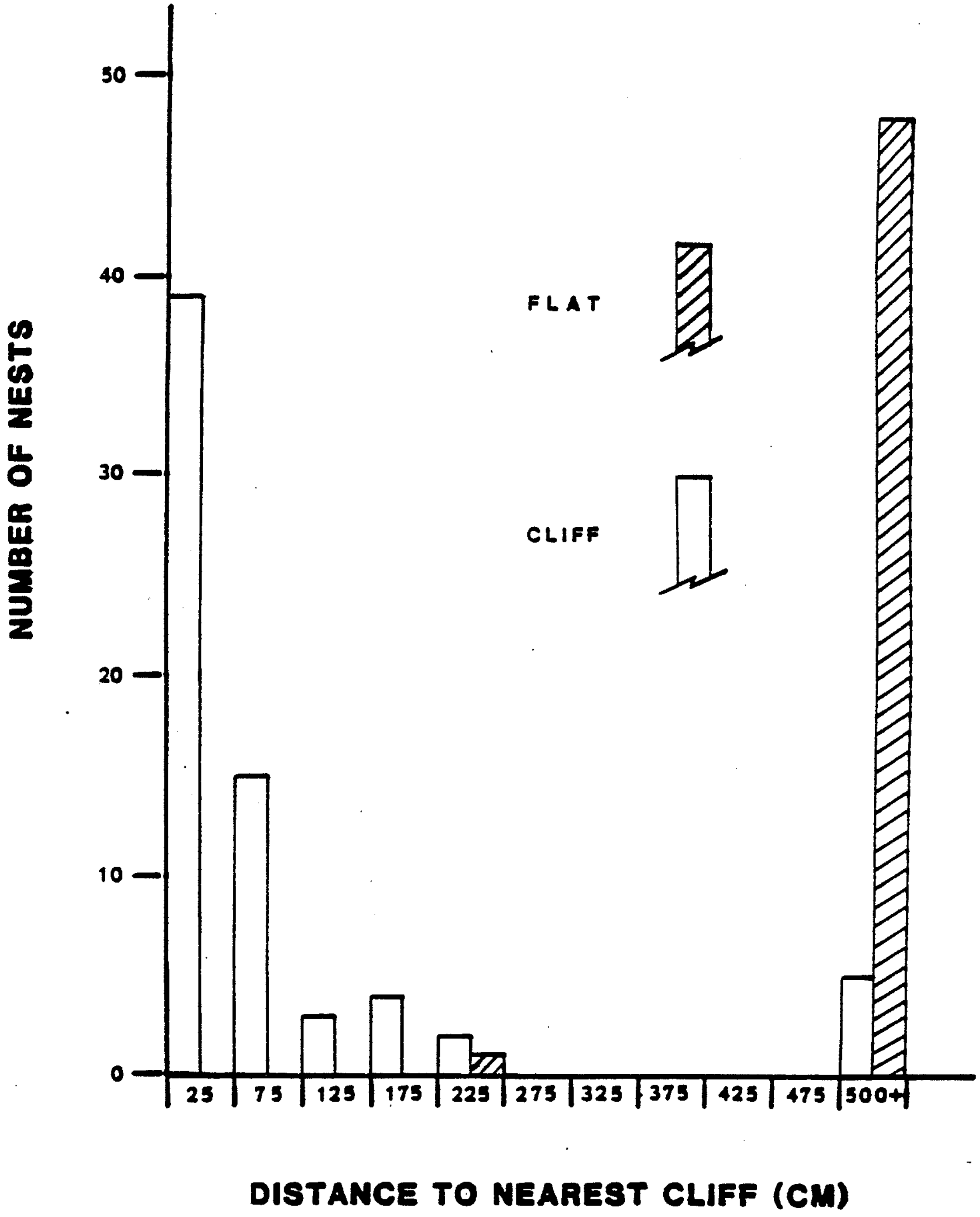
Both the cliff and flat areas were on the periphery of the colony, so there was no need to test assumptions regarding this factor.

The only data on the age of the breeding birds in both areas was that none showed mottling on the dorsal surface of the rectrices, the only indicator of being a young (three years old) breeding bird (Poor 1946).

The subjective creation of two areas, cliff and flat, was verified by the frequency distribution of the distances to the nearest cliff (Fig. 6). The distribution was sharply discontinuous, and the discontinuity was almost perfectly correlated with the flat-cliff dichotomy. Only five nests in the cliff area had no cliffs within 500 cm and only one nest in the flat area had a cliff within 250 cm. This discontinuity of distributions allowed the rejection by inspection of the null hypothesis that no difference was present between areas with respect to cliff-nesting hazards.

The mean height of the nearest cliff to each nest in the cliff area was 121.6 cm (SD = 124.4, n = 64). The mean height of the tallest cliff within 3.0 m of each nest in the cliff area was 178.5 cm (SD = 135.3, n = 64). Much of the magnitude of both the means and standard deviations was contributed by some nests which were close to a cliff which was 700 cm high. This cliff, and some others, presented the classic hazard of cliff-nesting to chicks. Any chicks falling over the edge would have died in the surf or on the rocks.

Fig. 6. The distance from nests to the nearest cliff in cliff and flat areas.



NUMBER OF NESTS
50
40
30
20
10
0
FLAT
CLIFF
25
75
125
175
225
275
325
375
425
475
500+
DISTANCE TO NEAREST CLIFF (CM)

The chronology of breeding was virtually identical in cliff and flat areas. The median date of hatching of the first egg in the clutch was 2 July for the flat area, and 3 July for the cliff area. In the flat area, all hatching was completed between 21 June and 24 July. In the cliff area, the comparable period was 15 June to 20 July.

In 1977 the mean clutch sizes for cliff and flat areas were 2.41 (SD = 0.27, n = 78) and 2.37 (SD = 0.36, n = 51), respectively. In 1978 the respective mean clutch sizes were 2.79 (SD = 0.17, n = 39) and 2.68 (SD = 0.32, n = 41). The differences between areas were not significant in 1977 (t = 0.79, n.s.) nor in 1978 (t = 1.90, n.s.). There is therefore no reason to suspect that any subsequent comparisons of reproductive performance in cliff and flat habitats include any confounding effects at the level of synchrony and clutch size.

Table 1 presents the group means and standard deviations from the discriminant function analysis of nesting habitat, along with the results of univariate F-tests for significant differences between groups. Significant differences in this table should be interpreted in the light of the inter-year differences in spacing reported below, suggesting that the denser nesting pattern on cliffs which appears in the 1978 data used for the discriminant function analysis cannot be taken as a characteristic difference between cliff and flat areas. It is more likely that the larger number of safe quadrants in the flat area is a long-term difference between the habitat types.

Table 1. Group means, sample sizes, standard deviations, and univariate F-tests for cliff and flat habitats for variables used in discriminant function analysis of habitat characteristics.

	Cliff (n=39)		Flat (n=41)			
	$\bar{x}$	SD	$\bar{x}$	SD	F	
Dangerous Quadrants	2.28	0.83	2.00	1.30	1.32	(n.s.)
Safe Quadrants	2.18	1.41	2.95	1.02	7.89	($p < 0.01$)
Neighbours Within 2.5 m	0.84	0.84	0.24	0.43	16.33	($p < 0.01$)
Neighbours Within 5.0 m	2.23	1.39	1.68	0.88	4.51	($p < 0.05$)
Distance (cm) to Nearest Neighbour	282.46	178.09	348.63	121.17	3.81	(n.s.)

The heavy growth of vegetation in the flat area would be expected to generate good hiding places during every breeding season.

Table 2 shows the correlation matrix for the variables employed in the discriminant function analysis. As would be expected, there is some negative correlation between the number of dangerous quadrants and safe quadrants, and considerably stronger correlation among the three variables measuring spacing: the distance to the nearest neighbour, the number of neighbours within 2.5 m, and the number of neighbours within 5.0 m. Note that as distance to nearest neighbour increases, the number of neighbours within 2.5 m and 5.0 m would be expected to decrease, hence the negative sign for the correlations between these variables (Table 2). Implications of these correlations for simulation (PART 3) are that a parsimonious description of a nest site would include one of the quadrant variables and one of the three spacing variables.

The standardized discriminant function coefficients (Table 2) show that when these data are used to distinguish between habitat types, the greatest contribution is made by the number of neighbours within 2.5 m, followed by the distance to the nearest neighbour. The two smallest contributions to the difference between habitats are made by the number of dangerous and safe quadrants.

A test on the discriminant scores generated for the two habitats by the above coefficients shows a significant

Table 2. Correlation matrix and standardized discriminant function coefficients for variables used in discriminant function analysis of cliff and flat nesting habitat in 1978.

	Dangerous Quadrants	Safe Quadrants	Nests Within 2.5 m	Nests Within 5.0 m	Distance to Nearest Nest	Coefficient
Dangerous Quadrants	1.00					-0.136
Safe Quadrants	-0.38	1.00				0.259
Nests Within 2.5 m	-0.08	-0.23	1.00			-1.030
Nests Within 5.0 m	-0.03	-0.29	0.41	1.00		-0.263
Distance to Nearest Nest	0.11	0.15	-0.71	-0.65	1.00	-0.503

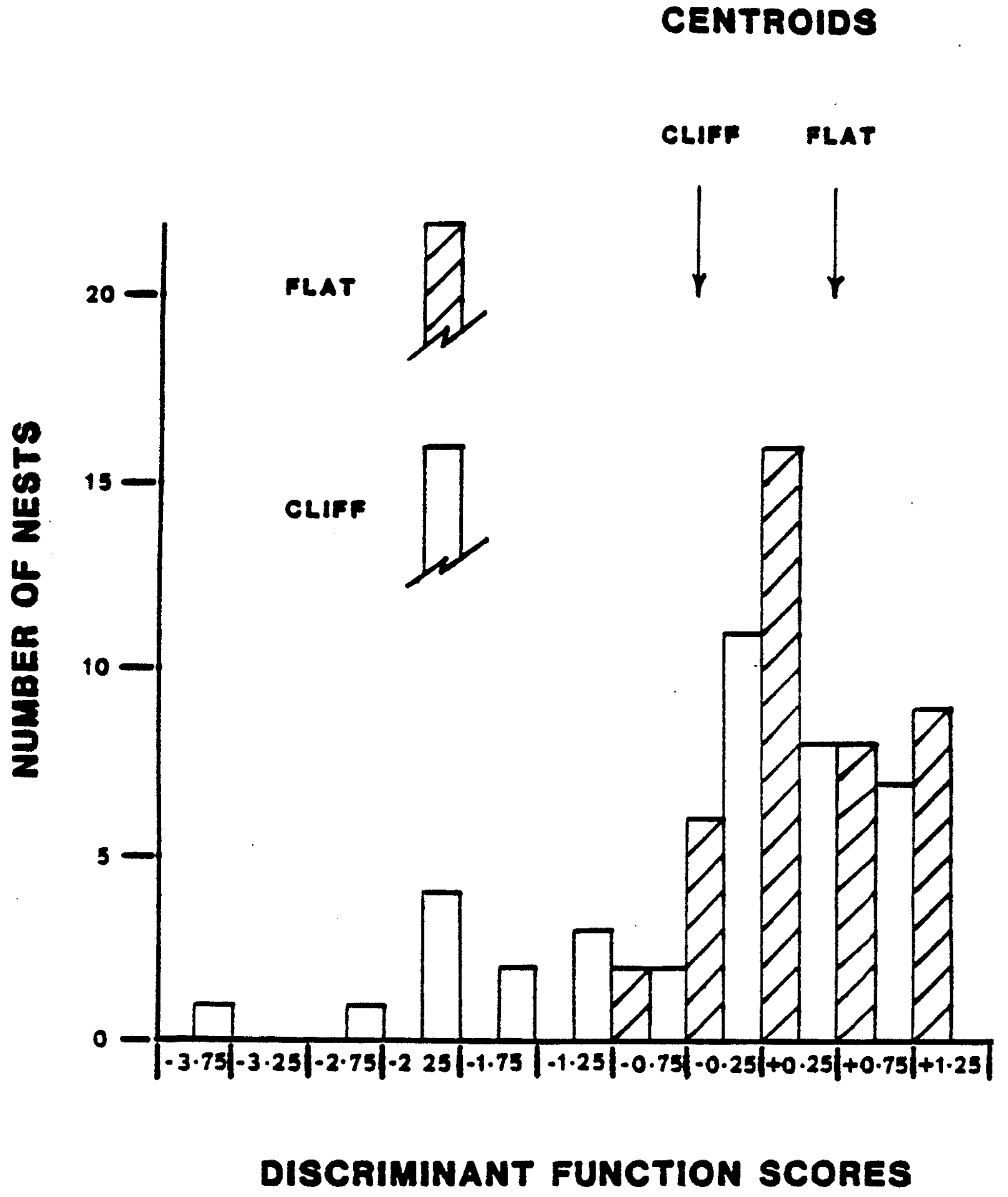
difference between habitats: the mean scores for cliff and flat were -0.487 and 0.462, respectively (Wilks's $\lambda = 0.7754$, $= 19.336$, d.f. = 4, $p < 0.001$). The biological significance of the above statistical significance is not immediately apparent, for the frequency distribution of discriminant scores (Fig. 7) shows that 60 of the 80 scores overlap. If one were to attempt to predict the habitat class to which a nest belonged solely on the basis of the five discriminant function analysis variables and the discriminant function, the error rate in classification would range from 20% to 40%.

In 1977 the mean distance to the nearest neighbouring nest in the cliff area was 305.4 cm (SD = 129.1, n = 69) and 294.2 cm in the flat area (SD = 231.9, n = 46). These means were not significantly different (t = 0.33).

REPRODUCTIVE SUCCESS

The primary purpose of measuring reproductive success in cliff and flat areas was to determine if cliffs were suboptimal habitat. On Kent Island there were clear examples of such habitat, which provided a useful qualitative benchmark regarding the use suboptimal habitat. Some nests were established on flat, rocky surfaces peripheral to both the cliff and flat areas. This rocky area was swept by water during storms, contained very few hiding places for chicks, and became extremely hot during sunny days. Almost none of the chicks and eggs in this rocky area survived.

Fig. 7. Frequency distribution of discriminant function scores for cliff and flat nesting habitats.


CENTROIDS
CLIFF
FLAT
FLAT
CLIFF
NUMBER OF NESTS
20
15
10
5
0
-3·75
-3·25
-2·75
-2 25
-1·75
-1·25
-0·75
-0·25
+0·25
+0·75
+1·25
DISCRIMINANT FUNCTION SCORES

Thirty-nine nest initiations were observed in the cliff area and 46 in the flat area (Fig. 8). There was no significant difference between habitats ($U = 88.5$, $z = 0.95$, n.s.) in the number of initiations per observation period, and therefore no evidence that one area is suboptimal, being utilized only by pairs which could not establish territories in more favourable areas.

The survival of eggs and chicks in cliff and flat habitat (Table 3) also provides no evidence that the cliff habitat is suboptimal. In fact, the one feature of the table which stands out is the very high survival rate of chicks in the cliff habitat in 1978, which generated a significant difference between habitats in chick survival and overall survival of chicks and eggs for that year.

COMPARISON OF NESTING BEHAVIOUR BETWEEN HABITATS

When measuring attendance of parents at the nest, 905 observations were made, 381 in the flat area and 524 in the cliff area. The areas were significantly different (Table 4), primarily in the increased frequency with which cliff nests had both parents present ($X^2 = 16.31$, d.f. = 2, $p < 0.01$).

We observed 167 feedings, of which 106 allowed a statement to be made about the parent's vocalizations: in 64 feedings birds were silent, in 39 they uttered a mew call, and in three they gave "long" calls. Because long calls were used

Fig. 8. The number of nest inititations in May 1977 in each observation period in the cliff and flat areas.

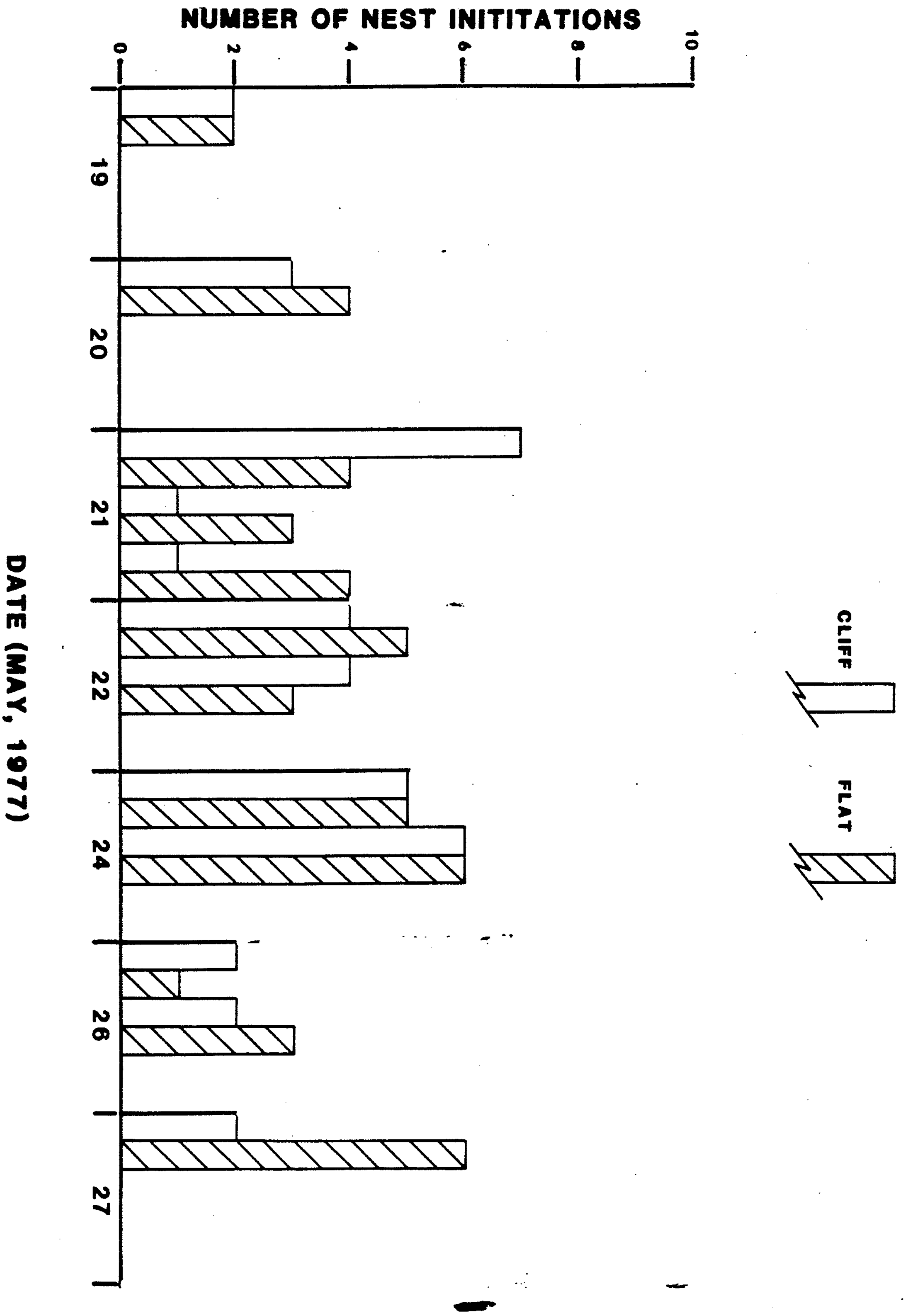

NUMBER OF NEST INITITATIONS
0
2
4
6
8
10
19
20
21
22
24
26
27
DATE (MAY, 1977)
CLIFF
FLAT

Table 3. The survival of eggs and chicks in cliff and flat habitat in 1977 and 1978. Probabilities are shown in parentheses under X^2 values.

	Cliff			Flat			Total
	1977	1978	Total	1977	1978	Total	
Number of nests	78	39	117	51	41	92	209
Eggs laid	188	115	303	121	110	231	533
Eggs hatched	100	75	175	73	68	141	316
% hatched	52.3	65.2	57.8	60.3	61.8	61.0	59.3
X^2 (cliff:flat)	1.52	0.28	0.58				
	(0.22)	(0.60)	(0.44)				
X^2 (1977:1978)		4.23			0.05		
		(0.04)			(0.82)		
Chicks surviving	24	37	61	25	21	46	107
% survival after hatching	24.0	49.3	34.9	34.2	30.9	32.6	33.9
X^2 (cliff:flat)	2.18	5.04	0.17				
	(0.14)	(0.03)	(0.68)				
X^2 (1977:1978)		12.11			0.18		
		(<0.01)			(0.67)		
Overall % survival	12.8	32.2	20.1	20.7	19.1	19.9	20.1
X^2 (cliff:flat)	3.44	5.03	0.004				
	(0.06)	(0.03)	(0.95)				
X^2 (1977:1978)		16.72			0.09		
		(<0.01)			(0.77)		
Chicks surviving per nest	0.31	0.95	0.52	0.49	0.51	0.50	0.51

Table 4. The presence of parents at the nest in cliff and flat areas.

Number of Parents Present	Cliff	Flat	Totals
0	45	27	72
1	398	327	725
2	81	27	108
Totals	524	381	905

infrequently, I deleted them from the analysis. Mew calls were given during 37.9% (n = 58) and 37.8% (n = 45) of the feedings in the cliff and flat areas, respectively.

Of the 167 feedings observed, 92 could be classified with respect to the movements of parents and chicks during feeding, (Table 5). There was no significant difference between the areas ($X^2 = 2.41$, d.f. = 4, n.s.).

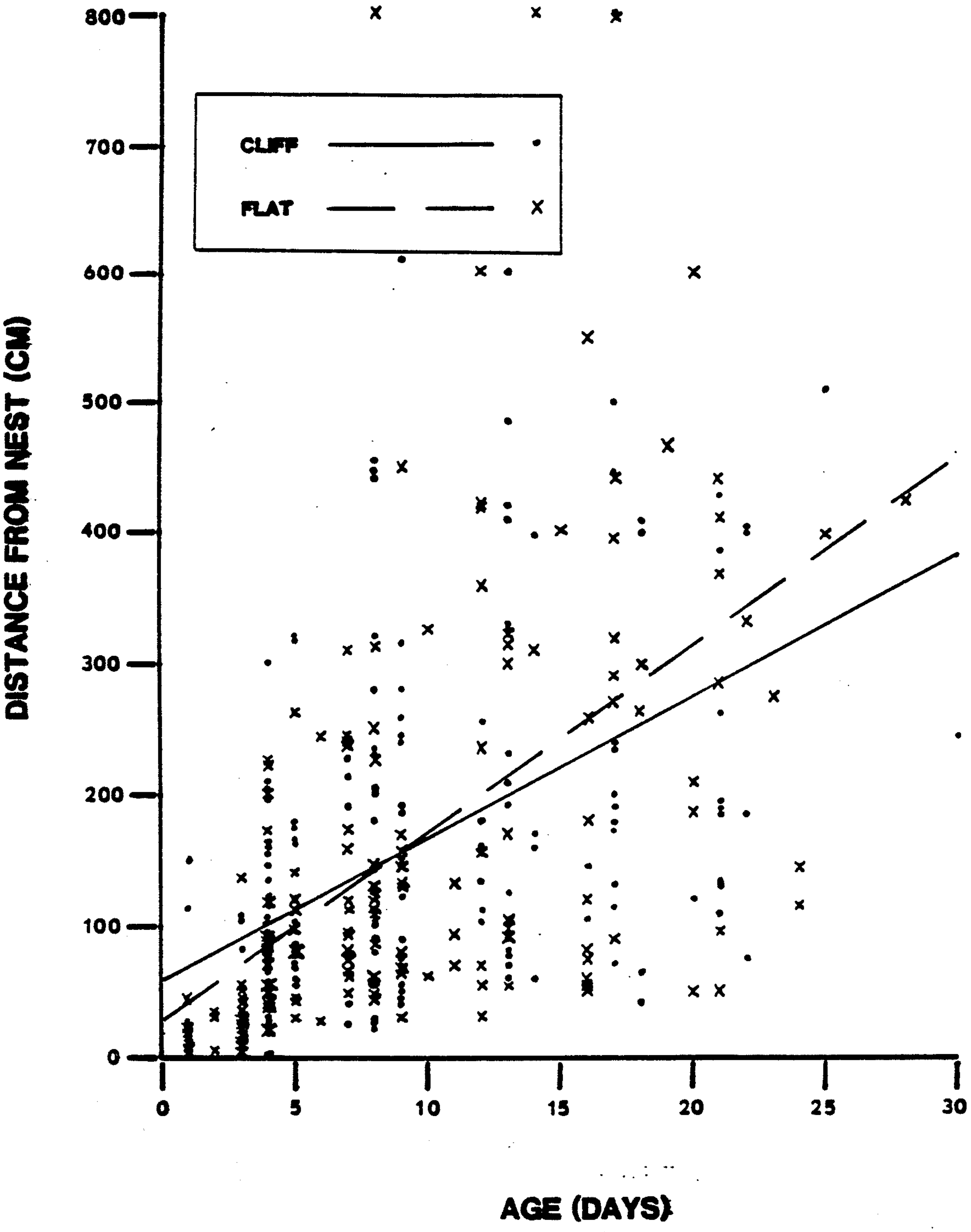
The distances involved in the movements of the parents and chicks during feedings were short with respect to the distance from the nest to the nest of the pair's nearest neighbour. Whereas the mean distance to the nearest neighbour was on the order of 3 m (Table 1), movements were rarely over 1 m. Only one movement (chick to parent) was over 2 m, and in the case of that family, the nearest neighbour was 16.2 m away.

The development of mobility, as indicated by the regression of distance (measured when I entered the territory) from the nest on age of chick, for 1977 data, is given in Fig. 9. The slope of the lines for cliff and flat areas are 10.9 and 14.4, respectively. Both slopes are significantly different from zero (cliff: $F = 55.6$, $p < 0.001$; flat: $F = 58.3$, $p < 0.001$), but not significantly different from each other ($F = 2.30$, $p = 0.13$). Although these distances were measured when I was in the vicinity of the nest, and therefore was disturbing the brood, there was no indication that these distances were different from distances from the nest when the

Table 5. Distribution of the types of movements of parents and chicks during feedings in cliff and flat areas.

	Cliff	Flat	Totals
Parent to chick	12	8	20
Chick to parent	16	13	29
Both moved	12	6	18
Neither moved	11	14	25
Totals	51	41	92

Fig. 9. Distance of chicks from the nest cup as a function of age. Distances were measured at the time the investigator entered the territory.


800
700
600
500
400
300
200
100
0
DISTANCE FROM NEST (CM)
CLIFF
FLAT
0
5
10
15
20
25
30
AGE (DAYS)

brood was undisturbed. On many occasions, while conducting nest checks, I was able to observe the reaction of broods to my approach. The hiding places to which chicks fled were usually only a few steps from the places where they were resting prior to my arrival.

HETEROGENEOUS PATTERNS OF MORTALITY WITHIN HABITAT TYPES

Some causes of mortality in chicks were evenly distributed throughout the colony, and were independent of the status of nests near the affected chick. An example is predation by gulls that regularly cruised over the colony at a height of a few meters. Such an incident typically began with a chick sitting in an open area, visible to me and neighbouring gulls. A gull would appear silently from behind a knoll and dip down to grab the chick in its bill. The chick would call, its parents would rush to its defence, and the chick would either be dropped or carried away.

Other aspects of chick mortality were less uniform. Although data were presented above as if they were representative of all mortality within cliff or flat areas, the pattern of mortality within a habitat type may not be represented correctly by a single value such as a mean or a ratio. One nest in the flat area provided the strongest evidence of heterogeneous mortality rates within habitat types in herring gull colonies. On 19 July 1978, the top half of a chick's body was lying beside this nest. The legs, body wall, and internal organs had been eaten. The skull had been crushed. The chick was too small to be resident at the nest. On 24 July 1978, the single resident chick (525 g) at this nest regurgitated the leg of another herring gull chick. The leg had been partly swallowed for some time, with the proximal portion of the tarsus digesting within the chick and the foot protruding from its mouth. The tarsus on the regurgitated leg was approximately the same size (74 mm) as the resident chick's tarsus (68 mm).

Chicks had been disappearing rapidly from neighbouring nests, so I searched the vegetation around the nest, and found scattered grey feathers, five more chick tarsi, and several other chick bones. On 28 July I found another chick leg beside the same nest, and on 29 July I found still another chick leg and some wing bones. By this time there were no neighbouring nests with living chicks, with the exception of one nest in which the chicks found hiding places further from the nest of the cannibalistic neighbours.

Other patches within the study area in which almost all chicks were killed occurred, but they took the form of gradually enlarging areas of complete mortality, without a successful nest in the middle. The high mortality in these areas therefore cannot be attributed to proximity to a single specialist in cannibalism. It appeared that these patches were caused by predation by parents who had lost all their young, but remained on their territories for a few days. Marked and unmarked birds usually were seen on their territories for two or three days after all their chicks were lost. Immediately after all chicks disappeared, the parents usually wandered the territory, with heads down, giving mew calls. After approximately a day of searching, the behaviour of bereaved parents was typically to stand on an elevated location, in an upright posture. Although bereaved parents were not seen killing or eating chicks, they were also not seen defending territory, sleeping, building nests, or courting - actions which would have suggested maintaining or reestablishing a breeding site. If they had been foraging elsewhere, and returned to their nesting territory only to loaf, sleep, and digest meals, one would expect that they would have usually been asleep or loafing. This information is anecdotal, because the primary objective of data collection at the time was not to gather data on the behaviour of bereaved parents, but to observe feeding behaviour, although the continual exhibition of alert behaviour, without giving mew calls, suggests strongly that the birds were foraging.

DISCUSSION

NASAL MARKERS FOR GULLS

There are a number of advantages of nasal markers over other markers for adult herring gulls. Nasal markers will last through several moults; plumage markers will not. Nasal markers can be seen easily by someone who is looking for them, but otherwise they are inconspicuous. Neck bands and wing markers can change the gross appearance of the marked bird and can potentially alter its social behaviour and susceptibility to predation. Neck, wing, and leg markers have a history of collecting ice and debris. Nasal markers have occasionally done this (Sherwood 1966), and have in some cases left diving ducks snagged (Erskine 1962; Sherwood 1966). Gulls appear unlikely to have problems such as these, because they do not dive into submerged vegetation. Another way in which gulls are well suited to wearing nasal markers is that unlike waterfowl, they have perforate nostrils. Wing markers have been shown to affect survival and reproductive behaviour adversely in ring-billed gulls (Larus delawarensis) (Southern and Southern 1985). These considerations, and the non-disruptive results of using nasal markers in this study, suggest that the nasal pins developed for this study merit further use.

COMPARISON OF CLIFF AND FLAT HABITATS

The assumption that the areas designated "cliff" and "flat" were in fact different with respect to cliff-nesting hazards, was verified by the rejection of the null hypothesis that there was no significant difference between the areas. The comparisons made below between cliff and flat sites are therefore objectively justified.

No significant differences were detected between cliff and flat areas in nesting chronology or clutch sizes. There is therefore no reason to suspect that the comparisons made between cliff and flat areas were invalidated by the effects of these confounding variables.

The objective of multivariate comparisons was to determine whether differences between habitat types, which appear to be great when the habitats are described as "cliff" and "flat", continue to be significant when the habitats are described quantitatively in terms of variables which reflect the actual hazards that chicks may encounter. Initial inspection of the discriminant function analysis results suggested that this was so, for the centroids of the cliff and flat groups were a significant distance apart in the space created by the five variables used.

Two considerations, however, indicate that the distinction is more a function of the sensitivity of discriminant function analysis than a factor of long-term selective importance to herring gulls. The first consideration is that the discriminant function which was generated relied heavily on measures of nesting density to distinguish between habitats, and yet the density in cliff and flat habitats, measured by the distance to the nearest neighbouring nest, was higher in the flat area in 1977 and in the cliff area in 1978. This suggests that nesting density is a labile quantity, rather than a fixed characteristic of one habitat, and that the discriminatory ability of the discriminant function might be very poor in some years.

The second consideration relates to the discriminatory ability of the function even within the year from which data were taken. If the discriminant function generated in 1978 were applied to 1978 nests, it would misclassify 20% to 40% of them. Even if between-year variability in relative density between habitats did not occur, the overlap in discriminant function scores presents a picture which is quite different from the one implied by the classical contrast between nesting on cliffs and flatland and illustrated in Fig. 6. If cliffs and flatland really presented herring gulls with two contrasting sets of threats to the survival of their chicks, a discriminant function such as the one conducted in this study should have generated a strongly bimodal distribution of scores.

On the basis of these characterizations of cliff and flat habitats, it does not seem that herring gulls on Kent Island require a specialized set of adaptations for one habitat or the other. This conclusion does not conflict with Cullen's (1957) analysis of adaptations to nesting on cliffs, for she clearly states that her work relates to the use of "tiny ledges on steep cliffs". Hailman (1965) was conscious of this fact, and listed the ways in which the habitat of the swallow-tailed gull (Larus furcatus) differed from the habitat of the black-legged kittiwake before he predicted which adaptations should occur in the former species. His comparison showed the swallow-tailed gull to be in an intermediate situation, between typical ground-nesting gulls and kittiwakes. It is clear from Hailman's qualitative comparisons and the quantitative results of this study that "cliffs" do not constitute a homogeneous type of nesting habitat, but rather consist of a variety of habitats, in which the importance of the cliffs to the overall breeding biology of the species varies considerably.

REPRODUCTIVE SUCCESS

The equal rates at which nests are initiated in cliff and flat habitats supports the hypothesis that neither is suboptimal nesting habitat for herring gulls. If cliff habitats were suboptimal, for example because of an absence of suitable behavioural characteristics in a predominantly flatland-nesting population, then there would be a benefit to those pairs attempting to establish first on flatland, and that trait would presumably have been selected in recent evolution. There was no evidence, however, of any clumping of early nesting attempts in flat habitat.

There was no evidence of lower reproductive success on cliffs. These results contrast sharply with studies of the use of suboptimal habitat. Krebs (1971) found that the nesting mortality of great tits (Parus major) nesting in woodland (optimal habitat) was 5 - 6%, whereas in hedgerows (suboptimal) it was 13 - 22%. No difference this great occurred between cliff and flat areas in this study, and in fact the largest difference, in 1978, occurred when cliff nests had a lower mortality of offspring. Robertson (1972) found a similar pattern with redwinged blackbirds (Agelaius phoeniceus). Nests in marsh (optimal) habitat were 50% successful in fledging at least one young. Nests in upland (suboptimal) habitat were only 30 - 35% successful. Robertson also found that this relationship applied to both the years of his study, providing a contrast with the strong inter-year differences found in the cliff habitat in this study.

Strong inter-year variability is only part of the heterogeneity in mortality herring gull offspring. There is also a strong intra-habitat variance. In one portion of the flat habitat there were virtually no chicks in 1978, while in another portion almost every nest produced a surviving chick.

This variability in survival of eggs and chicks does not make Kent Island herring gulls unique, but rather shows that they exhibit the same variability which has been found in most studies of the breeding biology of large gulls (e.g. Paynter 1966; Kadlec and Drury 1968; Gillett et al. 1975). Emlen (1956) specifically refers to this problem with published data as "distressingly variable". The mortality rate of eggs commonly ranges from 20 - 50% during the entire period of laying and incubation (Vermeer 1963; Brown 1967; Kadlec and Drury 1968; Hunt 1972; Robert and Ralph 1975; this study). Approximately 35 - 70% of the chicks which hatch are likely to die during the first three weeks of life (usually at weights <500 g) (Vermeer 1963; Drent et al. 1964; Davis and Dunn 1976; Hunt and Hunt 1975; Vermeer 1970). In some studies the mortality rate ranged from 75 - 89% for this period (Darling 1938 in Paynter 1966; Paludan 1951 in Paynter 1966; Drost et al. 1961 in Paynter 1966).

The analysis of reproductive success in the two habitats therefore leads not to a single answer, but to two questions: what mechanisms enable herring gulls to nest equally successfully on cliffs and flatland (below, and PART 2), and what are the causes and implications of the extreme variability in juvenile survival (PART 3)?

COMPARISON OF NESTING BEHAVIOUR BETWEEN HABITATS

It was shown above that there was no difference between habitats in the way in which parents and chicks interacted, or in the movement patterns of chicks, but that there was a greater attendance of parents at nests in the cliff area. It is interesting to note that the traditional view of cliff-nesting (Cullen 1957) would require that, in order for chicks to survive, they would have to restrict their mobility and change their patterns of vocalizing and movement during feeding. These things were not done by herring gulls, and yet survival was equal to, or greater than, survival in flat areas.

Increased attentiveness of parents was listed by Cullen (1957) as a genotypic adaptation to cliff nesting, in the sense that parents remained on the nest longer at the approach of a predator. In this study, parents at cliff nests were also more attentive, but the difference between parents in cliff and flat areas suggests that this was a phenotypic response to the fact that the cliff habitat had fewer safe quadrants around nests, and more dangerous quadrants around nests. Put in anthropomorphic terms, it appears that they "sized up the situation as risky, and doubled the guard". If it is a general characteristic of herring gulls to exhibit this kind of pheotypic response to dangers in their individual nesting environments, the ability of the species to nest in a wide range of habitats should be enhanced.

PART 2: INDIVIDUAL RECOGNITION AND MULTIVARIATE ANALYSIS OF HERRING GULL MEW CALLS

INTRODUCTION

Several studies have suggested that cliff-nesting should be restricted to specialist species (GENERAL INTRODUCTION), and yet herring gulls nest with equal success on cliffs and flatland (PART 1). The mechanisms that permit them to do this are not clear. One possibility is that cliff and flat habitats, despite their apparent dissimilarity, pose similar problems to nesting herring gulls. When one scrutinizes the problems associated with cliff-nesting to find an example of such a common problem, one immediately thinks of the danger of a chick's wandering and falling off a nesting ledge. Gulls which nest colonially on flatland also encounter problems with respect to the movements of their chicks. Wandering chicks are exposed to the attacks of neighbouring adults (e.g. Ward 1906; Kirkman 1937; Brown 1967; Hunt 1972; and others, reviewed in Evans 1980) and may be adopted inadvertantly (e.g. Brown et al. 1967; Hunt and Hunt 1975; Graves and Whiten 1980; Holley 1981, 1984).

It appears that regardless of nesting environment, the ability to control the movements of chicks would be a valuable asset to a generalist species such as the herring gull. If a nest should happen to be in a particularly dangerous location, near cliffs or exposed to predatory neighbours, parents would benefit from being able to confine their chicks' wanderings to absolutely necessary movements such as coming to be fed. Minimizing mobility would not minimize risk, however, for if the best hiding places for chicks were not in the immediate vicinity of the nest, there would be a selective advantage in allowing the chicks to wander and locate the most comfortable and secure hiding places. They would then be able to use landmarks to return to these locations quickly when in danger, and in fact have been shown to do this (Noseworthy and Lien 1976). This capability would be consistent with contentions that "birds meet environmental challenges with remarkable behavioral ..... plasticity" (Boag and Grant 1981), and plastic mechanisms are exactly the ones we would expect to have evolved in successful generalist species.

The linch-pin of the hypothesized system is some mechanism for controlling, rather than just restricting, the mobility of chicks. A simple and well-documented mechanism known for selectively controlling the movements of mobile chicks is one in which individual recognition occurs between parents and young (Beer 1970a; Evans 1980), with appropriate approach or other responses occurring after the evaluation of the stimulus. In spite of the apparent logic of the evolution of a system of individual recognition, and its apparent relevance for herring gulls, the existence of a system of individual recognition of vocalizations within families in this species has recently been questioned by Graves and Whiten (1980) and by Holley (1981, 1984). These authors used, as an indicator of failure of the parents and chicks to recognize one another, a large number of adoptions in herring gull colonies, and concluded that this high rate of adoption is maladaptive. However, none of these studies actually tested for recognition. Given Fetterolf's (1983) data which demonstrate that adoptions can be artifacts of disturbance by investigators, it has become necessary to test specific hypotheses regarding individual recognition in herring gull families. The specific null hypotheses tested in this section were: (1) herring gull chicks do not respond differently to the mew calls of their parents and the mew calls of other breeding herring gulls, and (2) the mew calls of herring gulls are not individually distinctive, when analysed using sonagrams and multivariate methods.

Two hypotheses are being tested because a complete system of recognition requires the evolution of both an adequate stimulus and selectively advantageous response. Both should therefore be demonstrated.

A brief report on the testing of the first hypothesis has now been published (Knudsen and Evans 1986). Further detail is provided below.

INDIVIDUAL RECOGNITION

Beer (1970a) has reviewed the considerable body of literature on the ability of birds to discriminate among the vocalizations of individuals of the same species. This discriminatory ability has been shown to exist among mates, siblings, and territorial neighbours, and between parents and young.

With respect to gulls, there are several reports that chicks recognize the vocalizations of their parents. These reports are based on a range of data, from suppositions based solely on observations (Goethe 1937) to field and laboratory experiments (Beer 1969, 1970b; Evans 1970a, 1970b). For details of the literature, and a discussion of individual recognition and its ecological significance, see Beer (1970a) and Evans (1980). As noted by both authors, it is important, when reading this literature, to determine which animal is sending the critical signal and which is receiving and recognizing it. Some discussions are ambiguous on this point. There can be substantial implications (see DISCUSSION below) arising from the direction in which recognition occurs.

In the following experiments, I will deal only with the recognition of the vocalizations of parents by their chicks (hereafter the restricted definition of individual recognition).

In the case of semi-precocial species such as the herring gull, there are also substantial implications associated with the time at which recognition begins to occur. It has been predicted (Davies and Carrick 1962; Evans 1970a, 1970b, 1977, Miller and Emlen 1975) that the development of individual recognition has been selected to precede or at least coincide with the development of mobility. Evans (1980) demonstrated that this is the case for a wide range of colonial waterbirds. The following experiments therefore test not only for the existence of individual recognition, but for the critical time (measured in age of the chicks in days) at which individual recognition is exhibited.

Data from this study show that chicks can travel far enough to reach neighbouring territories by the time they are eight days old (see inter-nest distances in Table 1 and development of mobility in Fig. 9). Before this age, chicks are protected by behavioural adaptations which ensure reduced spontaneous mobility (Uin 1984), and by low levels of responsiveness to calls of potentially dangerous adults (Evans 1973). If the hypothesis relating the development of individual recognition to the onset of mobility is correct, the chicks should have acquired the ability to recognize their parent's calls by no later than the age of eight days.

MULTIVARIATE ANALYSIS OF MEW CALLS

A system in which chicks must identify their parents' mew calls requires that any parent's mew call be much more similar to other mew calls of that parent than to mew calls given by other birds. As reviewed by Beer (1972), the importance of this concept has been recognized by authors for some time (e.g. Ramsay 1951; Hutchison et al. 1968; Evans 1970a), and there have been many different methods used to report cases in which inter-individual differences have been greater than intra-individual differences.

I used multivariate methods to test the uniqueness of herring gull mew calls.

METHODS

INDIVIDUAL RECOGNITION

Following Beer (1979), I subjected chicks to mew calls as they were being given by adults at nest sites (i.e. "live" instead of on tape) in 1979, between 25 June and 10 July. Nests in flat areas were staked and visited daily to obtain chicks whose ages were known. Forty nests were staked, from 28 June to 2 July, in an area of the colony which included the study area used in 1977 and 1978, and other undisturbed areas. I used a wide area so that it would never be difficult to select two chicks of the same age, each of which normally would not have heard the vocalizations of the other's parents. Chicks were tested at the ages of two, six, and eight days.

Trials were conducted as follows. One chick, to be the stranger, was taken from its nest and placed in a hardware cloth cage, a cube approximately 20 cm on a side. The cage was covered with a tight canvas cover which prevented seeing in or out. No shadows were visible through the thick canvas, even in bright sunlight.

The stranger was carried to the nest site of the resident chick for the trial. There, the resident was placed in a covered cage exactly as was the stranger. All other eggs and/or chicks were removed from the nest and taken far enough away that vocalizations the siblings might give would not be heard at the nest site.

The two cages, containing the resident and stranger, were placed approximately 1 m apart, and equidistant from the nest cup. Two cassette tape recorders (Sony TC-150), one for each chick, were started simultaneously. The two tapes were distinguished by reading the identity of each into its recorder's integral microphone. The tape recorders were placed inside tightly fitting canvas bags, which were acoustically transparent enough to transmit the sounds in the colony. One was placed beside each cage. With the recorders still running, I left the nest and walked away, usually to a point approximately 100 m from the nest, where I sat down and watched. Gulls were habituated sufficiently to the presence of humans in the colony that after my walking away and sitting down, one parent usually returned to the nest site and resumed normal behaviour. In 10 of 24 trials the parent continued to exhibit an alarm posture and I had to move out of sight before the parent calmed down. In these cases (blind trials) I had to interpret the results solely on the contents of the cassettes. In the other trials (visible trials) I could usually see the parent landing, calling, and walking around the cages.

After 15 min I returned to the nest and turned off the recorders. I returned any siblings and/or eggs to the nest and carried both cages to the nest from which I had taken the stranger. There the resident became the stranger, the stranger became the resident, and the experiment was repeated. Each chick was therefore tested once on its parents' territory and once on the stranger's parents' territory. At the end of the second trial, both chicks were returned to their nests. Neither these chicks nor any of their siblings were used again.

The tapes were later played to score the results of the trials. Both cassettes were rewound to the starting time and started simultaneously. As the cassettes played, any vocalizations by the parents were noted and the vocal responses of the chicks were recorded.

Results were analysed by means of 2 X 2 contingency tables. Significance was determined with the Fisher-Yates test of significance (Yates 1934; Fisher 1946), also called Fisher's Exact Test (Conover 1971). This test calculates the exact probability of the occurrence of a specific 2 X 2 table, rather than comparing a test statistic with a critical value, and therefore avoids the problems which can occur when the approximation is used for tables having small values in some cells. I generated probabilities with a small computer program, verified before use by comparison of test data with the tables published by Finney (1948).

MULTIVARIATE ANALYSIS OF MEW CALLS

I used principal component analysis (PCA) (Hotelling 1933) to express similarities within, and differences between, individual gulls. The benefits of PCA are the objective reduction of the dimensionality of a body of data while retaining as much of the original variance, the measurement of the contribution of each variable to the reduced-dimension data, and the illustration of inter- and intra-individual variability.

Mew calls were recorded at the nest site while chicks were present. Most recordings were made while chicks were being called out to receive food from a parent who had just arrived on the territory. The purpose of controlling context was to avoid any problems which might arise from grading in mew calls between feeding and aggressive contexts (Beer 1975).

All calls were recorded on a Uher stereophonic tape recorder, using shielded coaxial cables and microphones placed at the nest site. The microphones were covered by a thin cloth to hide them and avoid disturbing the parents or chicks. One track of the stereo tape was used to record calls and the other was used to record simultaneous annotation of the identity of calling birds and the context. By playing back both tracks during analysis, any possibility of misidentifying birds was eliminated.

Three or more satisfactory calls were obtained from each of 10 birds. To facilitate analysis and minimize problems with the validity of assumptions in parametric statistics (Glass et al. 1972), the sample size in analysis was fixed at three calls for each individual. In the case of birds for which more than three satisfactory calls were available, the calls to be analysed were chosen randomly.

Sonagrams of all the calls were printed on a Model 675 Kay Electric Missilyzer. Two sonagrams were made for each call: one with narrow band width for measuring frequency, and one with wide band width for measuring time. All sonagrams were made using the expanded scale.

Six variables were measured on each sonagram: (1) number of harmonics visible, (2) duration of the call, (3) the frequency range of the loudest harmonic, (4) the maximum frequency of the loudest harmonic, (5) the time from the beginning of the loudest harmonic until the point of maximum frequency, (6) the time from the beginning of the loudest harmonic until the point of minimum frequency.

All of the above measurements were made in mm directly from the sonagram, to avoid mixing units in the analysis and to avoid any errors of translation while converting linear units to s and kHz.

Data were standardized before analysis, to equalize the contribution of all variables to multivariate descriptions (Kleinbaum and Kupper 1978). To express, in two dimensions, the six-dimensional space and location occupied by the calls of each of the 10 individual gulls being analysed, two principal components were extracted from the data. The algorithm used to generate characteristic roots and vectors was Householder - Ortega - Wilkinson (Buhyoff et al. 1982). The scores for all 30 observations were calculated for both principal components, and the points plotted. The three points representing the observations for each individual were joined, so that an arrangement of 10 triangles showed the relative locations of the calls of the 10 gulls in two-dimensional principal component space.

As was the case in Hotelling's (1933) original application of the technique, no rotation of axes was performed on the components. The intention of the analysis was not to generate simple structure (Thurstone 1935, in Tatsuoka 1971; Kleinbaum and Kupper 1978), but only to illustrate spatial relationships in two dimensions and degeneracy in the correlation matrix for the six variables.

RESULTS

INDIVIDUAL RECOGNITION

Six chicks were tested at two days of age, 10 at six days, and eight at eight days. Chicks in the cages rarely moved and did not give any overt sign of distress.

In all trials at least one parent returned to the territory, but not always to the nest. After landing, usually near the nest and between the cages, the parent typically vocalized for a few minutes. These calls were a combination of call notes and alarm calls. During this period the general level of noise in the vicinity returned to normal as all parents gradually stopped vocalizing. Then the parent began walking around the territory, apparently searching for the missing chick(s). It was in this phase of the trial that mew calls were given. The time required for the parent to stop giving call notes and alarm calls and to begin searching ranged from 3 to 11 minutes in the trials during which mew calls were given. In the trials during which no mew calls were given, the parent usually continued to give call notes and/or alarm calls.

Mew calls were given in 12 of the 24 trials. All mews were monotonal (Appendix 2). Parents seemed more likely to give mew calls during blind trials (7 out of 10) than during visible trials (5 out of 14), but the difference was not significant ($p = 0.11$).

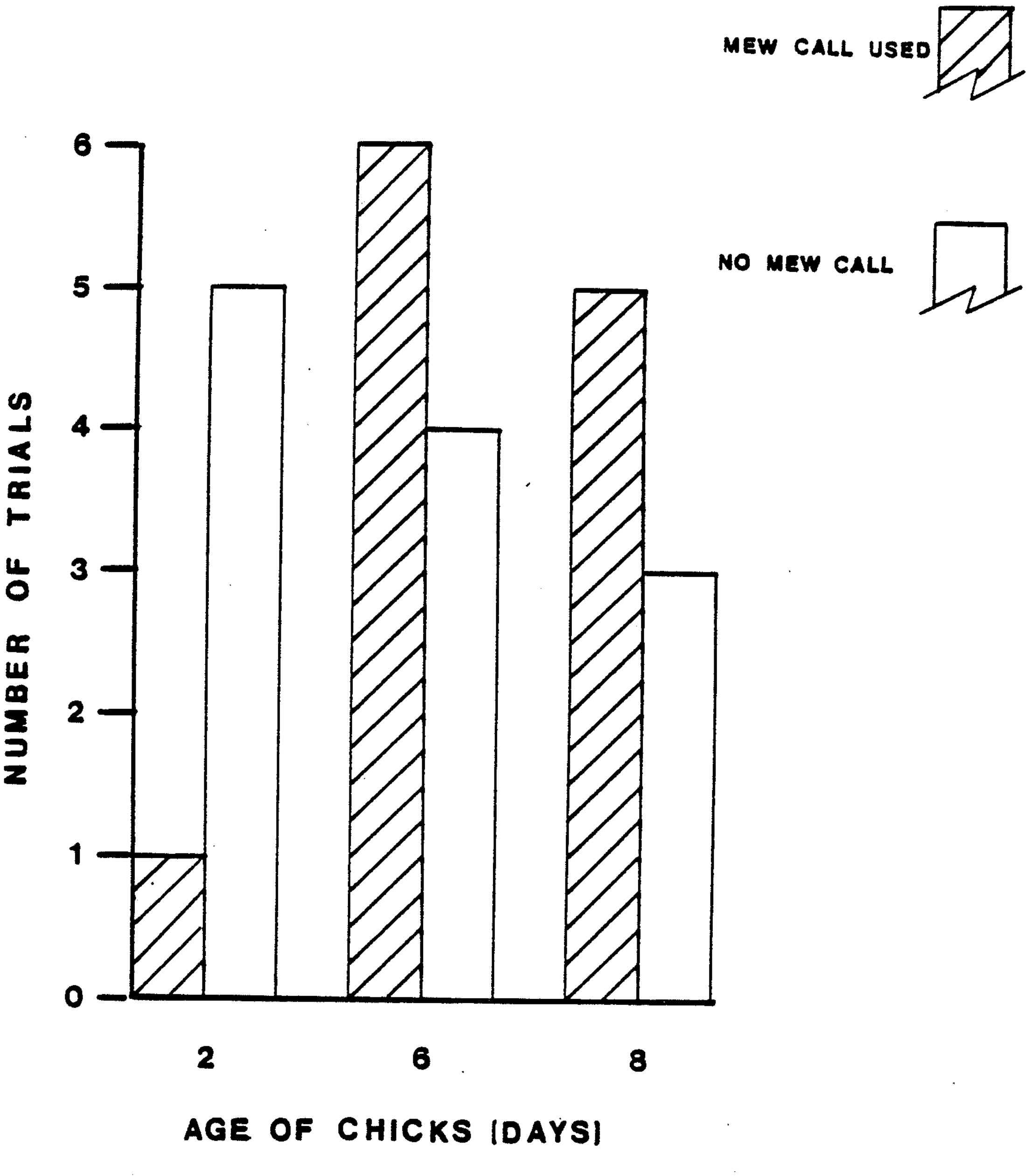
Hundreds of call notes and alarm calls were given by parents during the trials. There was never any response from the chicks to these calls. Several dozen long calls were given. One chick chittered after approximately a minute's silence following a long call. This is the only example of a chick's possibly responding to a call other than a mew call. One stranger chick began to vocalize in the absence of any calls from the resident parent. In only one of the 12 trials in which a mew call was given was there no response from either chick.

The use of the mew call by parents with chicks aged two, six, and eight days is shown in Fig. 10. There appears to be a change from infrequent use of the call at two days (1 out of 6 trials) to common use of the call when the chicks are six or eight days old (11 out of 18 trials). This trend was tested and found to be non-significant ($p = 0.08$).

The way in which parents return to the nest after a major disturbance, such as a visit to the nest by a human, changed as the chicks grew older. The parents of chicks two days old always returned directly to the nest as soon as I walked away (6 out of 6 trials). The parents of chicks six to eight days old usually returned to the territory, but not directly to the nest site (direct returns in 8 out of 18 trials, $p = 0.02$).

For the 12 trials in which mew calls were given, strangers responded in five trials to the calls of the resident chick's parent. Significantly more resident chicks vocalized (11 out of 12 trials, $p = 0.01$). This significant level of

Fig. 10. The use of mew calls by parents having chicks aged two, six, and eight days.


MEW CALL USED
NO MEW CALL
NUMBER OF TRIALS
0
1
2
3
4
5
6
2
6
8
AGE OF CHICKS (DAYS)

differential response to the chick's own parents indicates the presence of individual recognition of the parent's voice by the young.

Not only did the experiments demonstrate that chicks can recognize their parents' mew calls; they also suggest that parents do not recognize their chicks' voices. At three nests, where the resident young and parent exhibited particularly long and repetitive vocal exchanges while the stranger chick remained silent, the parent moved to the cage containing the resident chick and continued to mew and walk around the cage. At another nest, the stranger chick began to vocalize (apparently spontaneously, for no mew had been given by the parent), then the parent began to mew within 2 sec. In a trial where both chicks vocalized, the parent walked back and forth between the cages, continuing to mew. These data suggest that parents responded indiscriminately to any vocally active chick, and did not recognize vocalizations of their own chicks.

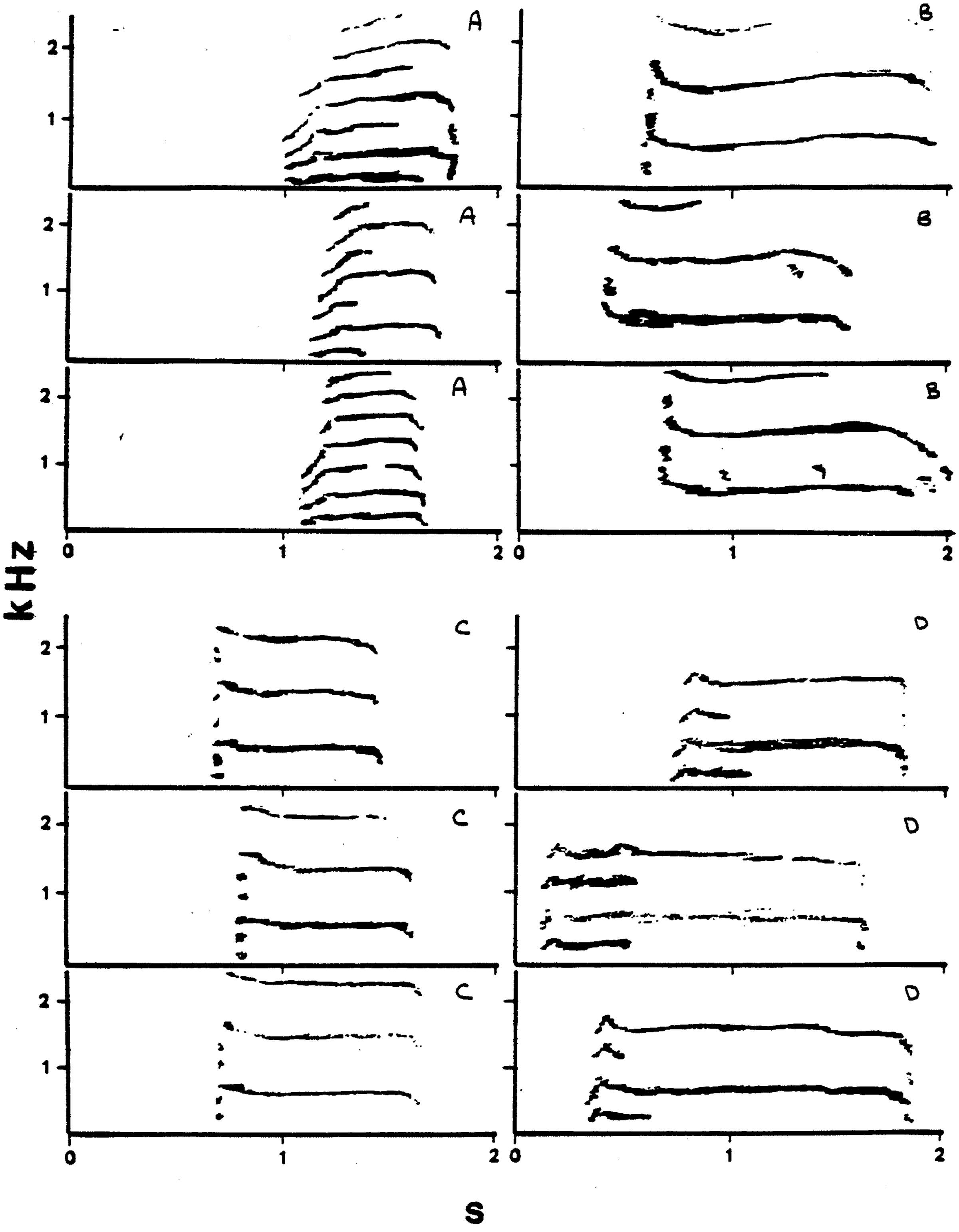
MULTIVARIATE ANALYSIS OF MEW CALLS

The essential qualities of the sonagram data on mew calls are that variation between individuals (distance between means) is high and variation within individuals (standard deviations) is low (Table 6). This pattern is also visible from the arrangement of sonagrams (Fig. 11); there are conspicuous similarities within birds and conspicuous differences between birds.

Table 6. The means and standard deviations (in parentheses) of the variables measured on sonagrams of mew calls. All variables except number of harmonics are given in mm, as they were taken from the sonagrams.

Bird	Harmonics	Duration	Frequency Range	Maximum Frequency	Time to Maximum Frequency	Time to Minimum Frequency
1	3 (0)	136.7 (7.6)	8.3 (3.2)	37.7 (21.1)	85.0 (5.0)	136.7 (7.6)
2	2 (0)	109.0 (25.1)	14.0 (4.4)	60.3 (0.6)	62.7 (16.2)	75.3 (61.9)
3	3 (0)	129.3 (17.6)	16.3 (2.1)	27.2 (0.6)	0 (0)	129.3 (17.6)
4	7 (0)	90.3 (21.4)	17.0 (1.7)	26.0 (0)	74.0 (13.9)	0 (0)
5	3 (0)	114.0 (7.0)	17.7 (1.5)	32.0 (1.0)	4.3 (1.5)	114.0 (7.0)
6	6 (0)	107.7 (6.1)	18.0 (2.0)	35.7 (1.5)	30.7 (47.2)	107.7 (6.1)
7	3 (0)	164.7 (14.6)	24.3 (1.2)	74.3 (1.5)	0 (0)	164.7 (14.6)
8	5 (0)	180.3 (28.4)	33.3 (2.1)	37.7 (0.6)	6.7 (0.6)	180.3 (28.4)
9	2 (0)	165.3 (5.0)	38.3 (3.8)	57.0 (4.6)	6.7 (1.2)	161.0 (5.6)
10	3 (0)	108.7 (11.0)	11.0 (1.0)	30.3 (1.2)	6.0 (1.0)	103.0 (10.4)

Fig. 11. Sonagrams of the mew calls of four of the gulls used in the principal components analysis. Three calls are shown for each gull, indentified as A, B, C, and D.


A
B
A
B
A
B
C
D
C
D
C
D
2
1
0
1
2
kHz
S

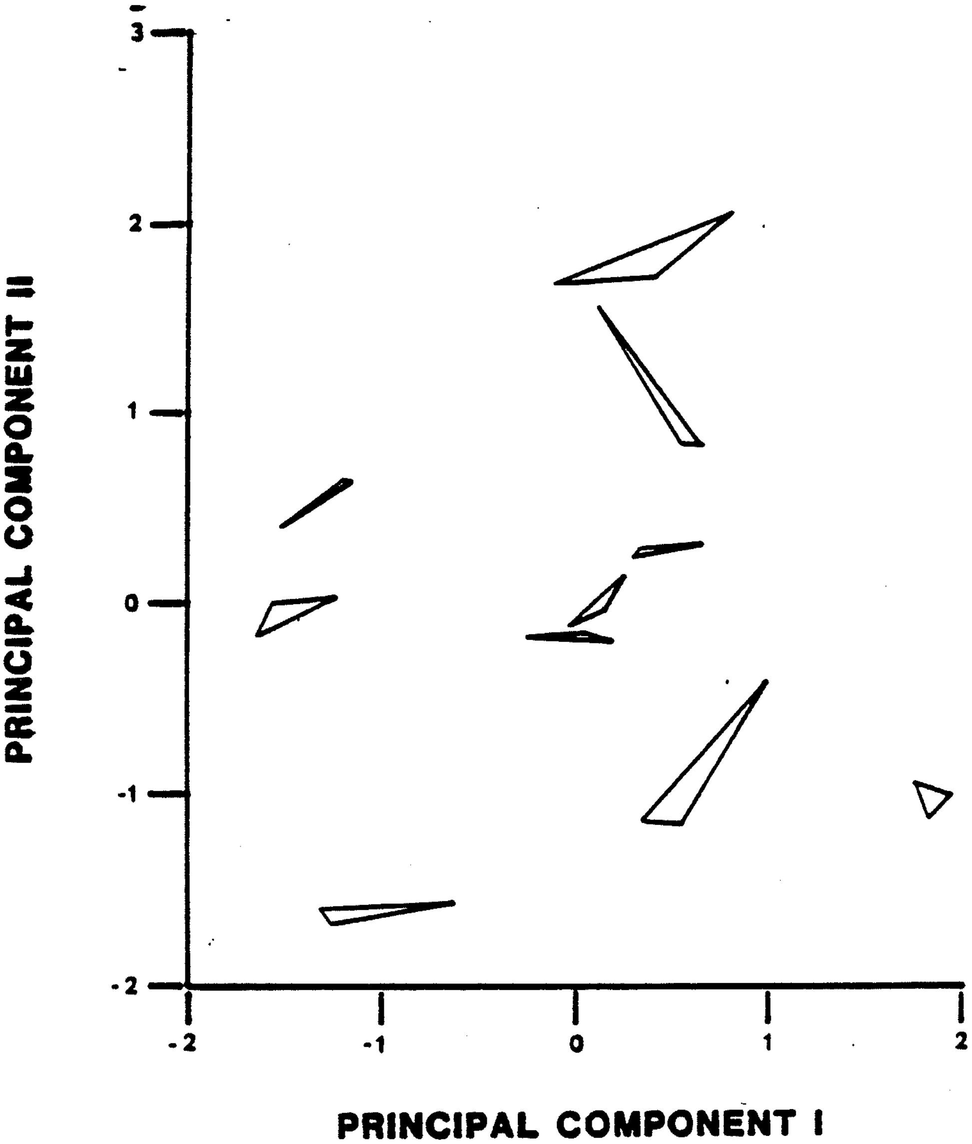
The structure of the two components created in the principal component analysis of mew call data is shown in Table 7. Each of the two columns of weights is a set of coefficients used in the linear combination of six original variables into one derived variable, or principal component score. The two columns of loadings are the correlations between each original variable and the derived variable created by the weights. The two derived variables included 69.8% of the total variation in the original six variables (51.2% in PC I and 18.6% in PC II). The loadings (Table 7) are similar in magnitude, showing that all variables contributed substantially to the components, with the exception of duration and minimum point in component II. This means that between gulls, mew calls differ with respect to many variables (at least six), rather than with respect to only one or two.

Fig. 12 illustrates the spatial relationships between the calls of individual gulls in the sample when PC I and PC II are used to present a two-dimensional representation of a system which is in fact at least six-dimensional. In this sample, separation between individuals is complete, meaning that for all 30 mew calls, measurement of the six variables used here would allow the identification of the calling bird with 100% accuracy.

Table 7. The factor weights and loadings for two principal components derived from the six original variables for herring gull mew calls.

Variable	Weight (PC I)	Weight (PC II)	Loading (PC I)	Loading (PC II)
Harmonics	0.1685	-0.6630	0.5178	-0.7407
Duration	-0.2820	-0.1248	-0.8661	-0.1395
Frequency Range	-0.2393	-0.4040	-0.7349	-0.4514
Maximum Frequency	-0.1973	0.4428	-0.6061	0.4947
Time to Maximum Frequency	0.1995	0.2814	0.6131	0.3144
Time to Minimum Frequency	-0.2858	-0.0390	-0.8778	-0.0436

Fig. 12. Individual distinctiveness of mew calls of 10 herring gulls, as demonstrated by principal component scores. Each gull is represented by a triangle, with a principal component score at each vertex.


3
2
1
0
-1
-2
PRINCIPAL COMPONENT II
-2
-1
0
1
2
PRINCIPAL COMPONENT I

DISCUSSION

INDIVIDUAL RECOGNITION

The system of recognition operating between herring gull parents and chicks, appears to consist of the following sequence. In the first four to five days of a chick's life, parents give mew calls during feedings and during normal contact at the nest site, but do not give mew calls when trying to locate chicks. By the age of six to eight days, chicks have developed the ability to discriminate between mew calls given by their parents and mew calls given by other gulls and vocalize selectively to their parents' mew calls. (The null hypothesis of inability to recognize calls is rejected.) When the chicks are at least six to eight days old, and are mobile enough that they often are difficult to find, parents give mew calls to locate their chicks. The parents feed and care for any chicks which respond appropriately to their mew calls.

Under this system, where adults apparently do not individually recognize their own young, chicks could respond to strangers as if they were their own parents, and be adopted in error. A similar recognition system has been suggested for the laughing gull (<u>Larus atricilla</u>) (Beer 1979). If an adult adopts the chicks of another brood, the adult is investing its resources in another gull's contribution to the next generation. This could decrease the probability of survival of the adopting parent and its own young (if still alive). Thus it seems anomalous that parents should not recognize their own young and be able to reject strange young seeking adoption. Further consideration suggests this does not happen because of the dangers inherent in a parent making an error and falsely rejecting its own young. Attacks by adults on chicks are often fatal (Kirkman 1937; Davis and Dunn 1976; Burger 1984). The selective cost of caring for an adopted chick is surely less than the selective cost of the death of one's own chick. Moreover, if a chick loses its parent, this system allows the chick to "cheat" when its situation becomes desperate: it can become less selective, respond to another gull's mew call, and increase its chances of being adopted. There would thus appear to be an overall advantage accruing to all individuals under the existing recognition system.

Note that in the recognition of calls being discussed here, species recognition is not important. Unlike vocal communication during mating, where species identification is critical, the only recognition which confers a selective advantage to a herring gull chick is the recognition of the calls of its two parents. This point renders more understandable the results of Evans (1975), which showed that parentally naive herring gull chicks stayed silent and still when exposed to herring gull mew calls. The logical default response to a mew call should be to remain silent and still. Chicks should respond only when sure that the call they hear is from one of their parents. The corresponding default response for a parent should be to feed a begging chick indiscriminately near the nest site. In the event of an adoption occurring because of these responses, the adopting parent is not being altruistic, as suggested by Pierotti (1980). It is just being careful not to hurt its own chick, and it is relying on its own chick's ability to recognize mew calls.

This interpretation of the recognition system in families of herring gulls suggests that interpretations of adoption in gulls as being maladaptive (Holley 1984) or based on non-kin altruism (Pierotti 1980) may be incorrect. As indicated by Waltz (1981) (tempered by Pierotti 1982), it is necessary to define terms clearly in analyses of this type. Traits which impose a cost on individuals which possess them are only maladaptive if the net result is fewer offspring in the next generation. A long-term examination of costs and benefits is required before claims of maladaption can be justified, and they do not appear to be so in the present instance.

MULTIVARIATE ANALYSIS OF MEW CALLS

When assessing the physiological basis for vocal recognition, Ramsay (1951) referred to "several factors, variation in any one of which upsets the recognition behavior of parents and young". Hutchison et al. (1968) examined seven variables taken from sonagrams of the "fish calls" of Sandwich terns (Sterna sandvicensis). They calculated coefficients of variation for all variables, and concluded that the three variables which contained the greatest variations were used for individual recognition. Evans (1970a) presented a 3 X 3 array of sonagrams of black-billed gull (Larus bulleri) mew calls, with columns representing individuals and rows representing replications. Consistency within individuals was readily apparent. Beer (1972), dealing with several calls of laughing gulls, also used sonagrams to illustrate inter-individual variability. Baker (1982) measured five variables from sonagrams of the "purr" calls of dunlins (Calidris alpina). He then selected the three variables with the largest standard deviations to create a three-dimensional plot of the calls of 17 individuals, illustrating the relative magnitude and orientation of differences between the calls of individuals.

All of the above methods for demonstrating the individual distinctiveness of calls make the essential point, but each has a drawback. Hutchison et al. (1968) arbitrarily selected three variables, and did not examine relationships between variables. This is a weakness of univariate statistics which is often cited by authors of texts on multivariate statistics (e.g. Tatsuoka 1971; Harris 1975). Evans (1970a) and Beer (1972) made clear visual points, but there was no quantitative measure of differences or similarities. Baker (1982) showed three-dimensional relationships, but was also arbitrary in selecting three variables and provided no estimate of intra-individual variance. Perhaps the individuals in Baker's plot should be represented, not by points, but by spheres which overlap considerably. Without some expression of within-individual variance, we do not know which representation, spheres or points, is more correct. Beer (1972) summarized the above difficulties when he stated "Frequency/time patterns displayed in some spectrograms are sometimes so complex that specification in quentitative (sic) terms is difficult or cumbersome.", and he relied on subjective evaluations such as the statement that, because of overlap, crooning calls appear "to be quite useless as a means of individual identification".

In contrast to Beer's results, the PCA analysis of mew calls used in this study rejected the null hypothesis of calls' not being individually distinctive and made two clear points. When feeding chicks, herring gulls give mew calls which are unique and consistent. Also, the unique nature of these calls is not determined by just one or two variables, but by at least six.

The implications for systems of individual recognition are substantial. Six or more dimensions allow sufficient "room" for a large number of unique calls. Each of the many adults whose calls would be audible to a chick in the first weeks of life therefore could occupy a unique location in the multidimensional space enclosing all mew calls.

By exhibiting variability between individuals in at least six dimensions, the adults' mew calls provide chicks with the possibility of uniquely identifying individual adults, even in colonies of thousands of breeding pairs. There would clearly be strong selection for chicks who developed improved auditory discrimination before the onset of mobility.

In future research, it would be useful to compare the auditory identification of adults by using mew calls, with the visual identification of chicks by using spotting patterns. Miller and Emlen (1975) found that adults did not respond to changes in the appearances of their chicks, but sample sizes were small, and no comparison of the relative uniqueness of spotting patterns and vocalizations was conducted.

In analyses of the adaptive significance of vocal recognition and the relative merits of visual and vocal systems of individual recognition, it is important to consider the implications of the fact that visual communication systems almost always present the possibility of two-way transmission of information, whereas vocal communications can readily be one-way. A gull chick can listen to an adult's vocalization without revealing its location, but to look at an adult, it must take the risk of being seen. Use of auditory recognition could thus be a highly adaptive means of reducing the risk of predation by neighbours (PART 1) in this species.

Vocal displays also appear likely to allow discrimination to occur more quickly. This is important in the context of the few seconds available for a chick to make a critical decision.

VOCALIZATIONS IN RELATION TO CLIFF AND FLAT NESTING HABITATS

The data presented above, in which chicks recognize the distinctive vocalizations of their parents, make the successful nesting by herring gulls on both cliffs and flatland less paradoxical. On flatland, this system provides the chicks, who must hide from predatory neighbours, with reliable criteria for deciding when to come out of hiding to be fed and protected by their parents. Individual recognition may be less important on cliffs, where potential brood mixing is less likely. Indirect evidence, from experimentally induced adoptions (Berens von Rautenfeld 1978) suggests that recognition may in fact be less well-developed at cliff nests, although cases of adoptions at cliff sites found by Berens von Rautenfeld may merely reflect lack of escape routes for chicks. Moreover, on cliffs, the safety of chicks is provided for primarily by their inclination to make repeated use of good hiding places and to avoid cliff edges, rather than avoiding neighbours. Individual recognition would presumably only come into play on cliffs if the arrangement of neighbouring nest ledges were to pose risks similar to those encountered on flatland. Thus a single set of vocal signals and responses exists which is evidently robust enough to allow herring gulls to nest on both cliffs and flatland.

PART 3: SIMULATION OF PATTERNS OF MORTALITY IN HERRING GULL CHICKS

INTRODUCTION

It was hypothesized in the GENERAL INTRODUCTION, and suggested by data in PART 1, that patches of massive juvenile mortality caused by chain-reaction cannibalism could be a significant mortality factor in herring gulls. Although this phenomenon has been reported in other studies (Davis and Dunn 1976; Burger 1984; Schoen and Morris 1984), it is difficult to use field data to test hypotheses regarding the magnitude of its importance because of its rarity and unpredictability, and because of the logistic difficulties and the time scales in herring gull population dynamics. It was feasible, however, to use computer simulations of the positive feedback system of chain-reaction cannibalism to indicate whether the hypothesis is plausible, and if so, at what levels of spacing and predation.

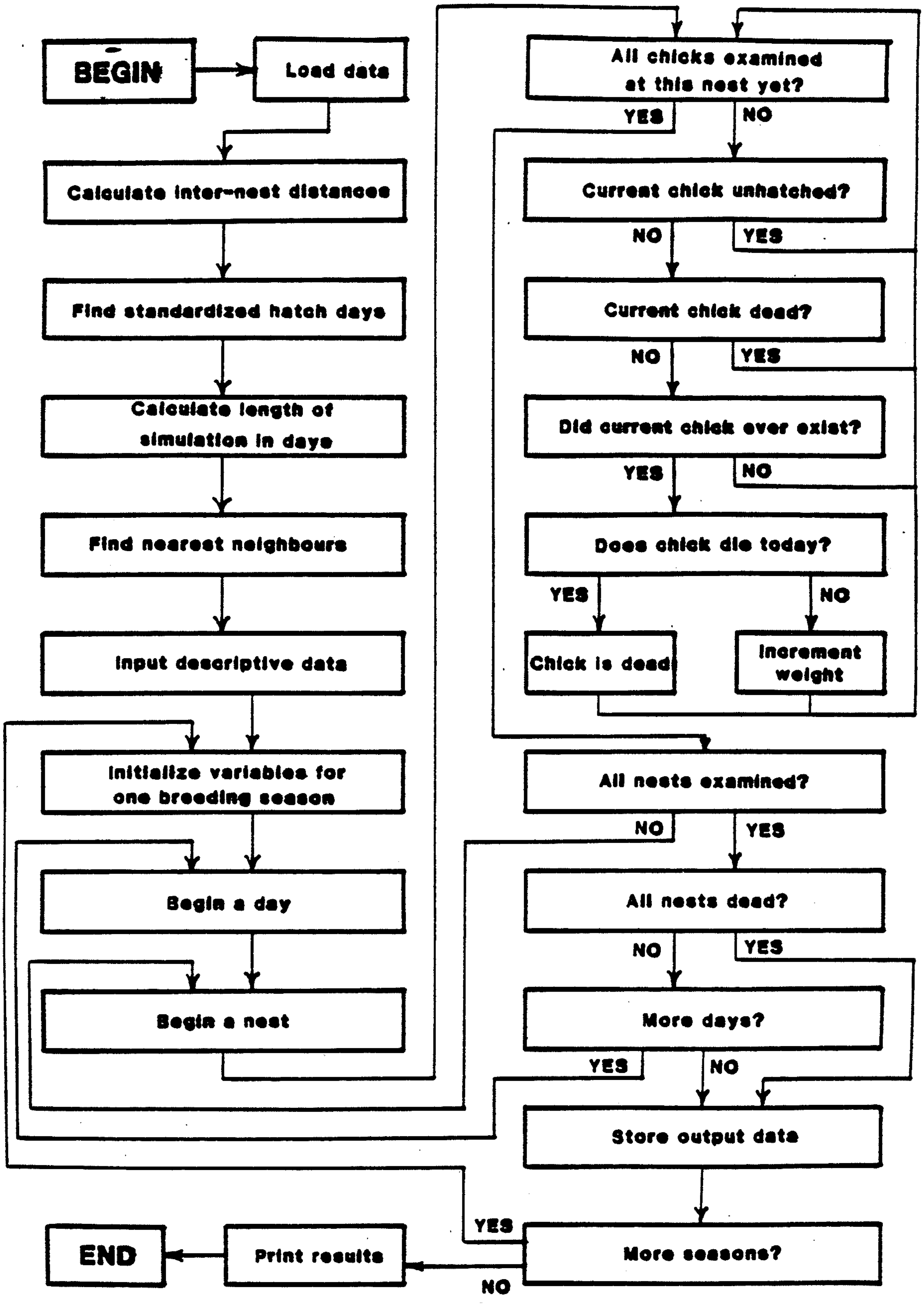
I addressed five questions in the simulation work. Can the proposed system of rare and unpredictable chain-reaction cannibalism generate a significant level of juvenile mortality? If significant juvenile mortality can be generated, at what nesting densities does it occur? In order for chain-reaction cannibalism to be a significant factor in the nesting of herring gulls, how long must parents remain on their territories after losing all their chicks? (This period will be referred to below as lag time, and parents who have lost all their chicks will be referred to as bereaved parents.) In order for chain-reaction cannibalism to be a significant factor in the nesting of herring gulls, how much must a chick's probability of survival be reduced when a neighbour has lost all its chicks and remains on territory? Is chain-reaction cannibalism likely to affect cliff and flat nesting herring gulls differentially?

METHODS

All simulation work was performed on a Compaq Deskpro 286 with programs (Appendix 5) (Fig. 13) written in Turbo Pascal. The general principle of operation was to have the model step through a breeding season day by day. On each day, each of 25 nests was checked to see if its chicks were hatched. If they were, each chick was checked to see if it was alive. If it was alive, its weight and its status relative to other nests were evaluated and the probability of its surviving the day was calculated. This calculation was based on a multiple regression equation which used the characteristics of the nest site before hatching, converted into a daily probability of dying, according to the distribution of age at death for the chicks known to have died in 1977 and 1978 at Kent Island (PART 1). The selection of variables for use in the multiple regression equation was performed by sequentially eliminating variables (from hatching weight, hatching date, number of chicks hatched, density variables, nest site variables) until only those which added at least 1% to the predictive capability of the equation were retained.

The overall probability of survival for each chick, calculated from the above regression equation, was distributed in the model among the 21 days during which the chick was considered to be vulnerable. The method used for distributing these probabilities was to fit a polynomial equation to the actual age-specific death rates for chicks in life, and use the

Fig. 13. Flow chart of the simulation program.


BEGIN
Load data
Calculate inter-nest distances
Find standardized hatch days
Calculate length of simulation in days
Find nearest neighbours
Input descriptive data
Initialize variables for one breeding season
Begin a day
Begin a nest
All chicks examined at this nest yet?
YES
NO
Current chick unhatched?
NO
YES
Current chick dead?
NO
YES
Did current chick ever exist?
YES
NO
Does chick die today?
YES
NO
Chick is dead
Increment weight
All nests examined?
NO
YES
All nests dead?
NO
YES
More days?
YES
NO
Store output data
More seasons?
YES
NO
Print results
END

y-values of this curve to generate day-specific probabilities of surviving which would have a grand product equal to the overall probability of the chick's surviving.

A number was chosen at random from a standard normal distribution (see procedure RANDNORM, Appendix 5). If the probability of drawing a number as large as, or larger than, the drawn number were smaller than the probability of the chick's dying on that day, the chick was classified as dead. If the chick survived the day, its weight was increased according to the growth equations fitted to field data obtained by weighing chicks every four days (PART 1). When a chick reached the age of 21 days or a weight of 500 g, it was assumed to be safe, and its probability of dying on all subsequent days of the breeding season was zero. Each breeding season continued until all chicks were dead or safe. At the end of each season, the status of each chick at each nest was printed.

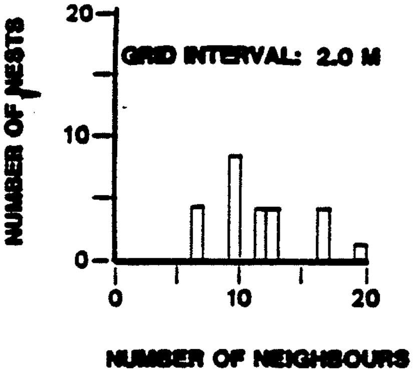
Three input variables were manipulated: density, the lag for bereaved parents, and the change in the probability of a chick's dying if a set of parents within 5.0 m became bereaved. Details of the values of these variables are given below. Fifty breeding seasons were conducted for each set of input variables. At the end of every set of 50 seasons the mean and standard deviation of the number of surviving chicks and the number of extant broods was printed.

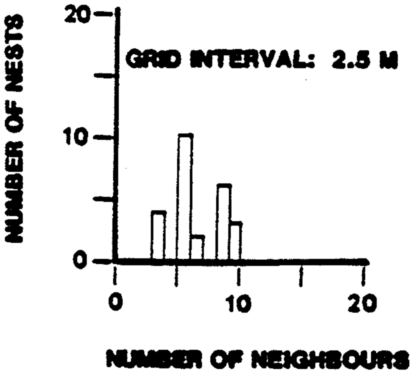
In many cases, data were not used in the model exactly as they were gathered in the field, but were simplified to make the model more tractable or the results more general. For example, in a real colony, a patch of 25 nests would show a range of inter-nest distances. In the model, the 25 nests were distributed approximately evenly on a square grid, within which the inter-nest interval (grid interval) could be varied between simulations to generalize about the effects of nesting density. Coordinates of each nest were given minor random deviations from grid line intersections to prevent nests from having perfectly equal distances to neighbours. This arrangement of nests falls between the perfectly even spacing of a set of hexagonally packed territories and the variable spacing of a real colony.

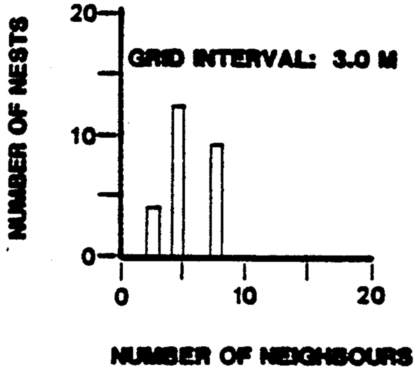
The grid interval was varied from 2.0 m to 5.0 m, at 0.5 m intervals. Fig. 14 shows the seven frequency distributions for the number of neighbours within 5.0 m at the beginning of each simulation. Note that the grid interval is the approximate distance to the nearest neighbour for every nest at the beginning of each season, and that the range of inter-nest intervals used (2.0 m to 5.0 m) brackets the overall mean distance to nearest neighbours in my study area, approximately 3 m (Table 1).

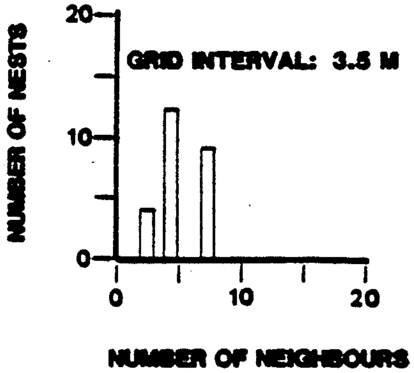
The lag for bereaved parents was varied from one to five days. This range included most values from my field data. Davis and Dunn (1976) reported birds remaining as long as seven days, but I observed that typically bereaved parents left in two to three days (PART 1).

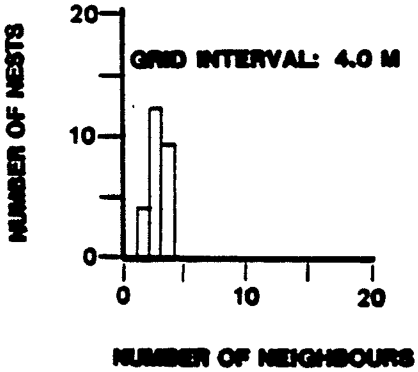
Fig. 14. Frequency distributions showing the number of neighbours within 5.0 m at the start of each season for each grid interval used in simulations.

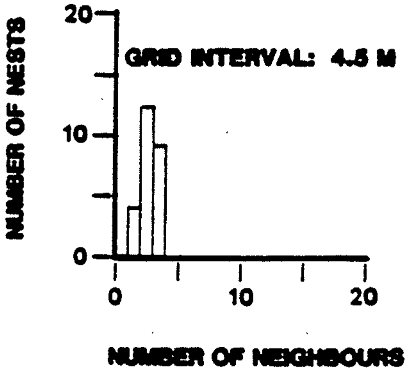

GRID INTERVAL: 2.0 M
NUMBER OF NESTS
NUMBER OF NEIGHBOURS
0
10
20
0
10
20

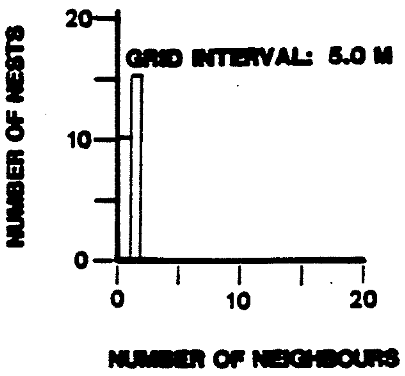

GRID INTERVAL: 2.5 M
NUMBER OF NESTS
NUMBER OF NEIGHBOURS
0
10
20
0
10
20


GRID INTERVAL: 3.0 M
NUMBER OF NESTS
NUMBER OF NEIGHBOURS
0
10
20
0
10
20


GRID INTERVAL: 3.5 M
NUMBER OF NESTS
NUMBER OF NEIGHBOURS
0
10
20
0
10
20


GRID INTERVAL: 4.0 M
NUMBER OF NESTS
NUMBER OF NEIGHBOURS
0
10
20
0
10
20


GRID INTERVAL: 4.5 M
NUMBER OF NESTS
NUMBER OF NEIGHBOURS
0
10
20
0
10
20


GRID INTERVAL: 5.0 M
NUMBER OF NESTS
NUMBER OF NEIGHBOURS
0
10
20
0
10
20

The values for the change in probability of a chick's dying were arbitrarily varied from 0% to 40%, in steps of 10%. At 0%, there was no change in the probability of a chick's dying regardless of the number of bereaved parents within 5.0 m. At 40%, the probability of a chick's dying on a given day was 40% greater than would have otherwise been calculated by the polynomial fit of the multiple regression prediction for that nest.

All nests were assumed to have 2 dangerous quadrants, the closest integral value to the mean number of dangerous quadrants in the cliff area (Table 1) and the exact mean number of dangerous quadrants for the flat area.

All nests and all eggs were assumed to hatch on the same day. Every nest was assumed to have two chicks hatch, the A and B chicks. All chicks were assumed to weigh the same at hatching and gain weight at the same rate, both of which parameters were determined by fitting the growth of chicks to a curve.

Although weight gain is most commonly fitted to sigmoidal curves (logistic, von Bertalanffy, Gompertz) (Ricklefs 1979; Ricklefs 1983; Zullinger et al. 1984) I did not use one of these curves because the growth of chicks during the first three weeks of life does not approach an asymptote, but continues to grow exponentially. The specific model I used to represent exponential growth was

$$w_t = ae^{bt}$$

where

w_t = the weight of the chick at time t
a = the y-intercept of the equation (hatch weight)
b = the coefficient of exponential growth
t = the age of the chick in days

All growth curves were estimated by a least squares fit. No data were used which involved chicks over 700 g or 21 days of age, to avoid using any data points which were past the likely inflection point of the long-term sigmoid pattern of growth of the chicks. Separate equations were not generated for A and B chicks for two reasons. An analysis of egg dimensions (Appendix 4) did not show a significant difference between A and B eggs; A and B eggs would therefore be expected to have the same y-intercept for their growth equations. Moreover, the distinction between A and B eggs and chicks in many clutches was not certain. If known A, B, or C chicks were the only data used to generate a growth curve, a very small sample would have been available.

When simulations were run using the above data, for every combination of lag and grid interval one run was made with the change in probability of a chick's dying set at 0%. This removed the effect of predation by neighbours on the survival of chicks, and provided a method of testing the model for bias.

For each grid interval, the expected value of the mean of the results of these 0% runs would be the value predicted by the multiple regression equation for that grid interval. The closer the mean to the deterministic prediction, the less bias there would be in the model.

RESULTS

Table 8 (parts A and B) shows the parameters of growth equations for all the categories of chicks, determined from 1978 field data. The equation chosen for use in simulations was the one describing growth of cliff A and B chicks that survived to 500 g. (Fig. 15), because the correlation coefficient of this equation was higher than the correlation coefficient for chicks in flat habitat (Table 8A). Note that any differences between simulations using equations from cliff and flat areas are likely to be trivial: one equation reaches 500 g in 17 days and the other in 18 days. All chicks were given a hatching weight (74 g) equal to the y-intercept for the growth equation of A and B chicks in cliff habitat.

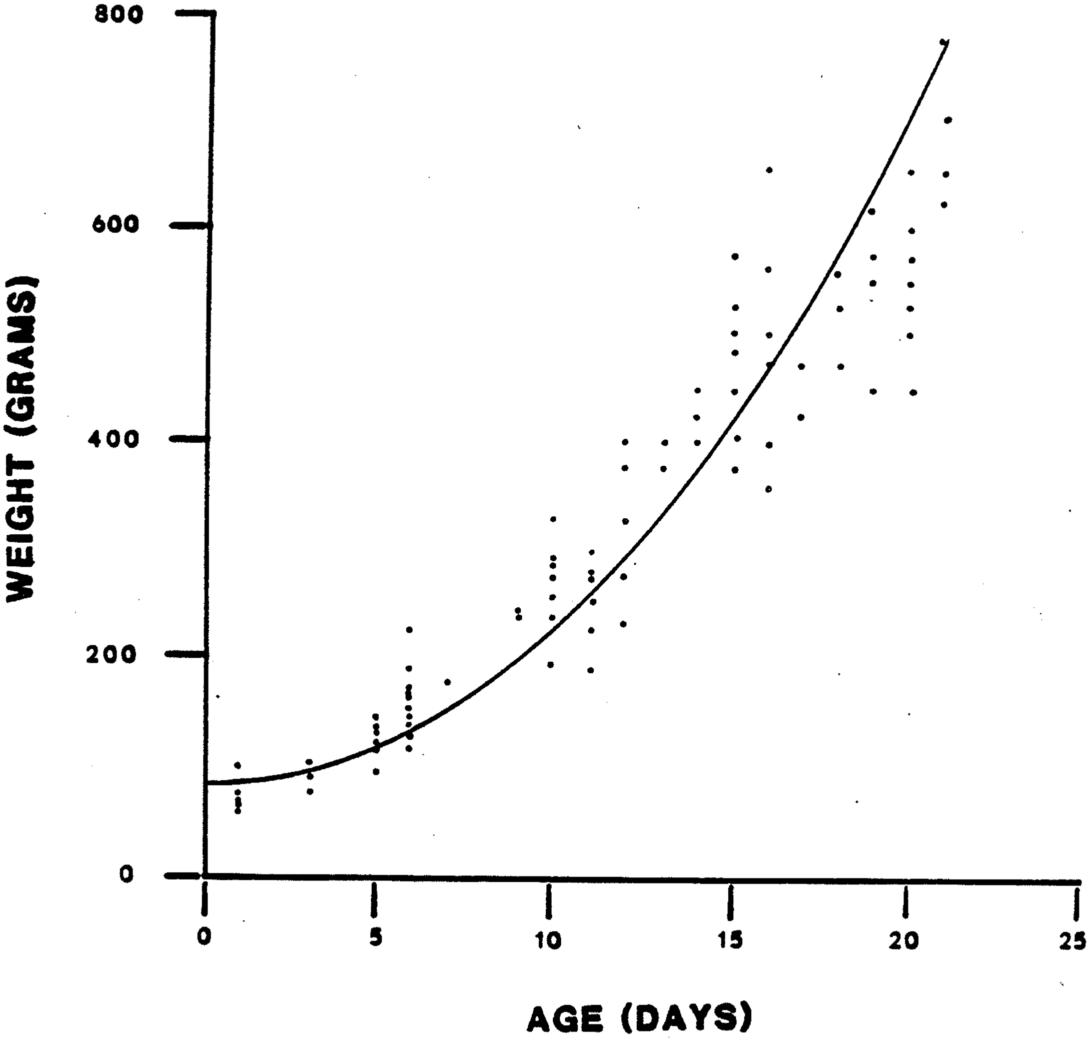
Table 8B shows growth rates for chicks which did not survive, indicating the problems which can be associated with pooling data from all gull chicks to estimate growth. The A and B chicks from the flat area (Table 8B) included several chicks which had been injured and failed to gain weight normally over a period of many days prior to their dying. Had they been included in the data, they would have decreased the slope of the fitted line by 10%: the slope for the flatland A and B chicks that reached 500 g was 0.111 and the slope for flatland A and B chicks that did not reach 500 g was 0.099. It is interesting to note that the C chicks did not follow the

Table 8. Intercepts (a), slopes (b), correlation coefficient (r) and quality of fit (r^2) for equations of growth rates of A, B, and C chicks.

Category of Chick	a	b	r^2	r	S.E.	n	Days to 500 g
A. Chicks that reached 500 g:							
Cliff, A & B	74.06	0.112	0.946	0.973	0.179	128	17
Flat, A & B	67.51	0.111	0.934	0.966	0.194	67	18
Cliff & Flat, C	62.92	0.118	0.946	0.973	0.182	22	18
B. Chicks that did not reach 500 g:							
Cliff, A & B	68.27	0.119	0.818	0.905	0.274	40	17
Flat, A & B	62.19	0.099	0.850	0.922	0.227	61	21
Cliff & Flat, C	56.77	0.126	0.856	0.925	0.255	28	17

Fig. 15. The fit of the growth equation to the scatter of weights for A and B chicks in the cliff area. The equation of the growth curve is

$$w_t = 74.06\ e^{0.112t}$$


800
600
400
200
0
WEIGHT (GRAMS)
0
5
10
15
20
25
AGE (DAYS)

same association between slow growth and failure to survive, exhibited by A and B chicks. The C chicks that died actually grew faster than the C chicks that survived; in fact they grew faster than any other group of chicks.

In the generation of a multiple regression equation to predict the number of chicks in a nest which will survive, 3 variables were rejected because they each contributed less than 1% to the predictive capability of the equation: the number of safe quadrants, the number of nests within 2.5 m, and the number of nests within 5.0 m. The accepted variables were the distance to the nearest neighbour, the number of dangerous quadrants, the hatch day, and the number of chicks hatched. (In this study, the only independent variable in the equation which was manipulated during simulation was the distance to the nearest neighbour, so the multiple regression as used here is effectively a simple linear regression. The details of the multiple regression equation were retained so that future simulations could be run with the same predictor, thereby generating results which will be suitable for comparison with this study.) The resulting equation was

$$c_s = 1.995 + 0.012d + 0.173q - 0.059h + 0.337c_h$$

where

c_s = the predicted number of surviving chicks,

d = the distance to the nearest neighbouring nest,

q = the number of dangerous quadrants around the nest,

h = the hatch day for the first egg in the nest, and

c_h = the number of chicks hatched.

Note that although the regression is significant ($F = 8.45$, $df = 4.65$, $p < 0.05$)), only 35% of the variability in the number of chicks produced per nest is accounted for by the equation ($r^2 = 0.349$), and therefore there are factors other than the site-specific variables measured here which strongly influence the number of chicks produced at a nest.

Because of the particular variables selected, there was no need to make separate specific predictions about survival in cliff and flat habitats. The distance to nearest neighbour and the number of dangerous quadrants were not significantly different between cliff and flat habitats (Table 1). Cliff and flat areas did not have significantly different hatch dates (PART 1). Direct measures of reproductive success (PART 1) showed that there was no consistent difference between habitats in the number of chicks hatched per nest. Thus all the variables used to predict chick survival occurred at the same mean level in both habitats. Differences in the magnitude of the variables represented differences between individual nests, not habitat types.

The polynomial equation which was used to adjust the overall probability of a chick's dying to match the pattern measured in the field was

$$w_t = b_0 + b_1(x_t) + b_2(x_t)^2 + b_3(x_t)^3 + b_4(x_t)^4$$

where

w_t = the weight used to adjust the overall probability of a chick's dying to the probability of that chick's dying on day t

x_t = the age of the chick on day t

b_0 = -1.26407108

b_1 = 2.63113166

b_2 = -0.325849884

b_3 = 0.0140932144

b_4 = -0.000203827235

The fit of this equation to data is shown in Fig. 16.

The results of testing for bias, by setting the change in the probability of a chick's dying to zero (Fig. 17), showed that the model contains a small and fairly consistent bias (5% to 8%) toward overestimating the survival of chicks. Given the substantial variability in survival of chicks in the field, I concluded that a bias of this magnitude was inconsequential to the objective of the study. The bias is unlikely to affect cliff and flatland differentially.

The results of the simulations over a range of grid intervals, lags, and values for the change in probability of a

Fig. 16. The age-specific death rates for A and B chicks from cliff and flat areas, and the fitted polynomial function (see text for equation).

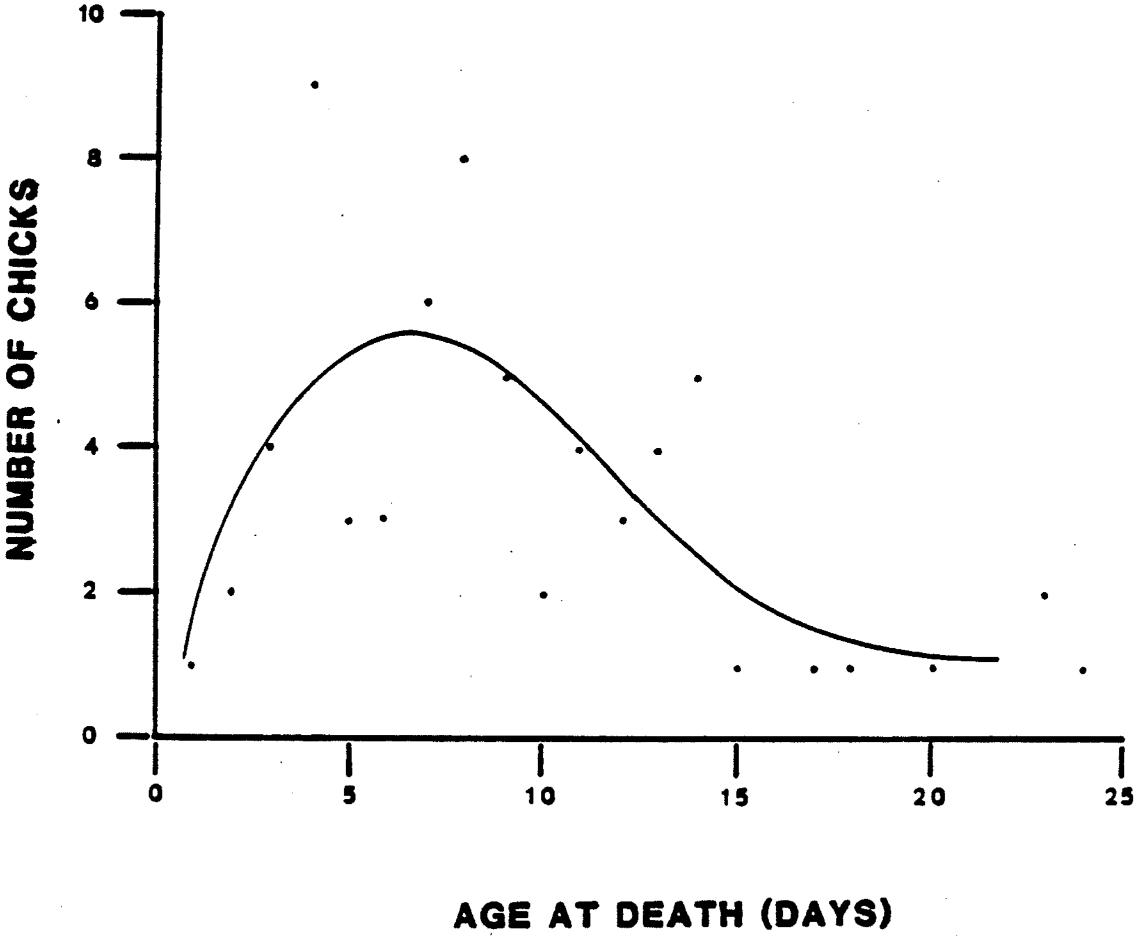
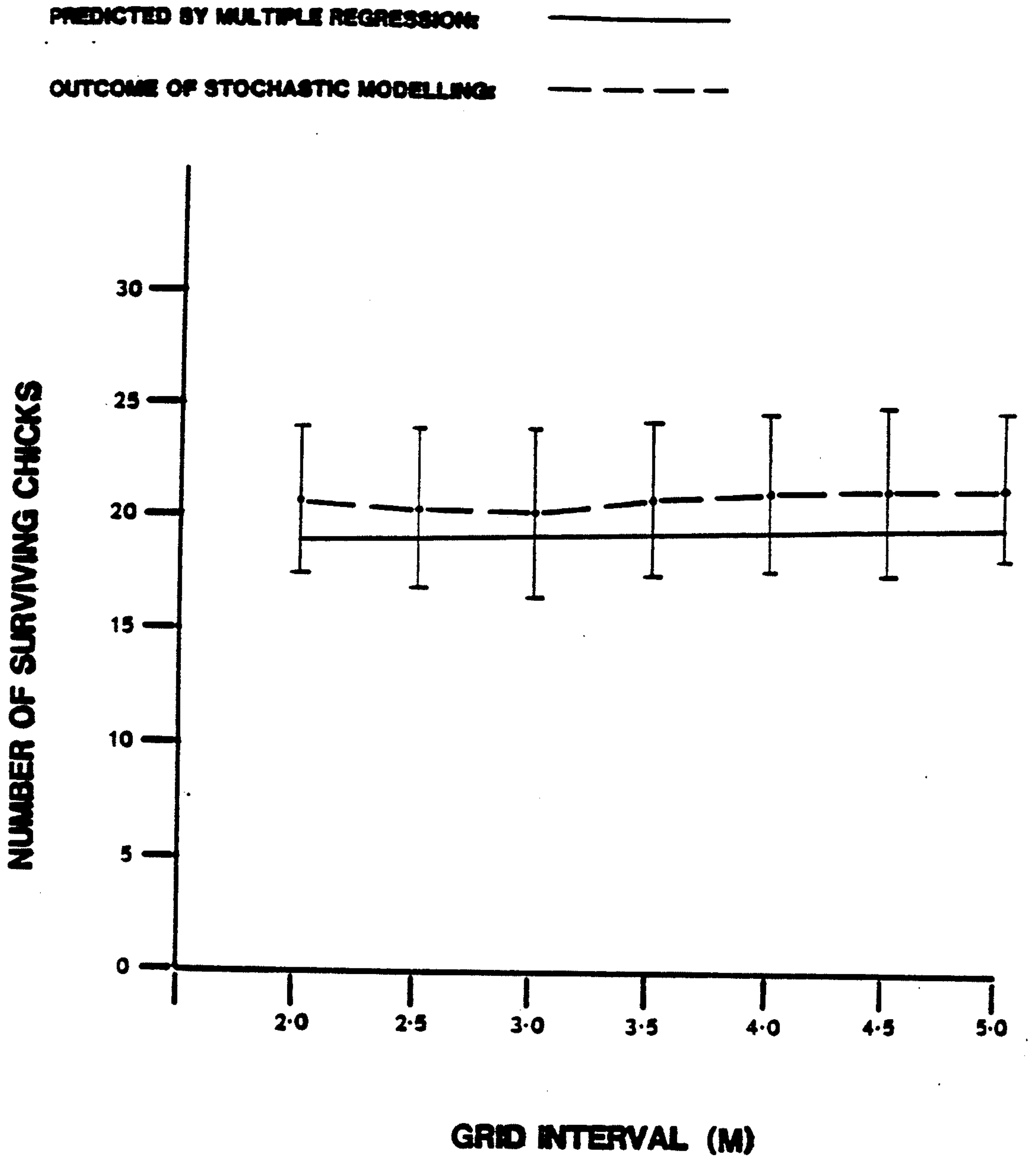

NUMBER OF CHICKS
10
8
6
4
2
0
0
5
10
15
20
25
AGE AT DEATH (DAYS)

Fig. 17. The fit of stochastic simulation results to the multiple regression line (see text for equation). Each point on the stochastic line is the mean number of chicks surviving for 50 breeding seasons, with the change in the probability of a chick's dying if a neighbour becomes bereaved set to zero. The vertical lines represent +/- one standard deviation.


PREDICTED BY MULTIPLE REGRESSION:
OUTCOME OF STOCHASTIC MODELLING:
NUMBER OF SURVIVING CHICKS
30
25
20
15
10
5
0
2·0
2·5
3·0
3·5
4·0
4·5
5·0
GRID INTERVAL (M)

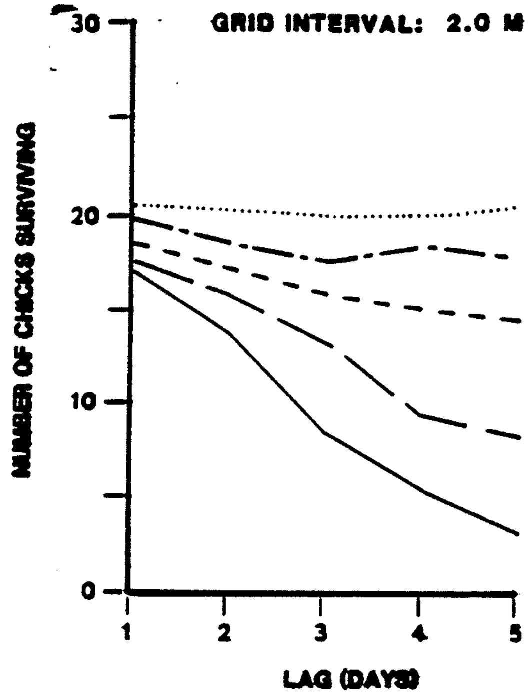
chick's dying are shown in Fig. 18 and 19. Fig. 18 shows the expected survival under each combination of input variables, Fig. 19 the degree of variability (uncertainty) associated with each combination. The figures can be assessed most effectively by comparing the graphs with respect to the degree to which the lines diverge as distance to nearest neighbour decreases. Survival decreases with lag and variability increases markedly as the probability of a chick's dying increases at small grid intervals.

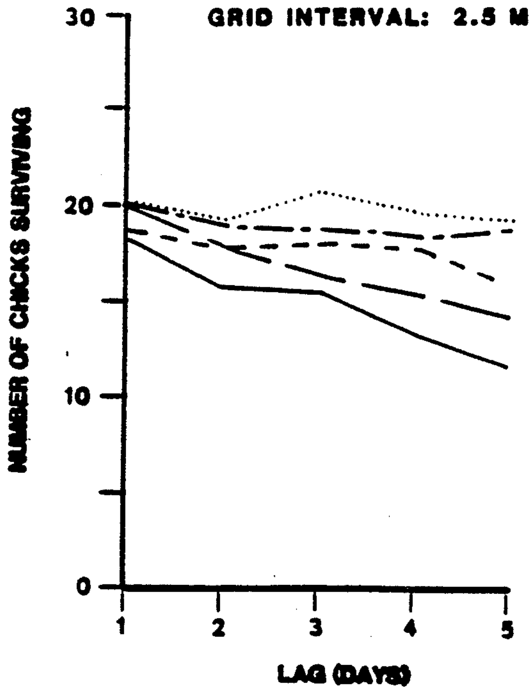
Two contrasts provide an index of how much difference should be expected between any two graphs in Fig. 18 and 19 on the basis of chance alone: the frequency distribution of the number of neighbours within 5.0 m (Fig. 14) is the same for 3.0 and 3.5 m grids, and for 4.0 and 4.5 m grids. The expected results for each of these pairs of grid intervals are the same, and so any differences in results within a pair are due to chance.

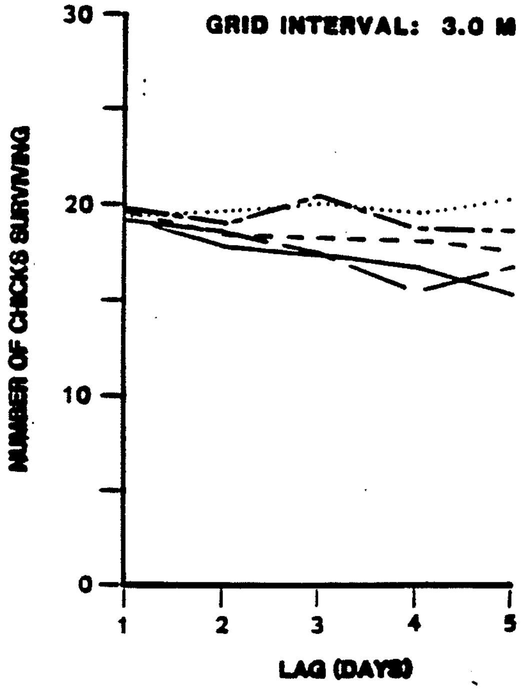
The simulation results illustrated in Fig. 18 and 19 can be related to data from cliffs and flatland by comparing the grid intervals used in the simulation with actual mean distances to nearest neighbours (Table 1), and by comparing the frequency distributions in Fig. 14 with the mean number of neighbours within 5.0 m (Table 1). Most of the nests in the Kent Island study area are represented by the graphs for grid intervals of 3.0 to 4.5 m, although some (either isolated nests or nests which were less than 1 m from the nearest neighbour)

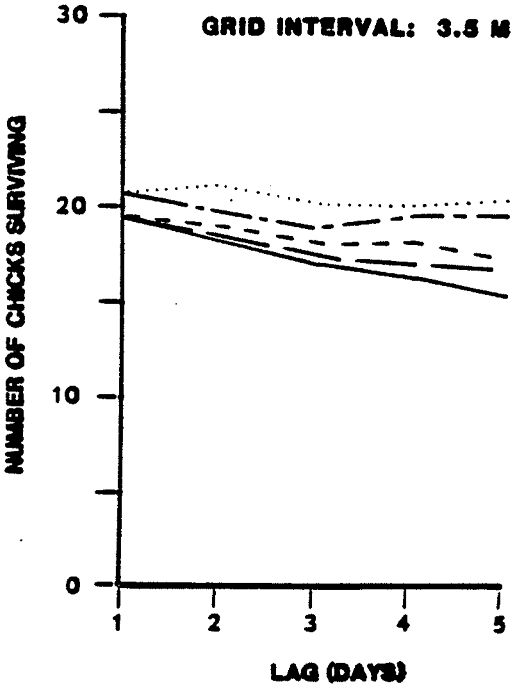
Fig. 18. The relationship between survival of chicks and changing levels of lag time, changes in the probability of a chick's dying when a bereaved parent was within 5.0 m, and grid interval. All graphs show the combined survival from 25 nests on the y-axis, the number of days a bereaved parent remains on territory (lag) on the x-axis, and a separate line for each of five levels of the change in probability of a chick's dying. The five levels, and the corresponding lines are:

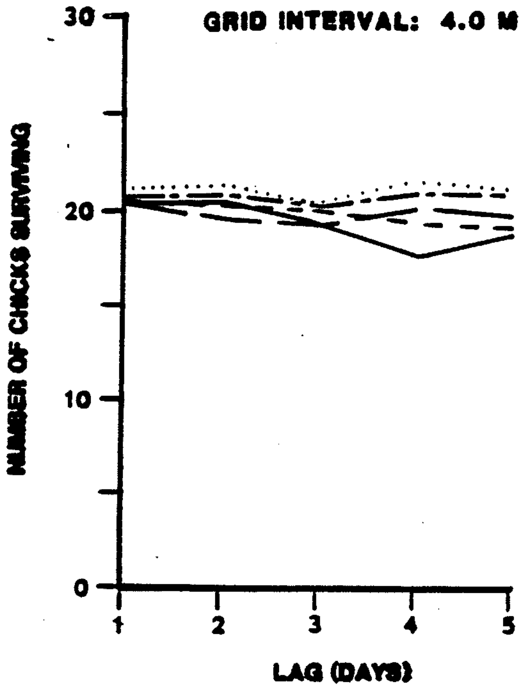
0% · · · · · · · · · · · ·
10% —·—·—·—
20% - - - - - -
30% —— —— ——
40% ————————

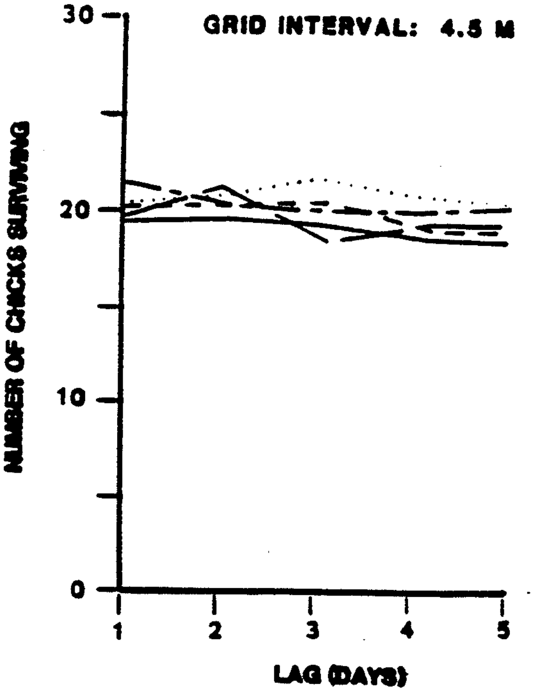

GRID INTERVAL: 2.0 M
NUMBER OF CHICKS SURVIVING
30
20
10
0
1
2
3
4
5
LAG (DAYS)


GRID INTERVAL: 2.5 M
NUMBER OF CHICKS SURVIVING
30
20
10
0
1
2
3
4
5
LAG (DAYS)


GRID INTERVAL: 3.0 M
NUMBER OF CHICKS SURVIVING
30
20
10
0
1
2
3
4
5
LAG (DAYS)


GRID INTERVAL: 3.5 M
NUMBER OF CHICKS SURVIVING
30
20
10
0
1
2
3
4
5
LAG (DAYS)


GRID INTERVAL: 4.0 M
NUMBER OF CHICKS SURVIVING
30
20
10
0
1
2
3
4
5
LAG (DAYS)


GRID INTERVAL: 4.5 M
NUMBER OF CHICKS SURVIVING
30
20
10
0
1
2
3
4
5
LAG (DAYS)

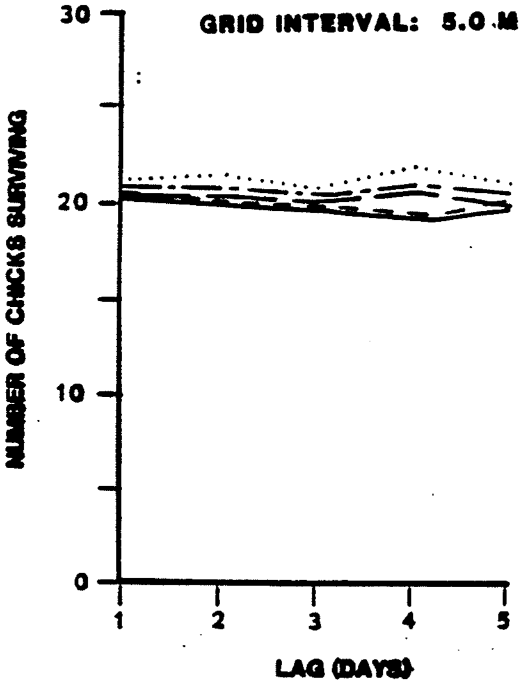
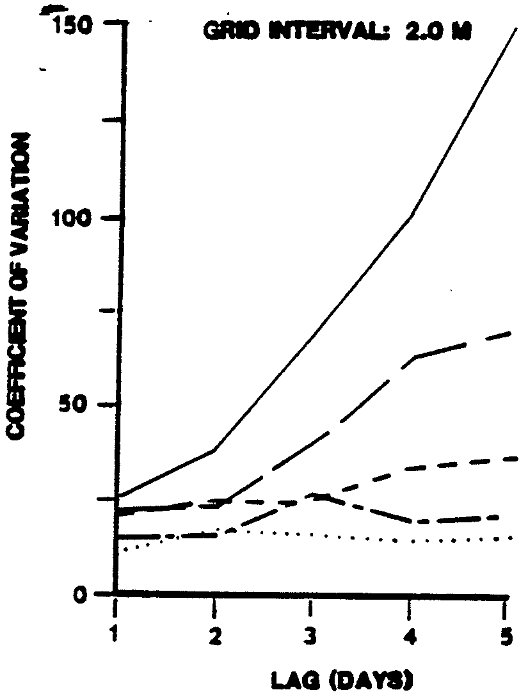
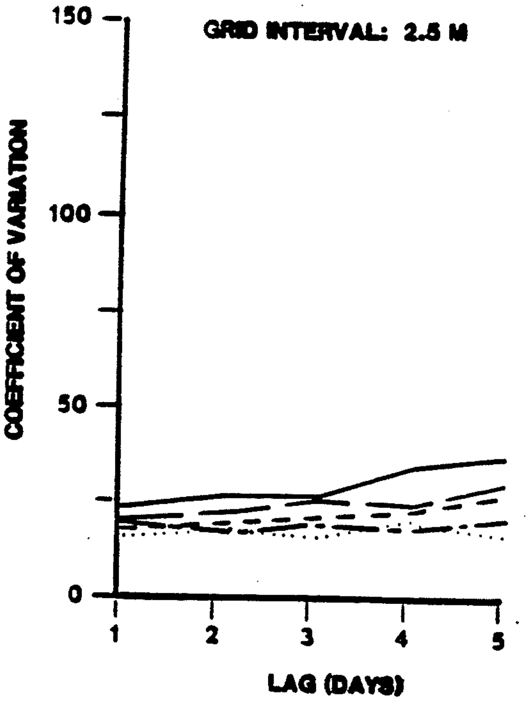

GRID INTERVAL: 5.0 M
NUMBER OF CHICKS SURVIVING
30
20
10
0
1
2
3
4
5
LAG (DAYS)

Fig. 19. The relationship between the variability of the survival of chicks and changing levels of input variables, as in Fig. 18. The y-axis expresses variability as the coefficient of variation for the number of chicks surviving a 50-season run: the standard deviation divided by the mean, multiplied by 100. The five levels of change in probability of a chick's dying, and the corresponding lines on the figure, are as in Fig. 18.


GRID INTERVAL: 2.0 M
COEFFICIENT OF VARIATION
150
100
50
0
1
2
3
4
5
LAG (DAYS)


GRID INTERVAL: 2.5 M
COEFFICIENT OF VARIATION
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100
50
0
1
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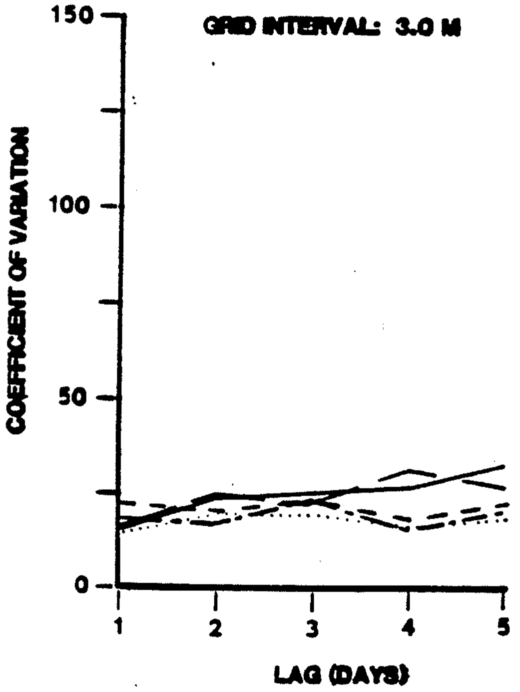
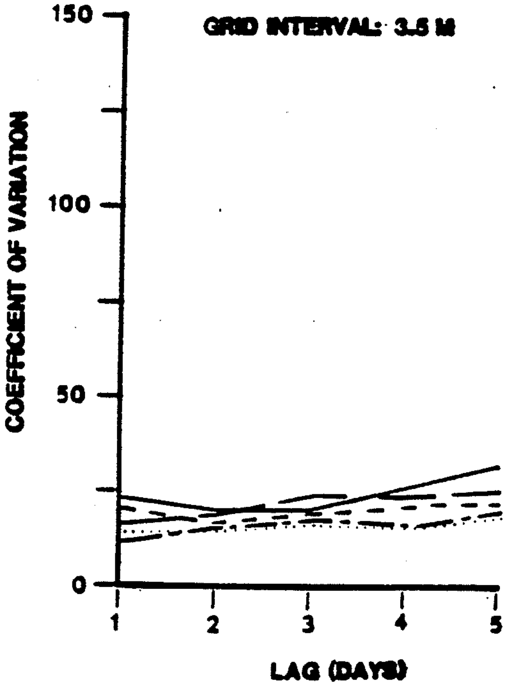
4
5
LAG (DAYS)


GRID INTERVAL: 3.0 M
COEFFICIENT OF VARIATION
150
100
50
0
1
2
3
4
5
LAG (DAYS)


GRID INTERVAL: 3.5 M
COEFFICIENT OF VARIATION
150
100
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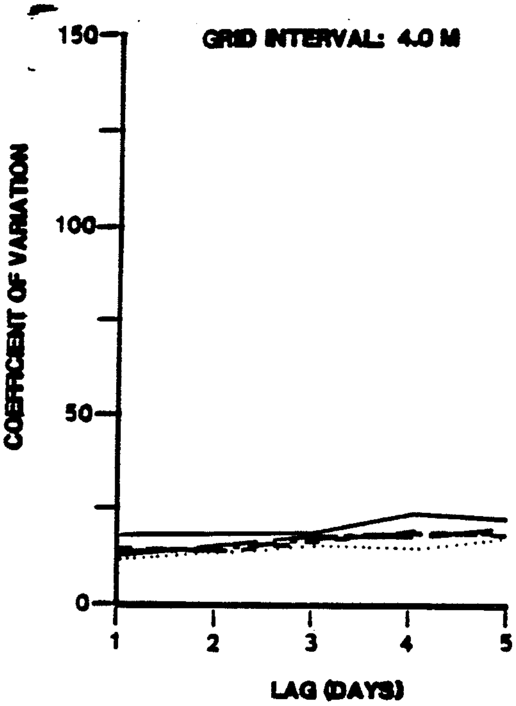
LAG (DAYS)


GRID INTERVAL: 4.0 M
COEFFICIENT OF VARIATION
150
100
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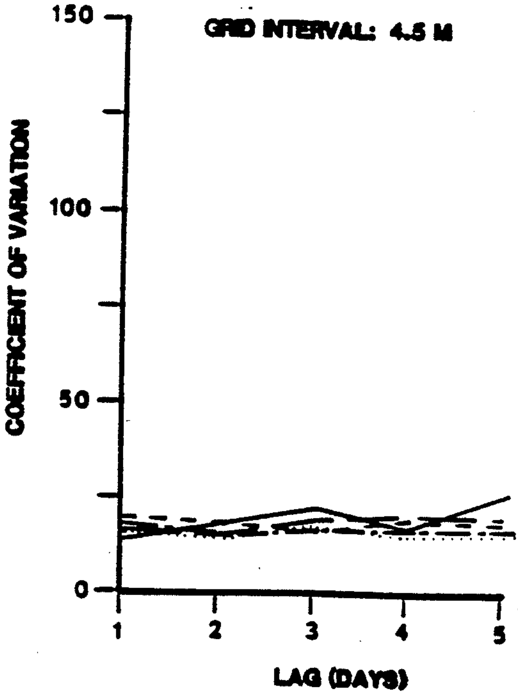
LAG (DAYS)


GRID INTERVAL: 4.5 M
COEFFICIENT OF VARIATION
150
100
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0
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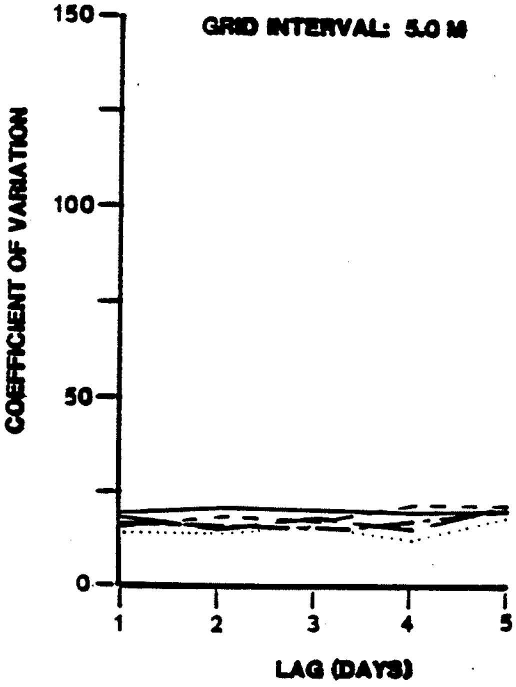
LAG (DAYS)


GRID INTERVAL: 5.0 M
COEFFICIENT OF VARIATION
150
100
50
0
1
2
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LAG (DAYS)

are described by the more extreme graphs.

The above simulation results, and the small and variable differences in nesting densities in cliff and flat habitats suggest that the phenomenon of chain-reaction cannibalism would not act differentially on cliffs and flatland. Differences in the frequency and severity of the process would rather be generated by factors not necessarily related to habitat type, but by factors influencing nesting density, disturbance, and foraging strategies.

DISCUSSION

APPLICATION OF SIMULATION TO HERRING GULL BREEDING BIOLOGY

The first question to be addressed by simulation work was whether conditions could be created under which significant juvenile mortality could be generated by chain-reaction cannibalism. Simulation clearly demonstrated that dramatic mortality could be generated, but this demonstration was performed with simplified systems, arbitrary magnitudes of parameters, and abstract quantities. If these results are to be useful, in terms of making inferences about effective reproductive strategies and the consequences of environmental changes, they must be related to real conditions in the nesting environment of herring gulls.

The second question posed in the INTRODUCTION deals with just such a connection with real data: at what nesting densities should we expect chain-reaction cannibalism? When densities exceeded the level of more than five neighbours within 5.0 m in simulation (grid intervals 2.0 to 3.0 m), chain-reaction cannibalism occurred often, and with dramatic effects, as shown by the lowered survival of chicks and the steep rate of increase of the coefficient of variation in the graph of the 2.0 m grid simulation. In 1977 and 1978, no nests in my study areas had more than five neighbours within 5.0 m, but several tolerated one or two neighbours less than 1 m away. Parsons (1976) studying herring gulls on the Isle of May, Scotland, found that most of the nests he observed (n = 819) had 4 - 7 nests within 5.0 m, and therefore provides data to test the model's predictions. In all of the periods of the breeding season, the nests with the greatest number of neighbours (3 - 4 within 2.5 m) had the lowest survivorship of chicks. Moreover, as the breeding season progressed and the number of bereaved parents increased, the survivorship of chicks in the densest category steadily decreased, from 42% early in the season to 0% at the end of the season. Davis and Dunn (1976), studying a lesser black-backed gull colony on Skokholm in South Wales, also report high densities (up to 10 nests within a 14 X 14 m square). They also found the association of the lowest survival with the highest densities, and specifically noted increasing predation by bereaved parents late in the breeding season.

If a change in the availability of nesting sites were to be created, perhaps by an agent such as the erosion of the banks of a nesting island or peninsula, an effective reproductive strategy for herring gulls would be to move and sacrifice some anti-predator protection by leaving a large group, rather than tolerate a dangerously high density of nests. This provides an interesting mechanism for the creation of new colonies during periods of population growth, such as the one exhibited by herring gulls in this century.

Of course, limiting the number of neighbours is simply another way of stating the previously demonstrated principle that there is a minimum acceptable territory size (e.g. Davis and Dunn 1976; Burger 1984), but the picture tends to be clearer in a set of simulation results than in field data, where samples are necessarily smaller, and paradoxical results are common. These graphs show the approximate point where the risk of becoming caught in a patch of chain-reaction cannibalism may balance the advantage of cooperative anti-predator behaviour.

The third question addressed by simulation was the length of the lag time required to initiate chain-reaction cannibalism. In simulation, lag times of four or five days caused occurrences of unpredictable high mortality. As mentioned earlier, Davis and Dunn (1976) found that parents commonly remained on their territories for seven days after losing all their eggs or chicks, so the lag times used in these simulations do occur in nature. The inclination of bereaved parents stay on their territories and forage for chicks on the colony would be expected to be sensitive to other foraging possibilities near the colony. If there were no source of abundant food near the colony, bereaved parents would be expected either to leave the general area of the colony quickly to search for food, or to remain longer at the colony, where they could specialize, at least for a time, in preying on surviving chicks. An inverse relationship between the vulnerability of chicks and the abundance of nearby food supplies could also arise from the activities of chicks and parents in surviving broods. If food were scarce, parents would have to spend more time off the territory. Their chicks, as they became more hungry, would be more likely to leave hiding places in search of food (cf. Hunt and Hunt 1976).

The fourth question listed early in this section dealt with the degree to which the probability of a chick's survival was decreased by the presence of a bereaved parent within 5 m. Extreme decreases in survival of chicks and extreme uncertainty regarding the outcome of a particular breeding season only occurred when the change in probability of a chick's dying was high (40%).

If chicks have secure hiding places, a large change in probability of survival cannot occur, because the typical pattern of behaviour for chicks, which is to hide and only appear when a parent vocalizes, places a ceiling on the effect a predatory neighbour can have, and reduces the probability of generating chain-reaction cannibalism. Again, Parson's (1976) data provide a confirmation of the model's predictions. Parson describes his study area as a "low flat rocky outcrop", which suggests that little cover was available for the chicks. This situation is consistent with the reduction of survival to 0% late in the breeding season: there was no ceiling on the effect of predatory neighbours. In contrast, Davis and Dunn found that chicks which had access to cover, with some open areas (presumably to allow parents to find and feed them) had much increased survivorship.

The last question with which simulation work was concerned was whether chain-reaction cannibalism could be expected to act differentially on cliff and flat habitats. There was no indication in field data or simulation results to suggest that there was sufficient difference between cliff and flat habitats in density, lag time, or vulnerability of chicks to cause this to be the case. Nesting densities differed between habitats, but not consistently. Foraging conditions near the colony, presumably a major factor in determining lag times, would be the same whether a parent nested on a cliff or a flat site. The abundance of hiding places for chicks, measured as safe quarters, is significantly greater in the flat habitat (Table 1), but the increased abundance of hiding places on flat sites is offset by the fact that the cover on flatland is annual vegetation, and the cover on cliff sites is crevices in rock. It is likely that a chick under vegetation could sometimes be attacked by an adult gull, but a chick in a rock crevice is invulnerable to attack. Thus the degree to which the probability of survival of a chick is decreased by the presence of a bereaved neighbour seems unlikely to be different on cliff and flat sites.

FUTURE USE OF THE MODEL

Although a simplified form of the model was used here to make a specific comparison between habitats, the model has the potential to be extended to other aspects of herring gull biology, such as the importance of the pattern of feeding chicks and the associated processes of sibling rivalry and the inclination of hungry chicks to wander. In this study, all chicks were equivalent, but an accurate representation of the biology of herring gulls must include differences in size, differences in growth rates, and competition among siblings (Werschkul and Jackson 1979; Ricklefs 1979, 1982 and Hahn 1981).

Of particular interest will be the importance of the C chick in such simulation. The high variability of growth rates (Hébert 1985; Hébert and Barclay 1986; this study) suggest that C chicks constitute a heterogeneous group, interacting in complex ways with the heterogeneous pattern of mortality in herring gull colonies.

GENERAL DISCUSSION

CLIFF AND FLAT HABITATS

The prime orientation of this study was to determine how herring gulls could reproduce with apparent success in two different habitats, cliffs and flatland, when previous studies (Cullen 1957; Emlen 1963; Hailman 1965; McLannahan 1973) indicated that breeding on cliffs required a set of very specialized characteristics. This presentation of the problem was based on two assumptions: that cliffs and flatland presented two different kinds of threats to the survival of chicks, and that the way in which selection operated on chicks was primarily a function of the type of habitat in which the chicks lived. Nothing in the study validated either of these assumptions. The only threat to the survival of chicks, which occurred in both habitats, was uncontrolled wandering. The survival of chicks was not a function of the habitat in which the chick lived, but rather of other characteristics of the immediate nesting environment of the chick, such as distance to neighbours, predatory actions by neighbours, and access to hiding places.

It appears that the use of gross habitat types, such as cliff or flat, as classes for sampling reproductive data in large gulls, can be a misleading approach. Survival is too variable within each habitat type to be properly represented by statements such as the mean number of chicks fledged in cliff versus flat habitats. Studies of survival of chicks in large gulls would perhaps be more appropriately organized by the approach of Wiens (1976), who contended that the views of nature presented by many biological studies ("mathematical stories") do not adequately account for the "environmental patchwork which exerts powerful influences on the distributions of organisms, their interactions, and their adaptations". Wiens was referring to patches of habitat, but his remarks apply to any patches, including patches defined as areas of low probability of survival for herring gull chicks. He promoted "intensive field studies undertaken with a conceptual foundation of environmental heterogeneity, with patches as the organizing framework" (ibid.). This approach contrasts with the assumption, implicit in some studies (e.g. Hunt and Hunt 1975) that within each nesting habitat, the nests constitute a population (in the statistical sense), within which variables relating to breeding biology are either normally distributed or do not vary at all. For many continuous variables, such as the depth of nest cups, the diameter of nest cups, the weights of parents, and the dimensions of eggs, this assumption is valid (Appendix 4). However, for many other variables, particularly related to survival and behaviour, the behavioural plasticity of parents and chicks means that field measurements are not samples from stable normal distributions, but samples taken from distributions which may change dramatically during the ongoing stochastic process of development and survival of chicks.

The uneven spatial arrangements of mortality cited by Davis and Dunn (1976), Burger (1984), Schoen and Morris (1984), and this study mean that parameters such as means and variances of chicks per nest or weights of chicks may not be a good represention of the real biology of the situation. The use of these parameters may overestimate survival by having a large patch of mortality fall outside the study area, underestimate survival by having a large patch fall inside the study area, or conceal the real process of mortality by representing multimodal data with a unimodal model.

To avoid these consequences, simulations can be used to analyse the population dynamics of species like herring gulls, in which dramatic spatial heterogeneity occurs. Wiens' "framework" can be used to organize both thinking and logistics in field studies. When single parameters are used to represent habitats or arbitrarily defined study areas, investigators can make use of existing methods of dealing with the problem of clumped dispersions (eg. Clark and Evans 1954; Poole 1974; Pielou 1977).

REPRODUCTIVE STRATEGIES AND VARIABLE JUVENILE MORTALITY

One implication of the variability in juvenile survivorship documented and simulated in this study bears directly on a major question which remains, which is how herring gulls have been so successful in the recent past. Even though different habitats have been shown to apply similar selective pressures to the gulls, one must still explain how the gulls have contended with the irregular occurrences of very high juvenile mortality, as documented in literature cited previously and as shown in field data and simulations from this study. Other simulations have shown (Murphy 1968, Meats 1971, Schaffer 1974) that the optimal reproductive strategy to cope with unpredictable mortality of juveniles is to delay reproduction, reproduce over several years, and have a small clutch size. These traits, which are characteristic of gulls in general, appear to have evolved under conditions of environmental uncertainty which no longer exist for herring gulls, who now usually use stable substrates for nesting. The value of these reproductive characteristics likely increased however, in this century, when the density at which herring gulls nested increased with expanding populations. The simulations reported here suggest that as densities increase, the variability in survival of juvenile herring gulls should also increase. If this were the case, the herring gull would have been preadapted to deal with its own success: in effect, it already had the optimal life history strategy to compensate for increased but unpredictable predation on juveniles caused by increasing numbers.

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APPENDICES

APPENDIX 1

POST-HATCHING AS A CRITICAL LIFE HISTORY PERIOD

This study focuses on the survival of chicks during the first three weeks of life. The choice of this period (following Dexheimer and Southern (1974) and Schoen and Morris (1984)) as being critical in the understanding of breeding biology in herring gulls was based primarily on survival rates for eggs, very young chicks, immature birds, and sexually mature birds. (See Paynter (1966) for a detailed treatment of the importance of chick mortality in creating life tables.)

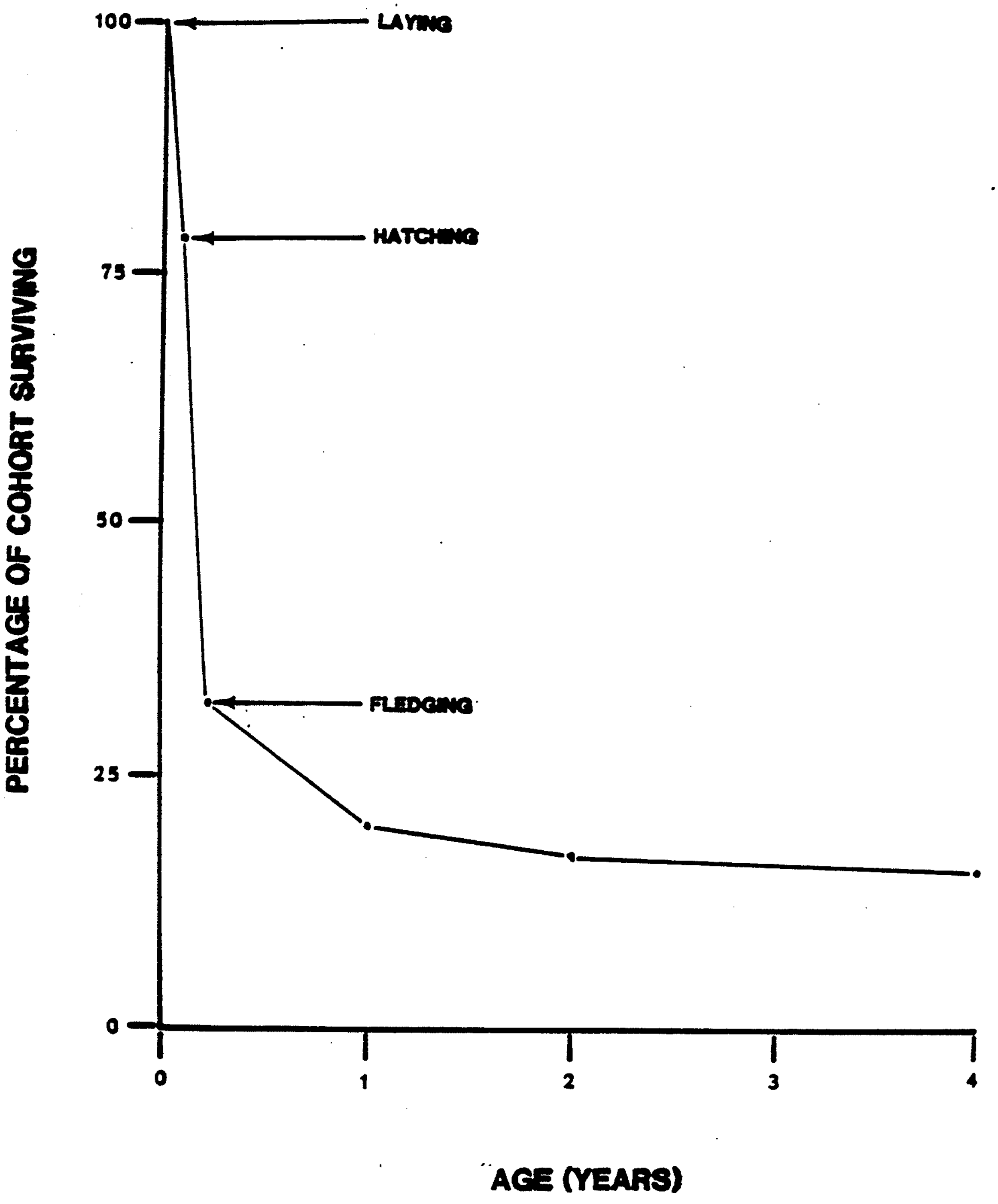
Mortality of eggs, from predation, breakage, cooling, etc. and the mortality of chicks in the first two to three weeks after hatching has been measured in several studies (PART 1) of herring gulls and other large gulls and has been found to be variable, and often very high. Gillett et al. (1975) summarize mortality after the first two weeks of life and before fledging by saying that deaths were "few and sporadic". The survival rate for the post-fledging portion of a chick's first year, and the annual rates thereafter, are high, 85 - 96% (Kadlec and Drury 1968; Parsons 1975; Chabrzyk and Coulson 1976; Kadlec 1976; Sibly and McCleery 1985).

When this pattern of survivorship is expressed graphically (Fig. 20), a very steep portion of the survivorship curve becomes apparent.

Meats (1971) showed that in situations in which mortality is already high, changes in mortality rates are more important than changes in fecundity. It is therefore likely that herring gulls are already exhibiting many behavioural mechanisms which reduce the mortality of their chicks during the dangerous first three weeks of life, and that searching for those mechanisms is likely to be rewarding.

Discovering a critical period upon which to focus a field study would be of little use if, during that period, sample sizes would be very small or if the measurements to be taken were of very small differences, so that null hypotheses would be unlikely to be rejected (i.e. large probability of Type II errors). Fortunately, the deaths of chicks in herring gull colonies are relatively easy to detect, and occur with a high enough frequency during the first three weeks of life that real differences between statistical populations have a reasonable probability of being detected in a short study.

Fig. 20. The survivorship of herring gulls from laying until reproductive maturity.


100
75
50
25
0
LAYING
HATCHING
FLEDGING
PERCENTAGE OF COHORT SURVIVING
0
1
2
3
4
AGE (YEARS)

APPENDIX 2

NOMENCLATURE AND CATALOG OF CALLS

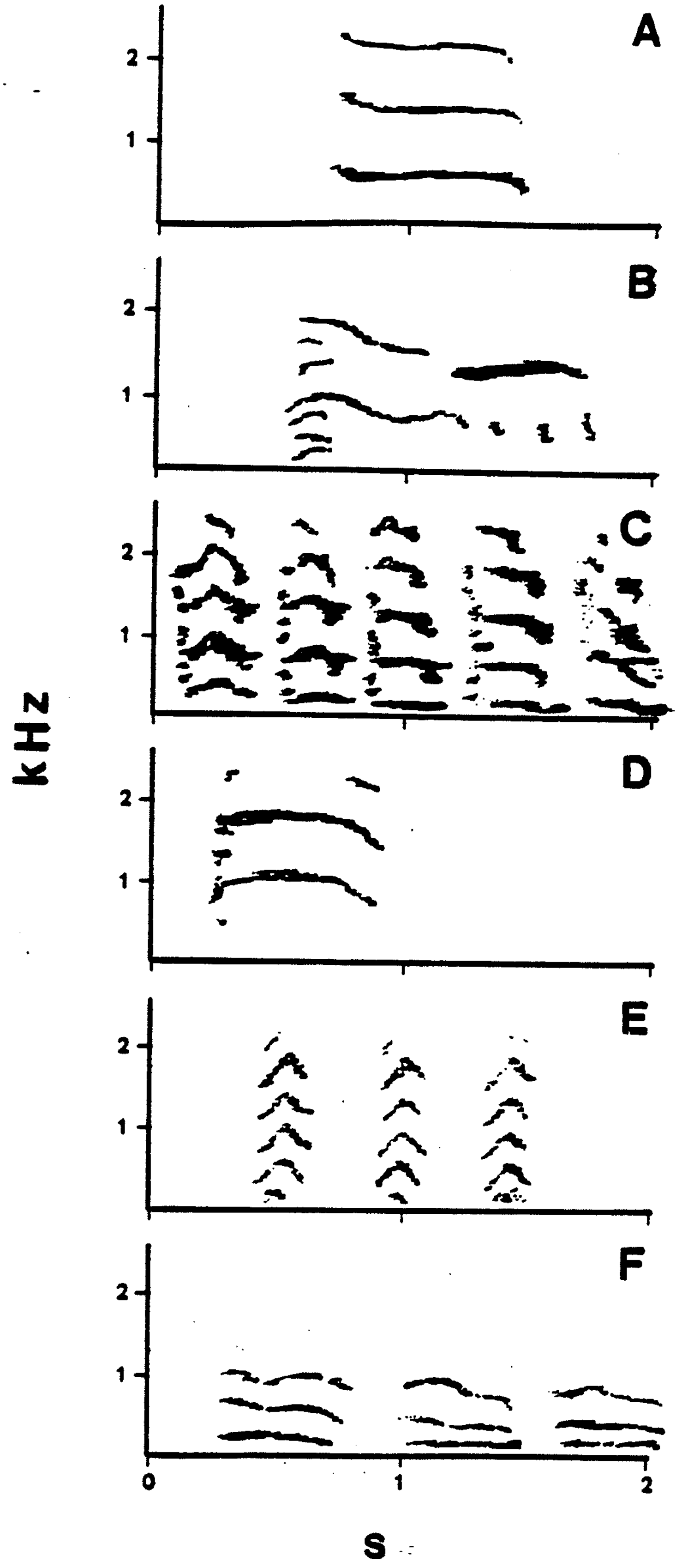
Several nomenclatures have been used to describe the vocalizations of herring gulls and closely related species. No single nomenclature has become standard, either implicitly or explicitly. Instead, common usage includes terms used in a variety of publications (e.g. Tinbergen 1953, 1959; Moynihan 1958; Stout et al 1969). In this paper I have tried to use terminology which reflects acceptable current usage. For the calls of adults, Tinbergen's terminology is the most widely used, with the exception of his use of the term "trumpeting call". Most authors now refer to this call as the long call.

The intention of this catalog is to provide, for readers unfamiliar with the vocalizations of gulls, unambiguous definitions of vocalizations discussed in this paper, and to outline the apparent significance of the calls in the communication of herring gulls. To the latter end, I have listed contexts (Smith 1965), messages (Smith 1965), and meanings (Cherry 1955, 1957; Smith 1963) associated with each call. The messages and meanings given below have not been rigorously determined (cf. Smith 1970a, 1970b), but have been inferred from literature and personal observations which allowed some reasonable conclusions to be drawn about messages and meanings.

MEW CALL

This call lasts from 1 to 3 sec (Fig. 21A & B). When

Fig. 21. Sonagrams of common herring gull vocalizations. A: unitonal mew call; B: bitonal mew call; C: a portion of a long call; D: call notes; E: alarm call; F: choking.


A
B
C
D
E
F
2
1
kHz
0
1
2
S

Tinbergen (1953) gave the name "mew call" to these vocalizations, he implied that the was referring to a homogeneous group of vocalizations. This may not be true. Evans (1973) found two types of vocalization which fitted Tinbergen's definition of a mew call: one which was unitonal (Fig. 21A) and one which he termed bitonal (Fig. 21B). He noted that the latter appeared to be given less frequently in the colonies he visited.

The mew call is given with the bill gaping widely. The head can be inclined up or down, or can be held level.

The characteristic site at which the mew call is given is on the home territory of a breeding adult. There are four common contexts: threat, courtship, nest relief, and feeding of chicks.

In the contexts of threat and courtship, the message appears to be that the sender is a male claiming a territory. The meaning for a rival is that if he approaches, he will get into a fight. The aggressive component has been shown experimentally for the closely related glaucous-winged gull (Larus glaucescens) (Moynihan 1958; Tinbergen 1959; Vermeer 1963; Moyle 1966; Stout et al. 1969; Stout 1975). The meaning for a female is that the sender is a potential mate. In the context of nest relief the message is that the sender is ready to incubate. The meaning is that the parent on the nest can leave the nest without endangering the eggs. When the mew call is used in feeding, the message is that the parent is present and has food to regurgitate. The meaning to the chick is that both food and protection are present so there is no reason to remain in hiding.

LONG CALL

The long call, referred to as the challenge by Strong (1914) and as the trumpeting call by Densing (1939) and Tinbergen (1953), is also a call which lasts several seconds (Fig. 21C). The first few syllables are given with the head pointed toward the ground. The series of louder, more piercing syllables are given with the head thrown back.

Long calls are given on the breeding grounds in three contexts: establishing or defending territory, greeting a returning mate, and guarding chicks. In the context of establishing or defending territory and guarding chicks, the message is likely the same: the sender is prepared to fight if approached by a stranger. The meaning for another gull is that there is a risk associated with trying to claim that territory or trying to attack a chick on it. In a greeting context, these calls probably function as exchanged "passwords", indicating arrival and also verifying the identities of both the arriving bird and the one in residence. Individual recognition of mates by long calls has been shown for laughing gulls (Beer 1970a), but remains unproven for herring gulls. Some anecdotal indications that adults can use the long call for individual recognitions is given by Tinbergen's (1953) observation of nest relief during incubation.

CALL NOTE

The call note (Fig. 21D) is the vocalization of gulls which is most often heard. It is approximately 1 sec long, and consists of a single syllable. It is used when feeding, when mobbing predators, and when mildly alarmed. The apparent message is that the sending bird is alert to some change in the immediate environment. The message is that the receiver should look out for food or a predator. The call is given from a wide range of postures on the ground, while flying, and while on the water.

ALARM CALL

The alarm call (Fig. 21E) lasts for approximately 1 sec, and consists of three short syllables, sounding like "kek-kek-kek". The call is usually given from an upright posture, or when flying. The most common stimuli are the presence of an intruding neighbour and the appearance of a predator or novel object. This call is commonly given in response to some disturbance coming from inside a blind. If disturbance continues, the call is usually followed by call notes and flight or attack. The message is that the sender is ready to fight or flee. The meaning is that the receiver should be ready to fight the sender, flee from the sender, or participate in mobbing a predator, depending on the context.

CHOKING

Choking (the terminology is attributed to Noble by Tinbergen (1953) without citation) is a vocalization (Fig. 21F) which is most commonly used in courtship, but which is also used in aggressive displays (Tinbergen 1953). In the former context, it is given by both members of a pair, standing over the nest site with the body held horizontal, the head pointing down, the mouth gaping, and the body bobbing with the vocalizations. The call consists of a series of gutteral elements. The male and female often vocalize simultaneously.

The message of choking appears to be that the sender is ready to mate, and the meaning appears to be that the receiver can consider the pair to be formed.

APPENDIX 3

EXPERIMENTAL METHODS IN VOCALIZATION STUDIES

In testing for individual recognition of voice, playbacks of the tape recorded calls often have been used as a stimulus, and have produced many important contributions. One such successful study was Beer's (1970b, 1970c) study of laughing gull chicks. Given his productive use of simultaneous presentation of calls to chicks in a testing arena, one might ask why I did not follow his playback methods, instead of his "live" method. I had four reasons.

There was a possibility that the artificial environment in the box might interfere with the chick's responses enough to obscure statistically significant differences which might be present. Such differences are difficult to detect at the best of times in behavioural experiments with sample sizes as small as these, because of the positive correlation between sample size and power.

Another aspect of context in this type of experiment is the method of simultaneous presentation. In natural situations within a colony chicks do not usually have to listen to two calls of equal volume at the same time. They characteristically hear the call of an adult while they are in hiding, and either reply in some form or crouch and continue hiding silently (Tinbergen 1953; this study). If the presentation of two calls at equal volumes were to give an ambiguous message to the chick, its responses would likely be variable or inappropriate. More noise would be injected into the data, and as a consequence of the low power of the tests, Type II errors would be expected.

Technical problems associated with the use of tapes could bias responses without any clue being given to the observer. These problems have been investigated by Espmark and Fonstad (1983), who investigated the degree to which inadequate reproduction quality can generate false negative results in playback experiments. They compared original recordings with playbacks of the same recordings, produced by a range of sizes of speakers. They found significantly different results, with respect to frequency parameters and amplitude. These differences were greater than differences detected by birds in individual recognition experiments, and therefore were definitely large enough to generate false negative results.

The scoring technique was not interpretable in terms of survival significance. Some simple response which would be selectively advantageous was needed.

APPENDIX 4

EGG MEASUREMENTS

In PART 3, when justifying the pooling of growth data on A and B chicks only, I referred to the fact that C eggs were significantly smaller than A and B eggs, and that the intercept of the growth equation (the weight of the chick at hatching) for C chicks would therefore be different from the intercept for A and B chicks. In this appendix, I present the MANOVA of lengths and widths of A, B, and C eggs which shows the significant difference claimed above. The specific null hypothesis tested was that there is no difference between the dimensions of C eggs and other eggs.

Lengths and widths used in this analysis were measured with calipers and recorded to the nearest 0.01 mm. Only measurements from eggs which could be classified with certainty as A, B, or C were used.

A graphic representation of the relationship of the sizes of eggs is shown in Fig. 22. The details of the MANOVA are given in Table 9. Within the three groups, there is a highly significant difference ($X^2 = 45.8$, $p < 0.001$). Inspection of Fig. 22 suggests that the significance in the above MANOVA is attributable to the C eggs. To confirm this impression, univariate ANOVAs and pairwise comparisons were conducted. For both lengths and widths, the ANOVAs indicated the presence of a significant difference (lengths: $F = 16.5$, $df = 2, 175$, $p < 0.01$; widths: $F = 17.2$, $df = 2, 175$, $p < 0.01$). A posteriori

Fig. 22. The relationship between length and weight data of A, B, And C eggs. For each group, the bivariate mean is indicated by a dot and and an identifying letter, and the scatter of data points is represented by a minimum convex polygon.

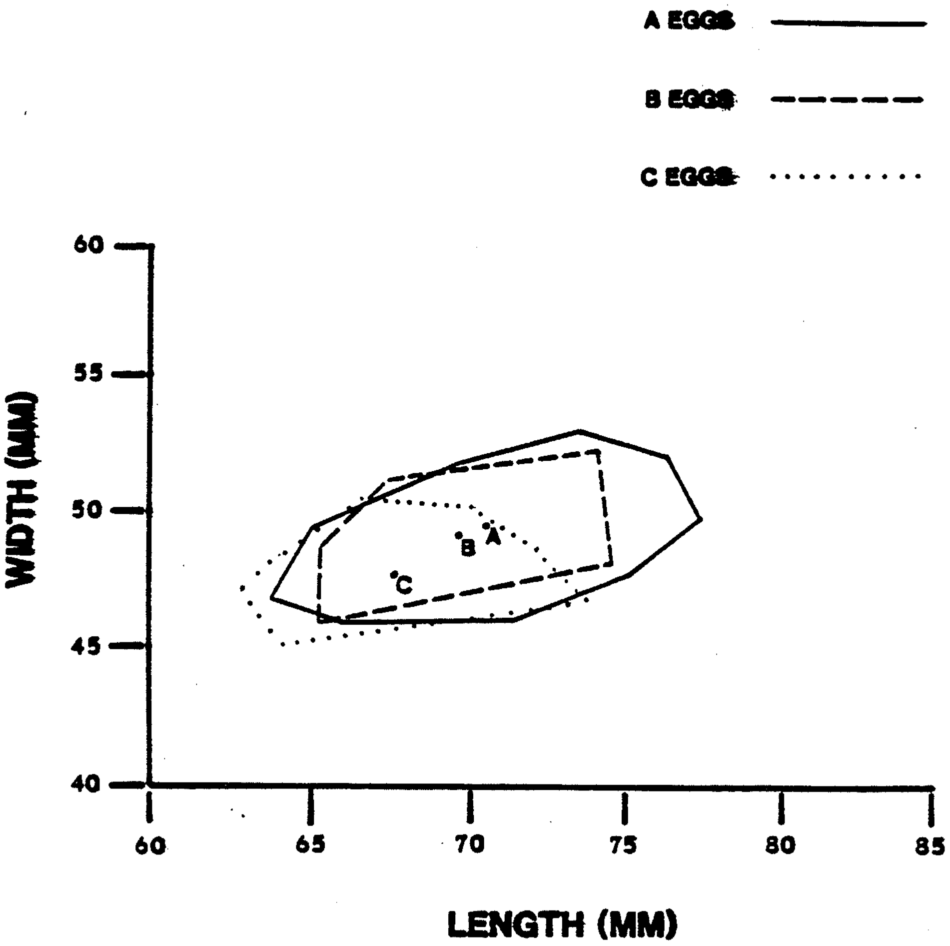

A EGGS
B EGGS
C EGGS
60
55
50
45
40
WIDTH (MM)
60
65
70
75
80
85
LENGTH (MM)
A
B
C

Table 9. The MANOVA of the lengths and widths of A, B, and C eggs.

Univariate Means:

	Egg			
	A	B	C	All
Mean Length (mm)	70.689	69.556	67.771	69.589
Mean Width (mm)	49.129	49.101	47.715	48.725
n	84	44	50	178

Sums of Squares Matrices:

	A		B		C		Total	
Within	761.9	148.1	256.9	68.5	395.6	80.5	1414.4	297.0
		196.3		71.6		93.3		361.3
Between							266.9	128.7
								71.0
Total							1681.4	425.7
								432.2

Wilks's λ : 0.775

Improved χ^2 : 45.8 ($p < 0.001$)

comparisons for both variables, conducted with $\alpha = 0.05$, rejected the null hypothesis of no difference between the A and C eggs and the B and C eggs, but did not reject the null hypothesis when A and B eggs were compared.

On the basis of these tests, it seems reasonable to assume equal hatching weights for A and B chicks for the purposes of simulation in this study.

APPENDIX 5

PROGRAM LISTINGS

Simulation Program

The following is a listing of the program PATCHSERIES, which conducts the simulations of gull breeding biology as described in PART 3.

```
PROGRAM PATCHSERIES;


(* DATE OF LAST EDIT: 3 FEBRUARY 1986 *)


 CONST FILL      = 'X';
       MAXNESTS  = 25;
       MAXSEASONS= 50;
       MAXLAG =5;


 TYPE  CHICKTYPE = (ACHICK,BCHICK,CCHICK);
       DISARYTYPE = ARRAY[1..MAXNESTS,1..MAXNESTS] OF REAL;
       DISTCLASSTYPE = (IN25,IN50,OUT50);
       NESTREC=RECORD
                NESTID:          STRING[5];
                NX,NY,DNEAR:     REAL;
                HDAY:                ARRAY[ACHICK..CCHICK]      OF
INTEGER;
                WT:                  ARRAY[ACHICK..CCHICK]      OF
INTEGER;
                DANGQ,SAFEQ:     0..4;
                ATTENT:          CHAR;
                N25,N50:         INTEGER;
                BRFT25,BRFT50:   INTEGER;
                NEARID:          INTEGER
               END;

       NESTATUSTYPE = (NORMAL,KILLERS,DEFUNCT);
       CHSTATUSTYPE = (PREHATCH,LIVING,DEAD,NOCHICK,HOMEFREE);


 VAR   ZARRAY:ARRAY[0..49] OF REAL;
       NNESTS,NEST,NDAYS,DAY,I,J  :INTEGER;
       SEASON,NSEASONS:INTEGER;
       LAG:0..MAXLAG;
       HOLDMAT:     ARRAY[1..MAXNESTS] OF NESTREC;
       NESTMAT:     ARRAY[1..MAXNESTS] OF NESTREC;
       DISTMAT:     DISARYTYPE;
       MRPRCH:      ARRAY[1..MAXNESTS] OF REAL;
       OUTMAT:       ARRAY[20..70,1..MAXNESTS,ACHICK..CCHICK]  OF
INTEGER;
```

```
        EXTANTLIST:  ARRAY[20..70,1..MAXNESTS] OF NESTATUSTYPE;
        (* NOTE THAT THE EXTANTLIST HOLDS THE STATUS OF NESTS AT
           THE BEGINNING OF THE DAY *)
        LASTSIMDAY:  ARRAY[1..MAXSEASONS] OF INTEGER;
        NFNAME: STRING[20];
        CH: CHAR;
        EDITFLAG:BOOLEAN;
        NESTFILE:FILE OF NESTREC;
        TITLE,DATE:STRING[20];
        CHICK:CHICKTYPE;
        KEYNEST, OTHERNEST:INTEGER;
        SLOPE,INTERCEPT: ARRAY[ACHICK..CCHICK] OF REAL;
        CURVEHEIGHT:ARRAY[1..21] OF REAL;
        HATCHCOUNT: ARRAY[1..MAXNESTS] OF INTEGER;
        BASE:ARRAY [1..MAXNESTS] OF REAL;
        MORTPROB:REAL;
        PR50,IDC,JDC,FIRSTHATCHDAY:INTEGER;
        PRCNTIN50,PRCNTIN25,PRCNTINNEAR:REAL;

(* FORWARD PROCEDURES*)

PROCEDURE PRESS;
FORWARD;

(*NORMAL PROCEDURES AND FUNCTIONS*)

PROCEDURE ZINIT;
BEGIN
 ZARRAY[0]:=0.0000;
 ZARRAY[1]:=0.0398;
 ZARRAY[2]:=0.0793;
 ZARRAY[3]:=0.1179;
 ZARRAY[4]:=0.1554;
 ZARRAY[5]:=0.1915;
 ZARRAY[6]:=0.2257;
 ZARRAY[7]:=0.2580;
 ZARRAY[8]:=0.2281;
 ZARRAY[9]:=0.3159;
 ZARRAY[10]:=0.3413;
 ZARRAY[11]:=0.3643;
 ZARRAY[12]:=0.3849;
 ZARRAY[13]:=0.4032;
 ZARRAY[14]:=0.4192;
 ZARRAY[15]:=0.4332;
 ZARRAY[16]:=0.4452;
 ZARRAY[17]:=0.4554;
 ZARRAY[18]:=0.4641;
 ZARRAY[19]:=0.4713;
 ZARRAY[20]:=0.4772;
 ZARRAY[21]:=0.4821;
 ZARRAY[22]:=0.4861;
 ZARRAY[23]:=0.4893;
```

```
  ZARRAY[24]:=0.4918;
  ZARRAY[25]:=0.4938;
  ZARRAY[26]:=0.4953;
  ZARRAY[27]:=0.4965;
  ZARRAY[28]:=0.4974;
  ZARRAY[29]:=0.4981;
  ZARRAY[30]:=0.4987;
  ZARRAY[31]:=0.4990;
  ZARRAY[32]:=0.4993;
  ZARRAY[33]:=0.4995;
  ZARRAY[34]:=0.4997;
  ZARRAY[35]:=0.499767;
  ZARRAY[36]:=0.499869;
  ZARRAY[37]:=0.499892;
  ZARRAY[38]:=0.499928;
  ZARRAY[39]:=0.499952;
  ZARRAY[40]:=0.499968;
  ZARRAY[41]:=0.499979;
  ZARRAY[42]:=0.499987;
  ZARRAY[43]:=0.499991;
  ZARRAY[44]:=0.499995;
  ZARRAY[45]:=0.499997;
  ZARRAY[46]:=0.499998;
  ZARRAY[47]:=0.499999;
  ZARRAY[48]:=0.499999;
  ZARRAY[49]:=0.500000;
  END;

PROCEDURE SHOW( VAR IR:NESTREC);
  BEGIN
   WITH IR DO
    BEGIN
     WRITELN('NEST NUMBER:                 ',NESTID);
     WRITELN('X-COORDINATE:                ',NX:6:2);
     WRITELN('Y-COORDINATE:                ',NY:6:2);
     WRITELN('CHICK A...HATCH WT.:         ',WT[ACHICK]);
     WRITELN('          HATCH DAY:         ',HDAY[ACHICK]);
     WRITELN('CHICK B...HATCH WT.:         ',WT[BCHICK]);
     WRITELN('          HATCH DAY:         ',HDAY[BCHICK]);
     WRITELN('CHICK C...HATCH WT.:         ',WT[CCHICK]);
     WRITELN('          HATCH DAY:         ',HDAY[CCHICK]);
     WRITELN('PARENTAL ATTENTIVENESS:      ',ATTENT);
     WRITELN('DANGEROUS QUARTERS:          ',DANGQ);
     WRITELN('SAFE QUARTERS:               ',SAFEQ);
     WRITELN('DISTANCE TO NEAREST:         ',DNEAR:6:2);
     WRITELN('NUMBER WITHIN 2.5 M:         ',N25);
     WRITELN('NUMBER WITHIN 5.0 M:         ',N50);
     WRITELN('BEREAVED WITHIN 2.5 M:       ',BRFT25);
     WRITELN('BEREAVED WITHIN 5.0 M:       ',BRFT25);
     WRITELN('NEARID:                      ',NEARID)
    END
  END;
```

```
 PROCEDURE DATALOAD;
  VAR ED,ENTRY:CHAR;
  BEGIN
   EDITFLAG:=FALSE;
   ASSIGN(NESTFILE,NFNAME);
   RESET(NESTFILE)
   I:=0;
   WHILE NOT EOF(NESTFILE) DO
   BEGIN
    I:=I+1;
    GOTOXY(0,12);
    WRITELN('ENTERING NEST:  ',I:2);
    READ(NESTFILE,NESTMAT[I]);
   END;
   CLOSE(NESTFILE);
   NNESTS:=I;
  END;
IF (LAG=1) AND (P50=0)
 THEN
  BEGIN
   WRITE('DISPLAY DATA?  (Y/N) ');
   READ(CH);
   WRITELN
  END
 ELSE
   CH:='N';
   I:=0;
   WHILE CH='Y' DO
    BEGIN
    CLRSCR;
    I:=I+1;
    GOTOXY(0,2);
    WRITELN('NEST:  ',I);
    GOTOXY(0,5);
    SHOW(NESTMAT[I]);
    IF I<NNESTS THEN
                   BEGIN
                   WRITE('MORE?  (Y/N) ');
                   READ(CH);
                   END
               ELSE
                   BEGIN
                   CH:='N';
                   PRESS;
                   END;
  END;(*DISPLAY DATA*)
 END;(*PROCEDURE*)

PROCEDURE GROWTHSET;
(* THESE ARE 1978 DATA *)
(* A AND B CHICKS ARE CLIFF DATA *)
```

```
(* C CHICKS ARE CLIFF AND FLAT DATA *)
BEGIN
 INTERCEPT[ACHICK]:=74;
 SLOPE[ACHICK]:=0.112;
 INTERCEPT[BCHICK]:=74;
 SLOPE[BCHICK]:=0.112;
 INTERCEPT[CCHICK]:=63;
 SLOPE[CCHICK]:=0.118;
END;

PROCEDURE SETUP;
 PROCEDURE MRPREDICTION;
  CONST  B0 = 1.995;
         B1 = 0.012;
         B2 = 0.173;
         B3 = -0.059;
         B4 = 0.337;
  VAR    ICH        : CHICKTYPE;
  BEGIN
   GOTOXY(25,17);
   WRITELN('PREDICTING...');
   FOR NEST:=1 TO NNESTS DO
    BEGIN
     HATCHCOUNT[NEST]:=0;
     WITH NESTMAT[NEST] DO
      BEGIN
       FOR ICH:=ACHICK TO CCHICK DO
        IF                  WT[ICH]<>-1                             THEN
HATCHCOUNT[NEST]:=HATCHCOUNT[NEST]+1;
       MRPRCH[NEST]:=B0+
                     (B1*DNEAR)+
                     (B2*DANGQ)+
                     (B3*HDAY[ACHICK])+
                     (B4*HATCHCOUNT[NEST]);
       IF MRPRCH[NEST]>HATCHCOUNT[NEST]
         THEN MRPRCH[NEST]:=HATCHCOUNT[NEST];
      END;
    END;
  END;

PROCEDURE POLYNOMIAL;
 CONST  B0 = -1.26407108;
        B1 =  2.63113166;
        B2 = -0.325849884;
        B3 =  0.0140932144;
        B4 = -0.000203827235;
 VAR    AGE:INTEGER;
        SUM,BASE:REAL;
 BEGIN
  GOTOXY(25,18);
  WRITELN('POLYNOMIAL..');
  SUM:=0;
```

```
   FOR AGE:=1 TO 21 DO
    BEGIN
    CURVEHEIGHT[AGE]:= B0+
                       (B1*AGE)+
                       (B2*AGE*AGE)+
                       (B3*AGE*AGE*AGE)+
                       (B4*AGE*AGE*AGE*AGE);
    SUM:=SUM+CURVEHEIGHT[AGE]
    END;
   FOR AGE:=1 TO 21 DO
    BEGIN
    CURVEHEIGHT[AGE]:=CURVEHEIGHT[AGE]/SUM;
    IF AGE=1 THEN BASE:=CURVEHEIGHT[AGE];
    CURVEHEIGHT[AGE]:=CURVEHEIGHT[AGE]/BASE;
    (* CURVEHEIGHT IS NOW THE WEIGHT FOR *)
    (* EACH DAY'S PROBABILITY OF DYING *)
    END;
 END;

PROCEDURE ITERATE;
 VAR INTERVAL,CUMPROB,DIFF:REAL;
     AGE:INTEGER;
 BEGIN
  GOTOXY(25,19);
  WRITELN('ITERATING..');
  FOR NEST:=1 TO NNESTS DO
   BEGIN
    INTERVAL:=0.1;
    BASE[NEST]:=0;
    REPEAT
     BASE[NEST]:=BASE[NEST]+INTERVAL;
     CUMPROB:=1.00;
     FOR AGE:=1 TO 21 DO
      CUMPROB:=CUMPROB*(1-(BASE[NEST]*CURVEHEIGHT[AGE]));
     DIFF:=(MRPRCH[NEST]/HATCHCOUNT[NEST])-CUMPROB;
     IF DIFF>0.005 THEN
       BEGIN
        BASE[NEST]:=BASE[NEST]-INTERVAL;
        INTERVAL:=INTERVAL/10.0
       END;
    UNTIL (DIFF<0.005) AND (DIFF>-0.005);
   END
 END;

 BEGIN(*SETUP*)
  MRPREDICTION;
  POLYNOMIAL;
  ITERATE
 END;

 PROCEDURE RUNPREP;
  VAR LAGSTR,P50STR: STRING[5];
```

```
 PTEMP: INTEGER;
 PROCEDURE HARDHEADER;
 BEGIN
  WRITELN('TITLE OF THIS RUN:  ',TITLE);
  WRITELN('CURRENT DATE:       ',DATE);
  WRITELN;
 END;

BEGIN
FOR NEST:=1 TO NNESTS DO HOLDMAT[NEST]:=NESTMAT[NEST];
GROWTHSET;
PRCNTIN50:=P50*10;
PTEMP:=TRUNC(PRCNTIN50);
STR(LAG,LAGSTR);
STR(PTEMP,P50STR);
TITLE:=CONCAT(NFNAME,'/',LAGSTR,'DAY/',P50STR,'%');
PRCNTIN50:=1+(PRCNTIN50/100);
HARDHEADER
END;

PROCEDURE DISSTDDAY;

PROCEDURE DISCALC;
 FUNCTION DISTANCE(NM1,NM2:NESTREC):REAL;
  VAR XD,YD:REAL;
  BEGIN
   IF IDC=JDC THEN DISTANCE:=0
              ELSE
               BEGIN
                XD:=NM1.NX-NM2.NX;
                YD:=NM1.NY-NM2.NY;
                XD:=XD*XD;
                YD:=YD*YD;
                DISTANCE:=SQRT(XD+YD)
               END
  END;

 BEGIN(*DISCALC*)
  CLRSCR;
  WRITELN('CALCULATING INTER-NEST DISTANCES');
  FOR IDC:=1 TO NNESTS DO
   BEGIN
   FOR JDC:=1 TO NNESTS DO
    BEGIN
    DISTMAT[IDC,JDC]:=DISTANCE(NESTMAT[IDC],NESTMAT[JDC]);
    WRITE(DISTMAT[IDC,JDC]:8:2);
    END;
   WRITELN;
   END;
 END;(* DISCALC *)

 PROCEDURE STDHATCH;
```

```
     BEGIN
     FIRSTHATCHDAY:=100;
     FOR NEST:=1 TO NNESTS DO
      BEGIN
      WITH NESTMAT[NEST] DO
        BEGIN
        IF (WT[ACHICK]=-1) AND (WT[BCHICK]=-1)
         THEN HDAY[ACHICK]:=HDAY[CCHICK]-2;
        IF (WT[ACHICK]=-1) AND (WT[BCHICK]<>-1)
         THEN HDAY[ACHICK]:=HDAY[BCHICK]-1;
        IF FIRSTHATCHDAY>HDAY[ACHICK]
         THEN FIRSTHATCHDAY:=HDAY[ACHICK];
        END
      END
     END;(*STDHATCH*)

  PROCEDURE DAYSCALC;
   VAR I:INTEGER;
   BEGIN
    WRITELN('CALCULATING THE TOTAL NUMBER OF DAYS');
    WRITE('REQUIRED FOR THIS SIMULATION:');
    NDAYS:=NESTMAT[1].HDAY[ACHICK];
    FOR I:=2 TO NNESTS DO
     BEGIN
      IF NESTMAT[I].HDAY[ACHICK]>NDAYS THEN
       NDAYS:=NESTMAT[I].HDAY[ACHICK];
     END;
    NDAYS:=NDAYS+21;
    WRITELN(NDAYS:4);
   END;(*DAYSCALC*)

 BEGIN(*DISSTDDAY*)
  DISCALC;
  STDHATCH;
  DAYSCALC
 END;(*DISSTDDAY*)

PROCEDURE MODEL;

VAR CC,CC2,NC,NC2:REAL;

 FUNCTION ALIVE(CH:CHICKTYPE):BOOLEAN;
  BEGIN
   WITH NESTMAT[NEST] DO
    BEGIN
    ALIVE:=TRUE;
    IF WT[CH]=0 THEN ALIVE:=FALSE
    END
  END;

 FUNCTION STATUS(CH:CHICKTYPE):CHSTATUSTYPE;
  BEGIN
```

```
  WITH NESTMAT[NEST] DO
   BEGIN
   IF(WT[CH]>0) AND (HDAY[CH]>DAY)  THEN STATUS:=PREHATCH;
   IF(WT[CH]>0) AND (HDAY[CH]<=DAY) THEN STATUS:=LIVING;
   IF(WT[CH]=0)                     THEN STATUS:=DEAD;
   IF(WT[CH]=-1)                    THEN STATUS:=NOCHICK;
   IF(WT[CH]=500)                   THEN STATUS:=HOMEFREE;
   END
  END;

 FUNCTION AGE (CID:CHICKTYPE):INTEGER;
 (* THIS ASSUMES THE CHICK HAS SURVIVED THE CURRENT DAY *)
 (* USE ONLY AFTER ROULETTE IN THE DAILY CYCLE *)
 BEGIN
  WITH NESTMAT[NEST] DO
  AGE:=(DAY-HDAY[CID])+1
 END;

 FUNCTION IPOWER(BASE:REAL;POWER:INTEGER):REAL;
 BEGIN
  IPOWER:=EXP(POWER*LN(BASE))
 END;

 FUNCTION DAYPROB:REAL;
 (* RETURNS THE PROBABILITY OF DYING *)
 (* FOR A SPECIFIC CHICK/NEST/DAY    *)
 VAR TEMPROB:REAL;
 BEGIN
  TEMPROB:=BASE[NEST]*CURVEHEIGHT[AGE(CHICK)];
  DAYPROB:=TEMPROB*IPOWER(PRCNTIN50,NESTMAT[NEST].BRFT50)
 END;

FUNCTION RANDNORM:REAL;
(* RETURNS A STANDARD RANDOM NORMAL NUMBER *)

VAR
  I : INTEGER;
  SUM : REAL;

BEGIN (* RANDNORM *)
  SUM := 0.0;
  FOR I := 1 TO 12 DO
    SUM := SUM + RANDOM;
  RANDNORM := SUM - 6.0;
END; (* RANDNORM *)

FUNCTION DIECALC (MORTPROB : REAL):INTEGER;
(* DETERMINES THE FATE OF A CHICK  BY COMPARING THE PROBABILITY
    THAT A STANDARD RANDOM NORMAL NUMBER (TESTPROP) LIES
    WITHIN A STANDARD NORMAL CURVE TO THE PROBABILITY OF A
    CHICK DYING ON A PARTICULAR DAY (MORTPROB).  IF
   RANDPROB IS LESS THAN MORTPROB THEN THE CHICK DIES.  *)
```

```
VAR
   NORMNUM, TESTPROB : REAL;
   NINTRVL,INTRVL,PHIGH, PLOW : REAL;
   ZINDEX : INTEGER;

BEGIN (* DIECALC *)
  NORMNUM  :=  ABS(RANDNORM);  (* GET A STANDARD RANDOM  NORMAL
NUMBER *)
  ZINDEX  := TRUNC(NORMNUM * 10.0);  (* FIND INDEX FOR Z  ARRAY
*)
  IF ZINDEX >= 49 THEN
    TESTPROB := 0.5
  ELSE BEGIN  (* INTERPOLATE *)
    PLOW := ZARRAY[ZINDEX];
    PHIGH := ZARRAY[ZINDEX + 1];
    INTRVL:=(PHIGH-PLOW)/10;
    NINTRVL:=10*((10*NORMNUM)-TRUNC(10*NORMNUM));
    TESTPROB := PLOW + (INTRVL * NINTRVL);
    END; (* ELSE *)
  TESTPROB := 0.5 - TESTPROB;
  IF TESTPROB <= (0.5 * MORTPROB) THEN
    DIECALC := 0
  ELSE
    DIECALC := 1;
END; (* DIECALC *)

PROCEDURE ROULETTE;
 (* DECIDES WHETHER A CHICK LIVES OR DIES *)
  VAR MORTRESULT:INTEGER;
  BEGIN
   WITH NESTMAT[NEST] DO
    BEGIN
    CASE CHICK OF
     ACHICK:BEGIN
            MORTPROB:=DAYPROB;
            IF MORTPROB<0.005 THEN MORTPROB:=0.005;
            MORTRESULT:=DIECALC(MORTPROB);
            IF MORTRESULT=0 THEN WT[CHICK]:=0
            END;
     BCHICK:BEGIN
            MORTPROB:=DAYPROB;
            IF MORTPROB<0.005 THEN MORTPROB:=0.005;
            MORTRESULT:=DIECALC(MORTPROB);
            IF MORTRESULT=0 THEN WT[CHICK]:=0
            END;
     CCHICK:BEGIN
            MORTPROB:=DAYPROB;
            IF MORTPROB<0.005 THEN MORTPROB:=0.005;
            MORTRESULT:=DIECALC(MORTPROB);
            IF MORTRESULT=0 THEN WT[CHICK]:=0
            END;
```

```
        END;(*CASE*)
    END
  END;

 PROCEDURE WTINCREM;
 BEGIN
  WITH  NESTMAT[NEST] DO
   BEGIN
    WT[CHICK]:=ROUND(INTERCEPT[CHICK]*EXP(SLOPE[CHICK]*AGE(CHICK)));
    IF (WT[CHICK]>=500) OR (AGE(CHICK)>=21) THEN WT[CHICK]:=500
   END
 END;

 FUNCTION ALLGONE(D:INTEGER):BOOLEAN;
 VAR N:     INTEGER;
     GONE: BOOLEAN;
 BEGIN
 GONE:=TRUE;
 N:=1;
 WHILE GONE AND (N<=NNESTS) DO
  BEGIN
  GONE:=(EXTANTLIST[D,N]<>NORMAL);
  N:=N+1
  END;
 ALLGONE:=GONE
 END;

 PROCEDURE CLOSENEST;
 VAR TEMPDAY:INTEGER;
 BEGIN
 FOR TEMPDAY:=(DAY+1) TO (DAY+LAG) DO
  EXTANTLIST[TEMPDAY,NEST]:=KILLERS;
 FOR TEMPDAY:=(DAY+LAG+1) TO NDAYS+1 DO
  EXTANTLIST[TEMPDAY,NEST]:=DEFUNCT;
 END;

 PROCEDURE UPDATEXTANT;
 VAR ELEMENT:   INTEGER;
     C:         CHICKTYPE;
     CLOSEFLAG: BOOLEAN;
 BEGIN
 IF EXTANTLIST[DAY,NEST]=NORMAL THEN
  BEGIN
  CLOSEFLAG:=TRUE;
  FOR C:=ACHICK TO CCHICK DO
   BEGIN
   ELEMENT:=OUTMAT[DAY,NEST,C];
   IF (ELEMENT=-2) OR (ELEMENT>0) THEN CLOSEFLAG:=FALSE;
   END;
  IF CLOSEFLAG THEN CLOSENEST;
  END;
 END;
```

```
PROCEDURE COMPLETE;
VAR LASTDAY:INTEGER;
BEGIN
CLRSCR;
GOTOXY(5,12);
WRITELN('COMPLETING OUTPUT MATRIX...');
LASTDAY:=DAY-1;
FOR DAY:= DAY TO NDAYS DO
 BEGIN
 FOR NEST:=1 TO NNESTS DO
  BEGIN
  FOR CHICK:=ACHICK TO CCHICK DO
      OUTMAT[DAY,NEST,CHICK]:=OUTMAT[LASTDAY,NEST,CHICK];
  END;
 END;
END;

PROCEDURE INITIALIZE;
BEGIN
FOR NEST:=1 TO NNESTS DO
 BEGIN
  NESTMAT[NEST]:=HOLDMAT[NEST];
 END;
FOR DAY:= 20 TO 70 DO
 BEGIN
 FOR NEST:=1 TO NNESTS DO
  BEGIN
  EXTANTLIST[DAY,NEST]:=NORMAL;
  FOR CHICK:=ACHICK TO CCHICK DO
  OUTMAT[DAY,NEST,CHICK]:=0;
  END
 END
END;(*PROCEDURE*)

PROCEDURE SEASNPREP;
BEGIN
INITIALIZE;
CLRSCR;
WRITELN('SEASON:   ',SEASON:3);
WRITELN('DAY NUMBER:    ');
WRITELN('NEST NUMBER:   ');
GOTOXY(5,12);
WRITELN('CONDUCTING SIMULATION...');
DAY:=20
END;

PROCEDURE CHICKDAY;
BEGIN
 CASE STATUS(CHICK) OF
  PREHATCH:OUTMAT[DAY,NEST,CHICK]:=-2;
  LIVING:  BEGIN
```

```
            ROULETTE;
            IF ALIVE(CHICK) THEN WTINCREM;
            OUTMAT[DAY,NEST,CHICK]:=NESTMAT[NEST].WT[CHICK];
            END;
   DEAD:    OUTMAT[DAY,NEST,CHICK]:=0;
   NOCHICK: OUTMAT[DAY,NEST,CHICK]:=-1;
   HOMEFREE:OUTMAT[DAY,NEST,CHICK]:=500
  END
 END;

FUNCTION CLASSCALC(ROW,COLUMN:INTEGER):DISTCLASSTYPE;
BEGIN
 IF DISTMAT[ROW,COLUMN]<=2.5
  THEN CLASSCALC:=IN25
  ELSE IF DISTMAT[ROW,COLUMN]<=5.0
      THEN CLASSCALC:=IN50
      ELSE CLASSCALC:=OUT50
END;

PROCEDURE INTERNEST;
(*RECALCULATES ALL INTER-NEST RELATIONSHIPS
FOR NORMAL NESTS AT THE BEGINNING OF
EACH DAY, USING DATA FROM THE EXTANTLIST
ARRAY, UPDATED ON THE PRECEDING DAY*)
BEGIN
 FOR KEYNEST:=1 TO NNESTS DO
 IF EXTANTLIST[DAY,KEYNEST]=NORMAL
  THEN
   BEGIN
    WITH NESTMAT[KEYNEST] DO
     BEGIN
      NEARID:= -1;
      DNEAR:= 10000.0;
      N25:=0;
      N50:=0;
      BRFT25:=0;
      BRFT50:=0;
      FOR OTHERNEST:=1 TO NNESTS DO
       BEGIN
        IF OTHERNEST<>KEYNEST THEN
          BEGIN (* IF *)
            IF (DISTMAT[KEYNEST,OTHERNEST] < DNEAR) AND
               (EXTANTLIST[DAY, OTHERNEST] <> DEFUNCT) THEN
             BEGIN
               DNEAR := DISTMAT[KEYNEST,OTHERNEST];
               NEARID := OTHERNEST;
             END; (* IF *)
           IF  DNEAR > 9500.0 THEN BEGIN (* NEAREST NEIGHBOR IS
ITSELF *)
             DNEAR := 0.0;
             NEARID := KEYNEST;
             END;
```

```
          CASE EXTANTLIST[DAY,OTHERNEST] OF
           NORMAL: CASE CLASSCALC(KEYNEST,OTHERNEST) OF
                   IN25: BEGIN
                         N25:=N25+1;
                         N50:=N50+1;
                         END;
                   IN50: N50:=N50+1;
                   OUT50:(*NO CHANGE*);
                   END;
           KILLERS:CASE CLASSCALC(KEYNEST,OTHERNEST) OF
                   IN25:BEGIN
                        BRFT25:=BRFT25+1;
                        BRFT50:=BRFT50+1;
                        END;
                   IN50:BRFT50:=BRFT50+1;
                   OUT50:(*NO CHANGE*);
                   END;
           DEFUNCT:(*DON'T CHANGE COUNTS*);
        END(*CASE*)
      END;(*FOR*)
      END(*IF THEN*)
    END(*WITH*)
  END(*IF THEN*)
END(*PROCEDURE*);

PROCEDURE DAYCYCLES;
BEGIN
 REPEAT
  GOTOXY(16,2);
  WRITELN(DAY:2);
  IF DAY>=FIRSTHATCHDAY THEN INTERNEST;
  IF (DAY=FIRSTHATCHDAY) AND (SEASON=1) THEN SETUP;
   FOR NEST:=1 TO NNESTS DO
    BEGIN
    GOTOXY(16,3);
    WRITELN(NEST:2);
    FOR CHICK:=ACHICK TO CCHICK DO CHICKDAY;
    UPDATEXTANT;
    END; (*CURRENT NEST*)
    DAY:=DAY+1;
   UNTIL (ALLGONE(DAY-1)) OR (DAY>NDAYS);
END;

 PROCEDURE SEASONPRINT;
 VAR NESTCOUNT,CHICKCOUNT:INTEGER;
 BEGIN
 NESTCOUNT:=0;
 FOR NEST:=1 TO NNESTS DO
  IF EXTANTLIST[NDAYS+1,NEST]=NORMAL THEN
   NESTCOUNT:=NESTCOUNT+1;
 NC:=NC+NESTCOUNT;
```

```
 NC2:=NC2+(NESTCOUNT*NESTCOUNT);
 CHICKCOUNT:=0;
 FOR NEST:=1 TO NNESTS DO
  FOR CHICK:=ACHICK TO CCHICK DO
   IF OUTMAT[NDAYS,NEST,CHICK]>0
    THEN CHICKCOUNT:=CHICKCOUNT+1;
 CC:=CC+CHICKCOUNT;
 CC2:=CC2+(CHICKCOUNT*CHICKCOUNT);
 DAY:=NDAYS;
(* IF (LASTSIMDAY[SEASON]=NDAYS) AND (NOT ALLGONE(NDAYS))
   THEN WRITELN('DAYS TO EXTINCTION:   NOT ALL GONE')
   ELSE WRITELN('DAYS TO EXTINCTION:   ',LASTSIMDAY[SEASON]);*)
 END;

 PROCEDURE STATPRINT;
 BEGIN
  WRITELN(LST,'NUMBER OF SEASONS:   ',NSEASONS);
  WRITELN(LST,'MEAN CHICKS LEFT:   ',(CC/NSEASONS):9:2);
  WRITELN(LST,'ST.             DEV.:               ',(SQRT((CC2-
(CC*CC/NSEASONS))/(NSEASONS-1))):9:2);
  WRITELN(LST,'MEAN NESTS LEFT:   ',(NC/NSEASONS):9:2);
  WRITELN(LST,'ST.             DEV.:               ',(SQRT((NC2-
(NC*NC/NSEASONS))/(NSEASONS-1))):9:2);
 END;

 BEGIN (*MODEL*)
  CC:=0;
  CC2:=0;
  NC:=0;
  NC2:=0;
  FOR SEASON:=1 TO NSEASONS DO
  BEGIN
  SEASNPREP;
  DAYCYCLES;
   IF DAY<=NDAYS THEN
                     BEGIN
                     LASTSIMDAY[SEASON]:=DAY-1;
                     COMPLETE
                     END
                 ELSE
                     BEGIN
                     LASTSIMDAY[SEASON]:=NDAYS;
                     GOTOXY(5,12);
                     WRITELN('NO COMPLETION REQUIRED.....')
                     END;
            SEASONPRINT;
    END;(*SEASON*)
  IF NSEASONS>1 THEN STATPRINT
 END;(*MODEL*)

PROCEDURE PRESS;
 VAR RESP:CHAR;
```

```
BEGIN
WRITELN('PRESS SPACEBAR TO CONTINUE....');
READ(RESP)
END;

(*BEGINNING OF THE MAIN PROGRAM*)

BEGIN
 WRITE('NAME OF NEST DATA FILE:  ');
 READLN(NFNAME);
 WRITE('NUMBER OF SEASONS:       ');
 READLN(NSEASONS);
 WRITE('CURRENT DATE:            ');
 READLN(DATE);
 FOR LAG:=1 TO 5 DO
   BEGIN
     FOR P50:=0 TO 4 DO
       BEGIN
       RANDOMIZE;
       ZINIT;
       DATALOAD;
       DISSTDDAY;
       RUNPREP;
       MODEL;
       END;
   END;
END. (*MAIN PROGRAM*)
```

Data File Creation Program

The following listing is for the program which created the data files used in the simulations run by PATCHSERIES.

```
PROGRAM BUILDEVEN;
(*BUILDS DATA MATRICES FOR PATCHSERIES
WITH NESTS EVENLY DISTRIBUTED IN A
5 BY 5 GRID*)

CONST NNESTS=25;

TYPE CHICKTYPE=(ACHICK,BCHICK,CCHICK);
     NESTREC  =RECORD
                NESTID:        STRING[5];
                NX,NY,DNEAR:   REAL;
                HDAY:              ARRAY[ACHICK..CCHICK]     OF
INTEGER;
                WT:                ARRAY[ACHICK..CCHICK]     OF
INTEGER;
                DANGQ,SAFEQ:   0..4;
                ATTENT:        CHAR;
                N25,N50:       INTEGER;
                BRFT25,BRFT50: INTEGER;
                NEARID:        INTEGER;
               END;
VAR IDARRAY:  ARRAY [1..5,1..5] OF INTEGER;
    ROW,COLUMN,I:  INTEGER;
    RESP:  CHAR;
    PRESENT:  ARRAY[ACHICK..CCHICK] OF BOOLEAN;
    SAMEWEIGHT:  BOOLEAN;
    STANDARDWEIGHT:  INTEGER;
    STNEST,NFNAME:  STRING{25};
    NESTMAT:  ARRAY[1..NNESTS] OF NESTREC;
    NFILES,STDQ,STSQ:  INTEGER;
    COUNT,GRIDGAP,NEST,STNDRDAY:INTEGER;
    XVECTOR,YVECTOR:  ARRAY[1..5] OF REAL;
    PREFIX,SUFFIX:STRING;
    NESTFILE:FILE OF NESTREC;
    INTERVAL1,NUMBERINCR,INCREMENT:INTEGER;
    CHICK:CHICKTYPE;
    CHICKLABEL:ARRAY[ACHICK..CCHICK] OF STRING{25};

PROCEDURE LABELS;
BEGIN
 CHICKLABEL[ACHICK]:=’A’;
 CHICKLABEL[BCHICK]:=’B’;
 CHICKLABEL[CCHICK]:=’C’;
END;
```

```
PROCEDURE MAKEIDARRAY;
BEGIN
 IDARRAY[1,1]:=25;
 IDARRAY[1,2]:=18;
 IDARRAY[1,3]:=17;
 IDARRAY[1,4]:=16;
 IDARRAY[1,5]:=24;
 IDARRAY[2,1]:=19;
 IDARRAY[2,2]:=7;
 IDARRAY[2,3]:=8;
 IDARRAY[2,4]:=9;
 IDARRAY[2,5]:=15;
 IDARRAY[3,1]:=20;
 IDARRAY[3,2]:=4;
 IDARRAY[3,3]:=5;
 IDARRAY[3,4]:=6;
 IDARRAY[3,5]:=14;
 IDARRAY[4,1]:=21;
 IDARRAY[4,2]:=1;
 IDARRAY[4,3]:=2;
 IDARRAY[4,4]:=3;
 IDARRAY[4,5]:=13;
 IDARRAY[5,1]:=22;
 IDARRAY[5,2]:=10;
 IDARRAY[5,3]:=11;
 IDARRAY[5,4]:=12;
 IDARRAY[5,5]:=23;
 WRITELN('NESTS  1 TO  9 HAVE 8 NEIGHBOURS');
 WRITELN('NESTS 12 TO 21 HAVE 5 NEIGHBOURS');
 WRITELN('NESTS 22 TO 25 HAVE 3 NEIGHBOURS');
END;

PROCEDURE GETINPUTS;
BEGIN
 WRITELN('ENTER SMALLEST GRID INTERVAL (CM): ');
 READLN(INTERVAL1);
 WRITELN('ENTER THE INTERVAL INCREMENT: ');
 READLN(INCREMENT);
 WRITELN('ENTER THE NUMBER OF INCREMENTS: ');
 READLN(NUMBERINCR);
 NFILES:=NUMBERINCR+1;
 WRITELN('YOU WILL MAKE ',NFILES,' FILES');
 FOR CHICK:=ACHICK TO CCHICK DO
  BEGIN
   WRITELN(CHICKLABEL[CHICK],' CHICK PRESENT? (Y/N)');
   READ(RESP);
   WRITELN;
   IF RESP='Y' THEN PRESENT[CHICK]:=TRUE
               ELSE PRESENT[CHICK]:=FALSE;
  END;
 WRITELN('ENTER THE HATCH DAY: ');
```

```
READLN(STNDRDAY);
WRITELN('MAKE THE HATCH WEIGHT CONSTANT? (Y/N) ');
READ(RESP);
WRITELN;
IF RESP='Y' THEN SAMEWEIGHT:=TRUE
            ELSE SAMEWEIGHT:=FALSE;
IF SAMEWEIGHT THEN
               BEGIN
                WRITELN('ENTER THE STANDARD WEIGHT: ');
                READLN(STANDARDWEIGHT);
               END;
WRITELN('ENTER THE FILE PREFIX: ');
READLN(PREFIX);
WRITELN;
WRITELN('ENTER DANGEROUS QUARTERS:  ');
READLN(STDQ);
WRITELN('ENTER SAFE QUARTERS:  ');
READLN(STSQ);
WRITELN('EVERY FILE CREATED WILL HAVE THIS');
WRITELN('PREFIX AND A SUFFIX SHOWING THE GRID');
WRITELN('INTERVAL IN METERS');
WRITELN('EG.  DUMMY2.25');
WRITELN;
END;

PROCEDURE VECTORBUILD;
VAR SIGN: INTEGER;
    DEVIATION: REAL;
BEGIN
 FOR I:= 1 TO 5 DO
  BEGIN
  XVECTOR[I]:=(I-1)*(GRIDGAP/100);
  SIGN:=1-(2*ROUND(RANDOM));
  DEVIATION:=0.01*(ROUND(3*RANDOM));
  XVECTOR[I]:=XVECTOR[I]+(SIGN*DEVIATION);
  YVECTOR[I]:=(I-1)*(GRIDGAP/100);
  SIGN:=1-(2*ROUND(RANDOM));
  DEVIATION:=0.01*(ROUND(3*RANDOM));
  YVECTOR[I]:=YVECTOR[I]+(SIGN*DEVIATION);
  END;
END;

PROCEDURE MATRIXBUILD;
BEGIN
 FOR ROW:=1 TO 5 DO
  BEGIN
   FOR COLUMN:=1 TO 5 DO
    BEGIN
     NEST:=IDARRAY[ROW,COLUMN];
     WITH NESTMAT[NEST] DO
      BEGIN
       STR(NEST,STNEST);
```

```
        NESTID:=CONCAT('EVN',STNEST);
        NX:=XVECTOR[COLUMN];
        NY:=YVECTOR[ROW];
        FOR CHICK:=ACHICK TO CCHICK DO
         BEGIN
          IF NOT PRESENT[CHICK]
             THEN WT[CHICK]:=-1
             ELSE
              BEGIN
               IF SAMEWEIGHT
                   THEN WT[CHICK]:=STANDARDWEIGHT
                   ELSE
                    BEGIN
                     WRITELN('WEIGHT OF ',CHICKLABEL[CHICK]);
                     READLN(WT[CHICK]);
                    END
               END;
           IF NOT PRESENT[CHICK]
              THEN HDAY[CHICK]:=0
              ELSE HDAY[CHICK]:=STNDRDAY;
          END;
         DANGQ:=STDQ;
         SAFEQ:=STSQ;
         ATTENT:='X';
         DNEAR:=0;
         N25:=0;
         N50:=0;
         BRFT25:=0;
         BRFT50:=0;
         NEARID:=0;
       END;(*WITH NESTMAT*);
     END;(*ROW*)
   END;(*COLUMN*)
 END;(*PROCEDURE*)

PROCEDURE STORE;
BEGIN
 STR(GRIDGAP,SUFFIX);
 NFNAME:=CONCAT(PREFIX,SUFFIX);
 WRITELN('THE FILE NAME IS:  ',NFNAME);
 WRITELN('OK?  ');
 READ(RESP);
 WRITELN;
 ASSIGN(NESTFILE,NFNAME);
 REWRITE(NESTFILE);
 FOR I:= 1 TO NNESTS DO
   WRITE(NESTFILE,NESTMAT[I]);
 CLOSE(NESTFILE);
END;

BEGIN(*MAIN PROGRAM*)
LABELS;
```

```
MAKEIDARRAY;
GETINPUTS;
GRIDGAP:=INTERVAL1;
COUNT:=0;
WRITELN('BEGINNING CYCLES...');
WHILE COUNT<NFILES DO
 BEGIN
  VECTORBUILD;
  WRITELN('VECTORBUILD COMPLETED');
  MATRIXBUILD;
  WRITELN('MATRIXBUILD COMPLETED');
  STORE;
  GRIDGAP:=GRIDGAP+INCREMENT;
  COUNT:=COUNT+1;
 END;
WRITELN('DONE');
END.
```