BREEDING SUCCESS OF THE PUFFIN ON DIFFERENT HABITATS

BREEDING SUCCESS OF THE COMMON PUFFIN (<u>FRATERCULA</u> <u>ARCTICA</u> L.) ON DIFFERENT HABITATS AT GREAT ISLAND, NEWFOUNDLAND

by

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ABSTRACT

The breeding success of puffins (Fratercula arctica) in different habitats was studied on Great Island, Newfoundland. A multiple regression analysis showed that puffin burrow density was negatively correlated with distance from the cliff edge, and positively correlated with angle of slope. The biological significance of these correlations was found to be that close to the cliff edge, where the angle of slope is steep, breeding success is significantly higher than on adjacent level habitat. The reasons for the difference in breeding success are, firstly, eggs and chicks are more exposed to gull predation on level habitat, and secondly, parents are more vulnerable to robbing by gulls when taking food to chicks on level areas than when taking food to chicks on slope habitat. Thus, during the breeding season, natural selection acts more strongly against birds nesting on level habitat away from the cliff edge than against those nesting close to the cliff edge. In the absence of gull interference puffins showed higher breeding success. A model is presented which relates the distribution of puffin nests to habitat characteristics in the presence and absence of gulls.

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I. INTRODUCTION

1. Outline of the Problem

Biologists have known for a long time that the total living world is characterized by order and organization. It is recognized that animals are dispersed in non-random patterns in time and space and occupy only a certain part of the available environment according to species-specific characteristics. This phenomenon of habitat specificity is presumed to be adaptive and to exemplify a fundamental principle of modern evolutionary theory, that animals tend to reside and breed in areas where values for survival and reproductive success are highest.

The question of what limits the distribution of a species has been considered by many biologists (e.g., Andrewartha and Birch 1954; Elton 1927, 1933; Fretwell and Lucas 1969; Hilden 1965; Hinde 1959; Klopfer 1962; Klopfer and Hailman 1965; Lack 1933, 1934, 1940; MacArthur 1958; Miller 1942; Shelford 1911; Svärdson 1949; Thorpe 1945), who have found two classes of environmental agents acting in a limiting fashion. These are biological interactions between individuals, species, populations, or any group, and physiological tolerances to critical physical and chemical properties of the environment. However, relatively few studies have been directed towards an analysis of what determines the distribution of a species within its total area of occupancy, although the above two classes of agents are probably involved.

Those investigations which have been conducted have usually been concerned with the description of habitats occupied in the breeding season by sympatric congeneric species of vertebrates to assess the extent of their segregation or overlap (e.g., Bédard 1969a; MacArthur 1958; Sturman 1968). Often abundance has been related to particular features of the environment in order to define habitat preferences, with rarely a clear demonstration of what portion of a species' observed distribution is maintained by the presence of its congeners or by other environmental factors. Furthermore, abundance alone is not always a reliable index of habitat suitability (see Dow 1969; Fretwell 1968, 1969). For example, density could be low, not for reasons of poor habitat but because few animals were available for invading the habitat. If habitat selection is an adaptive activity then the only measure of habitat quality during the breeding season is breeding success (i.e., the production of offspring surviving to fledging).

Thus to adequately describe the relationship between a species and the habitat is occupies, all the relevant environmental conditions throughout its total geographic range, as well as breeding success in representative areas, should be known. Although this requirement has yet to be met for any individual species, preliminary work towards this end has begun. For example, Sturman (1968), by using multiple linear regression techniques, has discovered the habitat characteristics which appear to be important in determining variations in abundance of chickadees (*Parus atricapillus* and *P. rufescens*) where they breed. However, the best attempt to determine the optimal breeding habitat of a species has been made by Southwood and his research team (see Blank *et al.* 1967; Southwood 1967; Southwood and Cross 1969) with partridge (*Perdix perdix*). They have not only shown a relationship between habitat and breeding success, but have also discovered the factor (insect abundance) which appears to be responsible for the observed differential survival of young (Southwood and Cross 1969).

Colonial seabirds make excellent study subjects for relating breeding success to environmental factors since they tend to breed in high numbers at traditional colonies where nests are abundant and the number of environmental variables small. Breeding success in relation to position in a colony has been found to vary in a predictable way (e.g., Brown 1967; Coulson and White 1956, 1958, 1960; Coulson 1968; Nelson 1966; Patterson 1965; Richdale 1957; Sladen *et al.* 1966; Snow 1960; Tuck 1960), but in most cases this appears to be determined by age and experience, which is correlated with position in the colony, and not by environmental factors. How breeding success varies in relation to physical features of the environment is not well known, nor the means by which the environment causes breeding success to vary. Because of this lack of knowledge, the relationship between habitat and breeding success was made the object of the present study. The species chosen for this purpose was the Common Puffin (*Fratercula arctica*).

The puffin is particularly suitable for examining breeding success in relation to habitat characteristics for three main reasons: first, the nesting habitat has been described throughout its geographic breeding range, which enables the associated environmental characteristics to be ascertained in general; second, puffins are relatively free from competitive interactions with other species for their nesting habitat; and third, colonies are usually large and free from human disturbance. The study was conducted at Great Island, Newfoundland, because the breeding habitat on this bird sanctuary encompassed almost all of the environmental conditions experienced by the species elsewhere in its breeding range. Some data on breeding were also collected on Funk Island and Small Island.

Based upon preliminary observations in 1967, which showed among other things that nest density varied and that gulls ate puffin eggs and chicks, the study was organized (and is presented) along the following lines:

1. Variations in nest abundance were studied in relation to several environmental factors which might be responsible for the variations.

2. Contrasting habitats, with respect to these factors, were delineated, and because nest abundance was found to be greatest on sloping ground (> 30°) and least on level ground (< 15°), slope and level ground were considered as the two habitats for the purpose of studying breeding success.

3. Factors likely to be important contributors to variation in breeding success were studied.

2. Summary of Puffin Breeding Biology

The following account of the nesting habitat of puffins is provided as a background to the present study of the puffin.

Descriptions of the nesting habitat of the puffin throughout its geographical range are abundant (North American mainland: Austin 1932; Bent 1919; Todd 1963; Newfoundland: Lucas 1888; Peters and Burleigh 1951; Tuck 1967; Greenland: Salomonsen 1950; Iceland: Gudmundsson 1953; Lack 1934; Faroes: Nørrevang 1960; Salomonsen 1935; Williamson 1948; British Isles: Lockley 1934, 1953; Perry 1946; Norway: Collett 1921; Løvenskiold 1947; Myrberget 1959a, 1961, 1962a; Murmansk region east of Novaya Zemlya: Belopol'skii 1957; Kartaschew 1960; Korneyeva 1967; Skokova 1967; Uspenski 1958; Spitsbergen: Jourdain 1922; Longstaff 1924; Løvenskiold 1954). In most areas puffins nest almost exclusively in burrows excavated in turf-covered maritime steep slopes and level tops of rocky coastal islets. At high latitudes, however, they are restricted to rock crevices in cliffs and interstices in talus slopes due to permafrost. The environmental conditions for nesting at Great Island, Newfoundland, are typical of other boreal colonies. Nests are concentrated on seaward grass slopes with lower densities on adjacent level ground.

The events of the breeding cycle of the puffin have also been studied in most parts of its breeding range, although seldom in great detail. The most useful accounts have been provided by Bannerman (1963), Belopol'skii (1957), Kartaschew (1960), Kozlova (1957), Lockley (1934, 1953), Myrberget (1959b, 1962a, 1962b), Perry (1946) and Salomonsen (1950). At Great Island, the seasonal cycle is as follows: adult puffins arrive in the vicinity of the island in early April, but the first synchronous mass landing does not occur until the last third of the month. Immature birds (< 3 years old, as judged by the aging technique of Lockley 1953 and Salomonsen 1944) do not appear until late May or early June. Nest-site establishment is accomplished by territorial agonistic behaviour among males. Courtship and copulation take place at sea close to the island. Eggs are laid from the second week of May to late June, with a strong peak in the first half of this period. The peak of hatching occurs during the last week of June and the first week of July. The first chicks are fledged in early August, and fledging continues through to the end of September. Except for the latest breeders, both breeding and non-breeding puffins depart in late August. The wintering range of the Newfoundland puffin populations is unknown, but Tuck (1967) suggests that it is the Grand Banks.

II. DESCRIPTION OF THE STUDY AREA

1. Location and Seabird Fauna

Fieldwork was done at Great Island, one of three uninhabited islands (other islands: Gull and Green) which comprise the provincial Witless Bay Seabird Sanctuary, located off the southeast coast of the Avalon Peninsula, Newfoundland (Figure 1). The precise location of Great Island is 47°11'N, 52°46'W, approximately 1.5 miles from the coastal settlement of Bauline East. In addition, three trips were made to Funk Island (49°46'N, 53°11'W) and Small Island (49°35'N, 53°46'W) in 1969 (Figure 1).

At least 100,000 pairs of puffins breed on Great Island. Nests are situated above the cliff; most of them are within 50 metres of the cliff edge. In addition to the Common Puffin, there are seven seabird species which breed regularly on the island: Leach's Petrel (*Oceanodroma leucorhoa*), Great Black-backed Gull (*Larus marinus*), Herring Gull (*Larus argentatus*), Black-legged Kittiwake (*Rissa tridactyla*), Razorbill (*Alca torda*), Common Murre (*Uria aalge*), and Black Guillemot (*Cepphus grylle*). Except for the gulls and petrels, there is little overlap in breeding habitats between these species and puffins. There are approximately 1,500 pairs of Herring Gulls and 40 pairs of Great Black-backed Gulls nesting on Great Island; both populations appear to be increasing (Dr. W. Threlfall, personal communication).

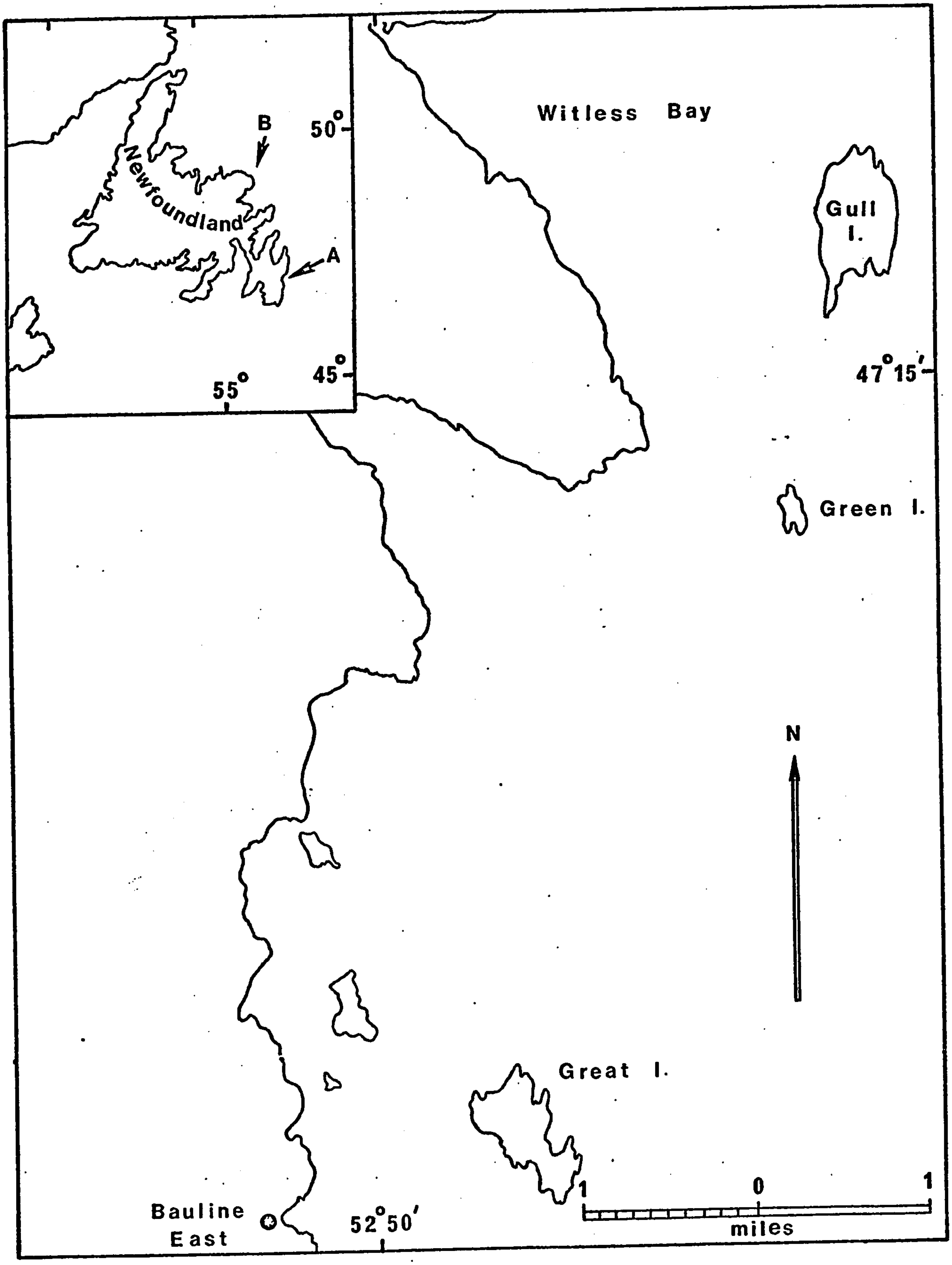


Figure 1. The Witless Bay islands, Newfoundland. . Inset map shows the general location of the Witless Bay islands (A) and Funk and Small Island (B) off the coast of Newfoundland.

2. Great Island

Topography

Great Island is approximately 0.85 mile long and 0.46 mile broad at its widest point and runs southeast-northeast along the greater dimension (Figure 1). The island has a rocky coastline of precipitous cliffs that reach their greatest height along the north facing shore (Figure 2). Numerous escarpments of granite rock form sharp irregularities with deep coves and bays. Except for the small areas of sand, gravel, and boulders, formed by wave action and cliff erosion at the base of these coves, there are no beaches. From the top edge of the rock cliffs a peat soil supports an often closed cover of grass-hummocked slopes which, proceeding inland, gradually give way to a Rubus-grass meadow and thick interior coniferous forest of predominantly dwarfed Balsam Fir (Abies balsamea) and Black Spruce (Picea mariana).

Habitats and vegetation

On the basis of the physical characteristics of the terrain and vegetative cover six major habitat types can be recognized. Conifers and shrubs account for some 51% of the surface area, maritime grass-hummocked slope 19%, Rubus-grass meadow 13%, exposed peat 9%, bare bedrock on the top of the island 6%, and eroded meadow 2% (Figure 3).

The characteristic physical features of the peripheral area of the island are shown in Figure 4. The maritime slope is covered mostly by grass hummocks (Bromus sp.), but sometimes it has undergone

Figure 2. Aerial view of Great Island, Newfoundland (Air Photo A 20967-11, 3 June 1969), showing location of main study areas: (1) Main Colony, (2-5) nests on slope habitat, (6-9) nests on level habitat. Areas 2, 3, 4, 6, 7, 8 and 9 were studied in 1968; areas 2, 5, 6, 7 and 8 in 1969.

Figure [illegible]. Aerial view of Great Island, Newfoundland (Air Photo [illegible]-67-11, 3 June [illegible]), showing location of main study areas. (1) Main colony, (2-4) nests on slope habitat, (5-9) nests on level habitat. Areas 2, 3, 4, 5, 7, 8 and 9 were studied in [illegible]; areas 2, 5, 6, 7 and 8 in [illegible].

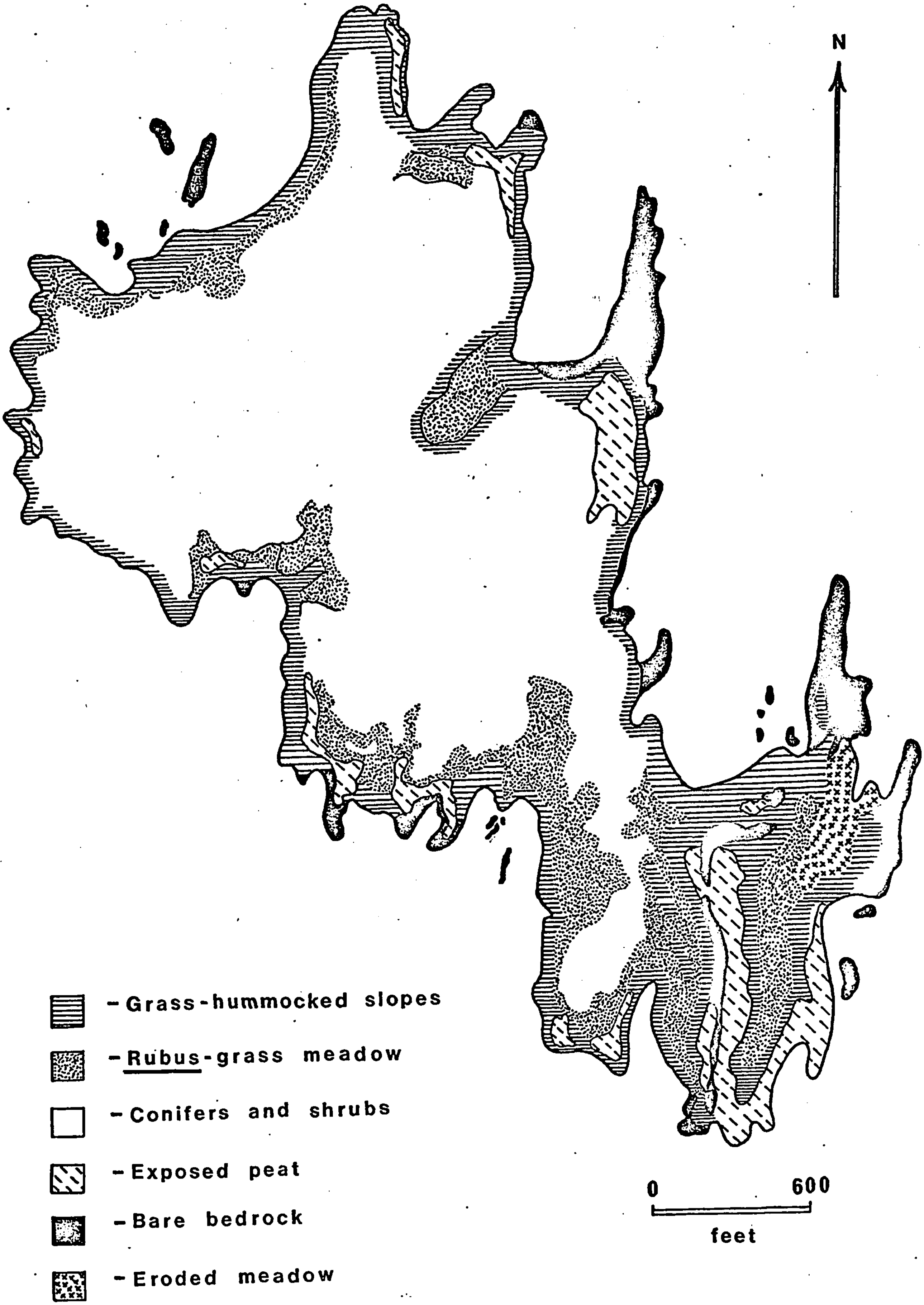


Figure 3. Sketch map of Great Island, showing principal habitats.

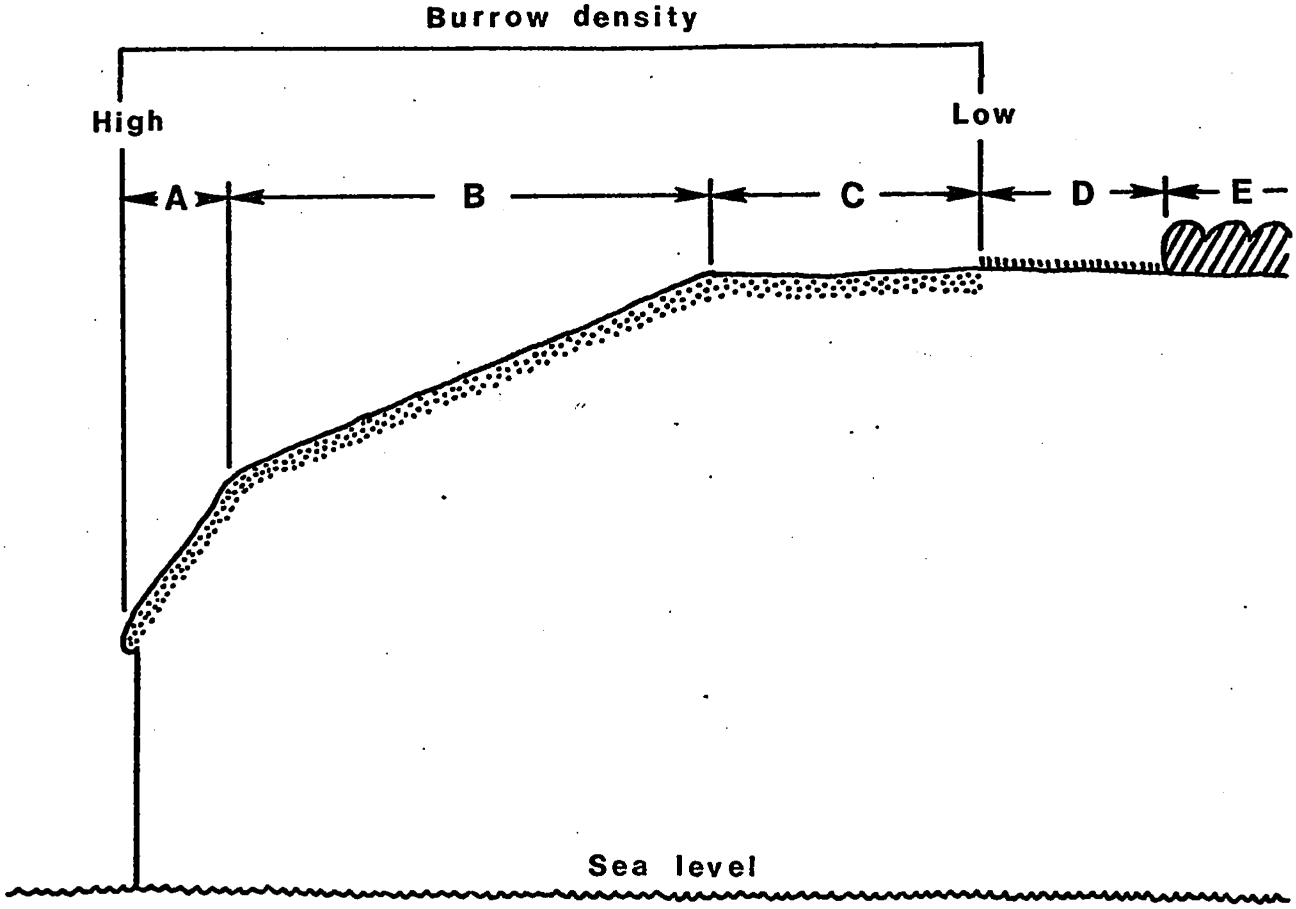


Figure 4. Comparison of puffin burrow density with habitat on a schematical section through the periphery of Great Island. Habitats: A - Maritime grass slope; B - Grass or Peat slope; C - Grass or Peat level; D - Rubus-grass meadow; E - Balsam Fir and Black Spruce forest.

partial erosion and supports almost no vegetation except for scattered grass clumps and a few Common Tansies (*Tanacetum vulgare*), Tansy Ragworts (*Senecio viscosus*), and Chickweeds (*Stellaria media* and *Cerastium vulgatum*). Inland slopes (Figure 4B) are usually less steep and covered by grass hummocks.

The dominant plant in the meadow region (Figure 4D), which extends from the grass or peat slope to the trees, is Wild Red Raspberry (*Rubus ideaus*) with a thick undergrowth of mixed grasses (*Deschampsia* sp., *Festuca* sp., and *Poa* sp.). In moist areas and in open valleys between conifer stands the soil supports a luxuriant growth of 3 - 4 foot high Reed Grass (*Calamagrostis inexpansa*), Fireweed (*Epilobium angustifolium*), Wood Fern (*Dryopteris clintoniana*), Clintonia (*Clintonia borealis*), and to a lesser extent Bunch-berry (*Cornus canadensis*), Goldenrod (*Solidago* spp.), and False Solomon's Seal (*Smilacina stellata*). On the southeast side of the island where a portion of the meadow has been eroded, the scattered vegetation is composed of dense stands of Common Tansy, Yarrow (*Achillea millefolium*), clumps of Angelica (*Angelica atropurpurea*), White Lettuce (*Prenanthes alba*), and short grasses. Stunted Balsam Fir, Black Spruce and associated shrubs form a thick forest over the interior of the island.

3. Experimental Islands

Funk Island

Funk Island is a flat-topped oblong granite rock situated some 35 miles out from the Newfoundland coast (Cape Freels) in roughly a NNE direction. It is 0.5 mile long, 0.25 mile wide, and approximately 46 feet high at its highest point. At the centre of the south end of the island on level ground, 500 to 1,000 pairs of puffins nest in shallow soil, covered by various short grasses, and in rock crevices. The shortest distance to the cliff edge from the periphery of the colony is over 400 feet. Funk Island is also a breeding site for the Gannet (Morus bassana), Great Black-backed Gull, Herring Gull, kittiwake, Razorbill, Common Murre, Thick-billed Murre (Uria lomvia), and possibly Black Guillemot (Garrity 1960; Gilliard 1937a, 1937b; Lucas 1888; Peters and Burleigh 1951; Russell 1965a, 1965b; Tuck 1960). The gull population is small (1969: c. 15 pairs) and does not appear to interact with puffins or other species on the island.(personal observation; Tuck 1960: 210).

Small Island

Small Island is the second outermost island of the six that comprise the Wadham Islands group located ten miles off the north coast of Newfoundland just east of Fogo Island. It is somewhat rectangular in shape and measures almost 0.5 mile long and 0.25 mile wide. The total surface is covered with luxuriant vegetation of hummock grasses, various herbs and mosses. Puffin nests are concentrated on the west half of the island and number at least 1,500 pairs. Our study burrows were in level, finely textured gravel some twenty to thirty feet from the shoreline along the southwest coast. The only other birds known to breed on the island are Common and Arctic Terns (Sterna hirundo and S. paradisaea).

4. Summer Climate

The summer temperature regime along the southeastern coast of Newfoundland is considerably lower than that of the adjacent continent. This is attributed to the frequent occurrence of fog and the cooling effect of the Labrador Current (Damman 1965). The summer climate can be described as cool and humid.

The weather at Great Island does not differ appreciably from meteorological records taken at St. John's, situated approximately 24 miles north of the island. Table 1 gives the monthly averages and extremes of temperature and precipitation of the months April to September 1967-1969 (breeding seasons studied), and the standard normals recorded at the St. John's Airport Weather Office.

Seasonal patterns of temperature and precipitation differ greatly between years. However, based on the standard normals for 1942-1960, the 1969 summer weather most closely approximated the average, while 1967 was significantly warmer and drier, and 1968 very much cooler and wetter. The poorest summer was 1968, when temperatures remained below normal for most of the season, snowfall and total precipitation in May and June was above normal, and the mean temperature for August was the lowest on record.

Table 1. Weather observations at St. John

Month	Temperature (°F)					
	Mean			Normal	Mean Extremes	
	1967	1968	1969	Mean*	1967	1968
April	29.4	34.7	33.5	34.1	24.1-34.7	28.2-41.2
May	41.2	40.0	40.9	42.1	34.0-48.3	32.4-42.5
June	54.1	46.6	54.3	50.6	43.0-64.6	38.6-54.5
July	64.1	57.3	56.5	59.7	55.8-72.3	48.1-66.5
August	65.8	53.6	59.1	59.8	58.1-73.2	47.5-59.6
September	55.2	53.6	52.1	53.6	48.2-62.1	46.5-60.6

*: Based as standard normals 1942-1960

at St. John's Airport (Torbay), Newfoundland.

Extremes		Normal Mean	Precipitation (inches)			
1968	1969	Extremes*	1967	1968	1969	Normal*
28.2-41.2	26.2-40.8	27.8-40.3	4.33	1.99	4.19	4.77
32.4-42.5	34.3-47.5	34.3-49.8	4.43	5.80	5.22	3.88
38.6-54.5	45.0-63.6	42.2-59.0	0.81	6.14	2.33	3.72
48.1-66.5	48.9-63.7	51.0-68.3	1.25	2.49	3.90	3.49
47.5-59.6	52.5-65.6	52.4-67.1	1.87	6.93	8.28	4.00
46.5-60.6	45.2-59.0	46.3-60.9	4.27	1.20	5.94	4.71

III. METHODS AND MATERIALS

Field work began in the second half of June 1967 and continued through the full breeding seasons (April to October) of 1968 and 1969. Small Island and Funk Island were visited in 1969.

The events of the puffin's breeding biology investigated at Great Island during this study separate clearly into two parts: measurements taken at one area of the island, designated the Main Colony (Figure 2), and measurements recorded at various locations around the island. The analysis of the breeding habitat (nest density and habitat characteristics), attendance (bird census), behaviour (fighting, panic-flights, nest-site tenacity, chick feeding rate, adult mobility), and gull interference (attacks and robbery) were conducted on the Main Colony. Data on time of egg-laying, breeding success, and fledging condition were obtained on the study areas shown in Figure 2. Collections of breeding birds, eggs, and food delivered to chicks were taken from nests off the study areas mentioned above, as were the egg displacement, chick movement, twinning and single-parented chick experiments. A detailed description of some of the procedures used are given below; the methods used for nest-site tenacity, chick feeding rate, twinning and single-parented chick experiments, egg displacement, and adult mobility are described in the appropriate location in the RESULTS.

1. Main Colony

The total area of this colony was divided into a grid of six metre squares by one-half inch polypropylene rope just before egg-laying began in 1968 (Figure 5). The grid was 60 metres long by 36 metres wide and covered the entire range of puffin nesting habitat, from the maritime cliff edge back through the *Rubus*-grass meadow into the edge of the coniferous forest. Strips 1, 2, and the front half of 3 were on maritime grass slope with the remaining strips on level ground.

2. Habitat Analysis

Late in the breeding season, 40 quadrats in the Main Colony grid were sampled by selecting at random one quarter of each quadrat (Figure 5) and measuring in each 9 m^2 sub-quadrat the following characteristics: puffin burrow number (Y), percent total vegetative cover (X_1), percent grass hummock cover (X_2), percent other vegetative cover (X_3), mean soil depth (X_4), mean grass hummock diameter (X_5), mean grass hummock height (X_6), grass hummock number (X_7), angle of slope (X_8), and distance from cliff edge (X_9). Only burrows over two feet in length and unconnected to adjoining burrows were used to determine Y. All mean values (X_4, X_5, X_6) were obtained from ten random measurements. The measurements were limited to Transects A to D because of their vegetative and topographic similarity (a semi-permanent stream ran along the entire length of Transect E, and Transect F was associated with an atypical inland slope).

An analysis of habitat selection based on simple linear

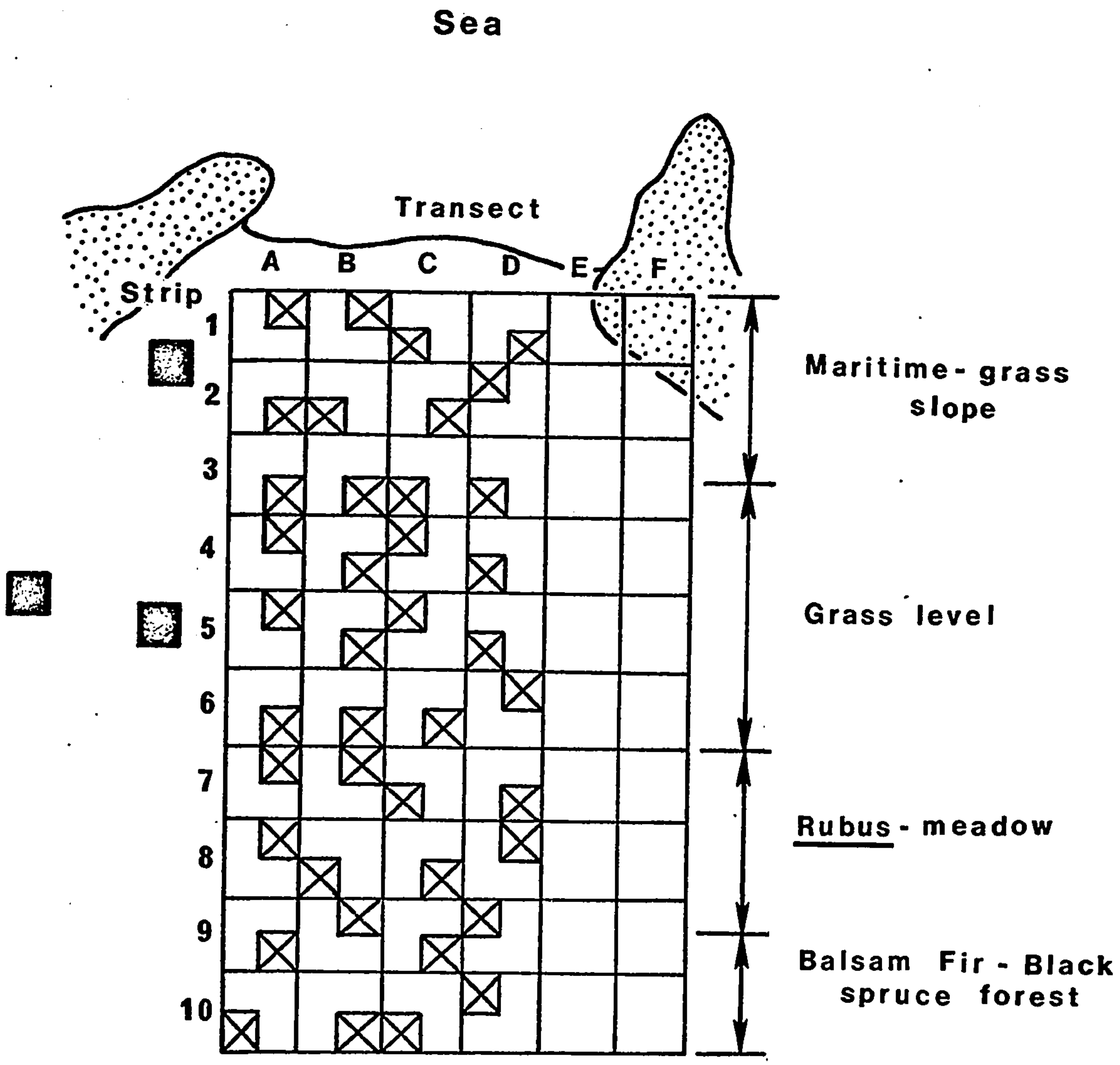


Figure 5. Grid system (60 m x 36 m) and habitat distribution on the Main Colony. Subdivisions (☒) of the quadrats were samples used in the habitat analysis. Shaded squares are permanent observation blinds and stippled areas at the front of the colony are exposed rock cliffs.

correlation is handicapped by the fact that each variable (X) measured in relation to the primary character (Y) is treated as an independent entity unrelated to other features of the nesting biotope. It is more likely that the variation in nest abundance of a species is determined by the resultant effect of the interaction of several characters rather than one factor alone (Sturman 1968; Power 1969). Therefore, puffin burrow numbers (Y) were regressed on the independent variables (X's) in a multiple linear regression analysis performed by computor (see Grant 1969).

The general equation for expressing the relationship between the independent and dependent variables is:

$$\hat{Y} = \bar{y} + b_1 (X_1 - \bar{x}_1) + b_2 (X_2 - \bar{x}_2) + b_3 (X_3 - \bar{x}_3) + \ldots b_n (X_n - \bar{x}_n).$$

Simple correlation coefficients (r) for all possible pairs of variables and significant ($P < 0.05$) partial regression coefficients (b) were calculated. The percentage contribution of the significant independent variables (X_i) to variations in Y was then determined by squaring the sum of the multiple correlation coefficients (R) and multiplying by 100. This value ($R^2 \times 100$) is the coefficient of determination (Steel and Torrie 1960), and is the percentage of the variation in Y that can be explained by the combined effect of the measured characteristics. To obtain R^2, the standard partial regression coefficient (b_i') was found by multiplying the partial regression coefficient (b_i) by the standard deviation (s) of X_i and Y: $b_i' = b_i (s_i/s_y)$. R^2 was then derived from the equation:

$$R^2_{y\,.\,1\,.\,.\,.\,k} = r_{y1}b_1' + r_{y2}b_2' + \ldots + r_{yk}b_k'$$

3. Census

Attendance at the colony was recorded by counting the number of birds on each quadrat of the grid each day (c. 1200 - 1400 hours) through the breeding season in 1969 from a permanent blind located above the colony (Figure 5). These census figures were used to determine variation in attendance at the colony, bird distribution, habitat occupation and utilization, etc. All day counts (number of birds in each quadrat counted every half-hour during the daylight period) were made on occasion for similar purposes.

4. Behaviour

Quantitative observation of behavioural interactions between puffins themselves and the puffin-gull association were made entirely on the Main Colony. The frequency of puffin fights (attacks and physical combat between two birds) and panic-flights (the simultaneous departure of birds from the colony towards the sea; Cullen and Ashmole 1963: 424) were observed at regular intervals (c. 4 - 5 days) through the breeding season in 1969 from two lower permanent blinds (Figure 5), one located directly adjacent to slope nesting habitat (A2) and the other beside level habitat (A5). Data were obtained simultaneously of birds in quadrat B2 (slope) and B5 (level) by one observer (myself and field assistant) in each of the two lower blinds (Figure 5). All watches were conducted in mid-afternoon (1400 - 1600 hours) for 60 consecutive minutes and commenced only after at least 20 minutes had elapsed from time of entering the blind.

5. Gull Interference

Gull cleptoparasitism (i.e., robbery or piracy of food) of puffins carrying food to the burrow for a chick was quantified by counting, in a four hour period, the number of puffin arrivals, deliveries of food to chicks, gull attacks, and gull robberies, across one strip (1, 2, 3, 4, 5, or 6) on the Main Colony. This was done each morning just after sunrise for six consecutive days in early August, 1968 and 1969. The watches were limited to a single strip to reduce error resulting from the observer's inability to accurately record all puffins arriving on a large observed area during this peak feeding period. Moreover, when an attempt is made by an observer to cover a large area, bias is introduced by the mere fact that a conspicuous interaction (gull attack) is less likely to be missed than a rapid, inconspicuous, successful, puffin delivery.

6. Collection of Adults

For a comparison of the morphological and physiological condition of breeding adults nesting on slope and level habitat early in the breeding season, birds incubating an egg were collected weekly between 26 May and 9 July in 1968 and just after the peak of egg-laying on 2 and 8 June in 1969. It was done at this time because correct identification of breeding status and nesting habitat for a bird can only be made once an egg has been produced and incubation begun.

7. Measurement of Eggs

Eggs laid in nests on slope and level habitat were compared to reveal possible differences between the two groups of breeding puffins (see Coulson 1963; Coulson et al. 1969; Fisher 1969; Nelson 1966; Richdale 1955, 1957; Serventy 1967 for similar work on other seabirds). Fertile eggs were collected between 28 May and 3 June 1968 and length, breadth, and weight were measured. From these the shape index and volume was derived according to the method described by Coulson (1963).

8. Time of Egg-laying

In 1968 all nests under observation were used in calculating the egg-laying period, whereas the 1969 data were derived from nests on the study areas alone (Figure 2). Time of laying was estimated by subtracting 42 days (incubation period: Myrberget 1962a) from hatching dates. This method eliminates nest failures from the analysis, but avoids the bias created by human disturbance on the colony during the egg-laying period (i.e., nest desertion) experienced by other workers (Lockley 1934; Myrberget 1962a; Korneyeva 1967). Late egg dates are less accurate than early ones because the data from which they are calculated may include some replacement clutches.

9. Breeding Success

Great Island

Breeding success (the production of offspring surviving to fledging) was determined by following the fate of 150 nests in 1968 (Slope = 90; Level = 60) and 402 nests in 1969 (Slope = 200; Level = 202) at various locations around the island (see Figure 2). Only complete burrows (i.e., unconnected to adjoining burrows) with an egg were selected for study. They were marked in early June and not re-examined until late June. Thus figures for hatching success do not take into account egg loss and subsequent replacement during the period from nest marking to the first inspection. However, I doubt if this source of error is significant, because no obvious replacement clutches were detected from hatching dates. From late June onwards regular checks were made at four-day intervals, weather permitting, until the egg disappeared, chick disappeared, or chick fledged. Towards the end of the fledging period chicks were checked at two-day intervals. This procedure was adopted to reduce nest desertion and avoid causing premature departure of young that has hampered other studies (e.g., Lockley 1934; Myrberget 1962a; Korneyeva 1967). Searching effort on our part was equal at all nests, as burrows were always opened and examined thoroughly before the fate of an egg or chick was recorded as disappeared if the first inspection failed to reveal it.

Hatching data were grouped into early (21-30 June)and late (post-30 June) period for the purpose of analyzing fledging success; the latter period was subdivided to compare chicks within this longer time period.

Funk Island and Small Island

The figures for puffin breeding success were derived from 106 nests at Funk Island and 147 nests at Small Island. Complete burrows were selected and marked on 17 (Funk) and 18 (Small) June 1969. They were re-examined on 18 (Funk) and 19 (Small) July to determine egg survival, and again on 29 (Funk) and 30 (Small) August for chick survival and fledging.

10. Fledging Condition

Great Island

Chicks at nests studied for breeding success were weighed with a Pesola Spring Balance (100, 300, or 500 g capacity) and their wing lengths were measured along a flattened left wing. Measurements were taken at four-day intervals until primary wing length exceeded 120 mm, from which time the chick was measured every two days until it fledged. Data used for fledging condition (i.e., bodyweight and winglength just prior to fledging) are in most cases taken from the chick one or two days before actual fledging (time of deserting the nest); rarely, chick measurements were known only within four days of fledging.

Funk Island and Small Island

All the 166 young still in study nests on the final visit to Funk Island (29 August) and Small Island (30 August) were weighed, their winglengths were measured and classified as to stage of feather development. For comparison of condition at fledging with chicks on Great Island only fully feathered chicks (little or no down present) estimated to be within a few days of fledging were used.

11. Food for the Chick

Food samples delivered by parents to the young were examined systematically through the chick rearing period (late June to early September) to determine the composition, seasonal variation and size of the meal. Immediately an adult puffin entered a burrow carrying food, the nestling was removed, any partially swallowed items extracted, and the burrow floor checked for additional food. In most cases the adult had left the burrow before we reached the nest-site. Each food item in the meal was identified, weighed and measured, and then returned to the burrow with the chick. Partially eaten loads, recognizable by the chick's swollen gullet, are not included in this analysis.

12. Chick Movements in Relation to Food Supply

The construction and arrangement of artifical burrows used in the chick activity experiment is shown in Figure 6. Each burrow consisted of a rectangular wood frame of 2 x 1 inch strapping 3 feet long, 6 inches wide and 6 inches high. One end and the two sides were enclosed with wire screening. The roof was covered with one-way viewing aluminum foil (supplier: Edmund Scientific Co.) and the bottom was left uncovered so the floor of the burrow would be entirely soil. The four burrows were placed side by side with soil packed tightly between and around them to prevent light from entering except through the burrow entrance. A black canvas tent was then erected over the burrows, with one edge of the tent attached to the front frame of each burrow roof.

Chicks (age: 25-30 days) were removed from natural nest-sites and one placed in each of the four experimental burrows. Acclimation was apparently rapid, as the chicks ate fish thrown to them from the burrow entrance on their first day of captivity. Nevertheless, to

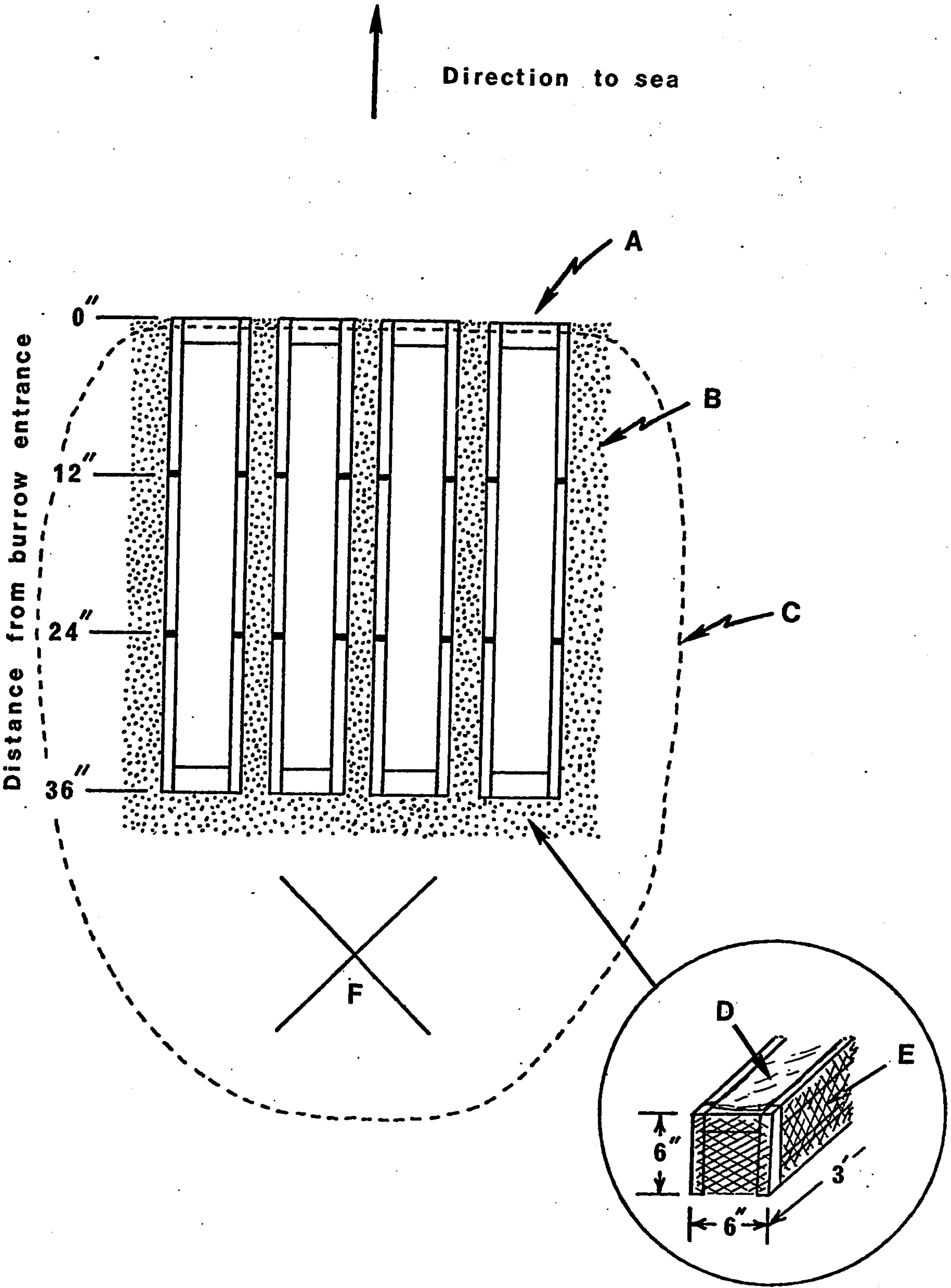


Figure 6. Design of the artificial burrows, showing: A open burrow entrance; B - soil; C - perimeter of tent enclosure; D - one-way view aluminum foil roof; E - wire screening; F - observer's position inside tent. Inset shows end of one artificial burrow with soil removed.

ensure adjustment to the new burrow environment and feeding method, the activity measurements were not started until seven days after capture.

The movements of the four chicks were observed through the burrow roofs from inside the darkened tent enclosure for three hours (1400-1700 hours) for eight consecutive days (22-29 August 1969). The first four days (control period) the chicks were fed 75-100 grams of fish per day while no food was given to them during the second half (starvation period) of the experiment. Position of the chicks in their separate artificial burrows was recorded each minute throughout the daily watches.

13. Statistical Analysis

The statistical tests used, including the multiple linear regression analysis, are from Ferguson (1959) and Steel and Torrie (1960). Chi-square values (X^2) shown with tables have been derived from 2 x 2 contingency tables testing the significance of the difference between the proportions indicated, unless stated otherwise.

IV. RESULTS

A. Comparative Breeding Performance of Puffins at Great Island

1. Nest and Adult Distribution

Nest distribution

The results of a multiple linear regression analysis show that 65.6 percent of the variation in nest abundance is accounted for by distance from cliff edge (X_9) alone (Table 2). The three significant variables (X_9 - distance from cliff edge, X_8 - angle of slope, and X_4 - soil depth) in combination account for 80.6 percent, to which the greatest contribution is made by distance from cliff edge (X_9), as shown by the standard partial regression coefficients (b_i'). Soil depth (X_4) was entered second into the multiple linear regression equation which means that it is more important in reducing the residual variation than the third significant independent variable, angle of slope (X_8).

Adult distribution

To determine if adults standing on the colony are distributed in the same way as nest density, the total number of birds observed across each strip of the Main Colony census area (Quadrats A-D: 1-6) during an all-day watch (25 May 1968: 0530 - 2000 hours) was compared with nest density figures for the same strips (Table 3). A chi-square test (2 x 6 contingency table) showed the differences between the observed and expected distributions to be highly significant ($P < 0.001$, $X^2 = 112.33$).

Adult puffins appeared more frequently in Strip 3 ($P < 0.001$,

Table 2. Multiple regression analysis*
to three significant variables
and distance from cliff edge (

Independent variables	Standard partial regression coefficients (b'_i)			Multiple correlation coefficients (R)			Tota R
	X_4	X_8	X_9	X_4	X_8	X_9	
X_9	--	--	0.38	--	--	0.8099	0.80
X_9, X_4	0.25	--	0.40	0.0054	--	0.8755	0.88
X_9, X_4, X_8	0.20	0.11	0.34	0.0044	0.1498	0.7442	0.89

*Significant independent variables are entered
linear regression equation in decreasing order

ession analysis* of puffin nest density (Y) in relation
ificant variables: soil depth (X_4), angle of slope (X_8),
from cliff edge (X_9), in 40 quadrats on the Main Colony.

n (R) X_9	Total R	Total R^2 x 100	Multiple linear regression equations
0.8099	0.8099	65.6	$\hat{Y} = 7.3-0.38(X_9-31.87)$
0.8755	0.8809	77.6	$\hat{Y} = 7.3-0.40(X_9-31.87)+0.25(X_4-80.12)$
0.7442	0.8984	80.7	$\hat{Y} = 7.3-0.34(X_9-31.87)+0.20(X_4-80.12)$ $+0.11(X_8-14.45)$

es are entered into the multiple
ecreasing order of their b_i' values.

Table 3. Comparison of observed and expected frequencies in distribution of adult puffins and nests over the Main Colony on 25 May 1968.

Strip	Observed values		Expected values		
	No. Nests	No. Birds	No. Nests	No. Birds	X^2 (1 df)
1	65	970	47.1	987.8	7.12
2	80	1789	85.1	1783.8	0.31
3	43	2178	101.1	2119.8	34.97
4	40	669	32.2	676.7	1.96
5	41	313	16.1	337.8	40.32
6	19	118	6.2	130.7	27.65
Totals	288	6037	287.8	6036.6	112.33 (df = 5)

$X^2 = 34.97$) than expected and less frequently in Strip 1 ($P < 0.01$, $X^2 = 7.12$), Strip 5 ($P < 0.001$, $X^2 = 40.32$), and Strip 6 ($P < 0.001$, $X^2 = 27.65$). The observed distribution did not differ significantly in the other two strips. Thus the distribution of adults does not match the distribution of nest-sites.

2. Pre-laying Period

Habitat occupation in spring

Puffin numbers at Great Island varied in a quasi-cyclical fashion during spring occupation and settlement; the birds were present for several consecutive days, followed by an equal time period when the nesting habitat was deserted (Figure 7). Once egg-laying was initiated some puffins were continuously ashore, although the cyclic pattern of attendance at the colony continued throughout most of the breeding season.

Birds appeared to occupy all parts of the nesting habitat simultaneously at the first landing, with no unusual strife in one part of the colony and dispersion from this part. Neither was there any obvious variation in the time of nest-site establishment on different parts of the Main Colony.

To determine how the nesting space is occupied in spring, the number of birds on each strip of the Main Colony grid was recorded each day of the attendance periods and related to habitat characteristics. The data for each attendance period are presented in Table 4. The differences in distribution between the first full visit (24 April) and the last one prior to the commencement of egg-

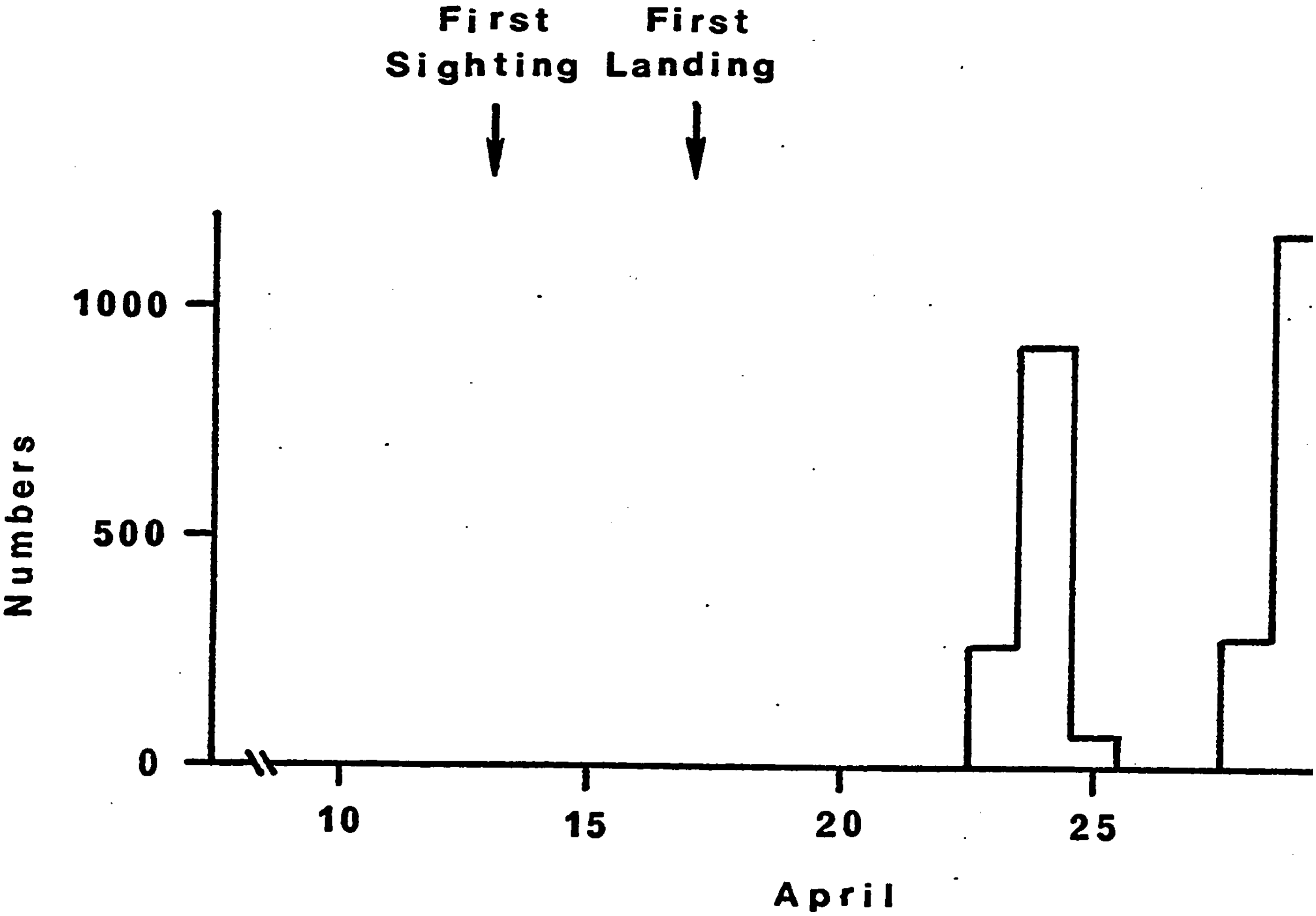
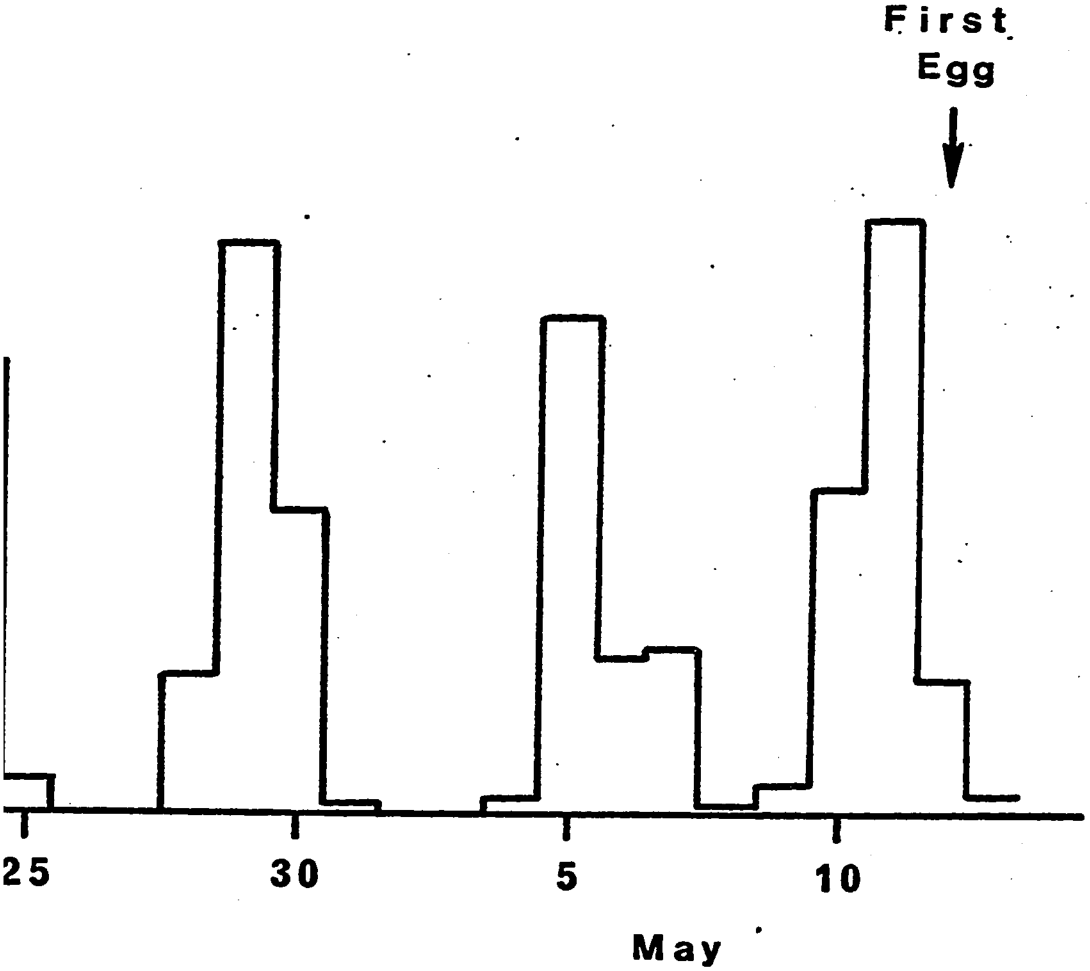


Figure 7. Attendance at the Main Colony during the
12 May) in 1969.



during the pre-laying period (9 April -

Table 4. Distribution of adult puffins on eac
during the pre-laying period (9 Apri
days not shown total attendance was
brackets are percentages for each pe

		APRIL			APRIL			
Habitat	Strip	23	24	25	28	29	30	
Slope	1	64	118(12.9)	28	68	131(11.4)	157	1
	2	105	205(22.5)	36	73	254(21.9)	213	1
Slope and level	3	80	187(20.5)	5	77	292(25.2)	197	-
Level	4	13	167(18.4)	-	42	193(16.6)	27	-
	5	1	164(18.0)	-	24	205(17.6)	7	-
	6	-	63(6.9)	-	5	81(7.0)	1	-
	7	-	6(0.8)	-	-	4(0.3)	-	-
Total attendance		263	910	69	286	1160	602	34

ins on each strip of the Main Colony grid
od (9 April - 12 May) in 1969. (N.B., On
dance was less than 10 birds. Figures in
or each peak day of attendance.)

	MAY				MAY			
30	4	5	6	7	9	10	11	12
157	18	166(16.6)	80	112	30	102	143(11.9)	42
213	16	260(26.0)	90	113	20	139	260(21.6)	100
197	-	285(28.0)	67	78	12	178	301(25.0)	88
27	-	146(14.6)	47	20	-	118	194(16.1)	33
7	-	112(11.2)	28	-	-	88	201(16.7)	9
1	-	31(3.1)	3	-	-	41	96(8.0)	1
-	-	1(0.1)	-	-	-	5	9(0.7)	-
602	34	1001	310	323	62	671	1202	273

laying are small and are therefore not analyzed statistically.

Morphology of breeding birds

Measurements of bodyweight and winglength of breeding adults collected early in the breeding cycle are shown in Table 5. The average bodyweight of males from nests on slope habitat was higher than those from nests on level habitat in both years (1968: $P < 0.02$, $t = 2.56$; 1969: $P < 0.01$, $t = 3.37$), although the difference in variation was not significant (1968: $P > 0.10$, $F = 1.31$; 1969: $P > 0.10$, $F = 1.09$); differences in winglength were not significant. Bodyweight and winglength of females were similar in the two habitats.

Nest-site tenacity

Puffins at Great Island displayed a high degree of nest-site tenacity. The return of breeding birds to the same grid quadrat and nest-site on the Main Colony in 1969 where they had been banded and colour coded the previous season (captured brooding an egg or chick) is summarized in Table 6. These data show that birds not only returned to the same local area (island and colony), but also nested in the identical habitat situation. All colour-banded birds observed back on the Main Colony in 1969 settled in the same habitat used in the previous year and none of the missing 1968 colour-banded birds were observed in other locations on the island.

Burrow establishment

The dispersion of breeding males over the nesting habitat appeared to be accomplished by territorial agonistic behaviour. The

Table 5. Comparison of morphological measure
nesting on slope and level habitat

Year (collection dates)	Values	MALES			
		Bodyweight (g)		Winglength (	
		Slope	Level	Slope	Leve
1968 (26 May-9 July)	N	18	21	18	21
	$\bar{x}$	491.6	468.3	172.4	173
	s	30.11	25.06	5.68	4.
	range	432-524	429-513	166-180	164-
	t	2.56		0.88	
	P	< 0.02		> 0.30	
1969 (2-8 June)	N	29	23	29	23
	$\bar{x}$	497.9	463.7	173.1	172.
	s	34.35	30.52	3.60	4.
	range	434-562	384-530	168-181	163-1
	t	3.37		0.39	
	P	< 0.01		> 0.50	

logical measurements of breeding birds
level habitat at Great Island.

		FEMALES			
Winglength (mm)		Bodyweight (g)		Winglenght (mm)	
Slope	Level	Slope	Level	Slope	Level
18	21	29	28	29	28
172.4	173.6	439.9	451.4	168.9	171.0
5.68	4.65	31.63	25.88	3.57	7.99
166-180	164-182	386-511	402-498	161-176	163-179
0.88		1.55		1.33	
> 0.30		> 0.10		> 0.10	
29	23	21	56	21	56
173.1	172.7	422.9	438.1	170.2	170.6
3.60	4.22	21.67	27.77	3.14	3.58
168-181	163-181	407-485	372-510	167-179	163-180
0.39		0.79		0.49	
> 0.50		> 0.40		> 0.50	

Table 6. Nest-site tenacity of birds on the Main Colony in 1969.

Nest habitat	Strip	No. birds colour-banded 1968	No. birds returned to nest-site 1969	% return
Slope	2	28	22	78.6
Level	4 and 6	33	25	75.7
Totals	2, 4 and 6	61	47	77.0

male puffin defended a small area at the burrow entrance against intruders by threat (physical presence, head-flicking, bill-gaping) and physical combat (fighting with beak and claws).

Figure 8 shows the frequency changes in fighting (No. fights/bird/hour) on slope and level areas of the Main Colony during the settlement, egg-laying, and incubation periods. In 1969, fighting was more frequent on slope habitat than level habitat during the 22 April - 24 May pre-laying period ($P < 0.01$, $t = 3.19$, $df = 16$). However, the most intense fighting early in the season occurred between the start and peak of egg-laying earlier on the slope than level habitat. Fighting declined to a low point over the entire colony during the incubation period.

3. Egg-laying Period

Morphology of eggs laid on slope and level habitats

The morphological data of fertile eggs removed from nests on slope and level habitats are summarized in Table 7. The differences in egg size and shape between the two groups are small and not statistically significant.

Time of egg-laying on slope and level habitats

The characteristics of the egg-laying regime of slope and level birds are shown in Figure 9. In both groups the median laying dates are very similar; there is no statistically demonstratable difference in median egg-laying dates (median test) within either habitat between years ($P > 0.10$) or between the two nesting groups themselves ($P > 0.10$). The most obvious difference between patterns

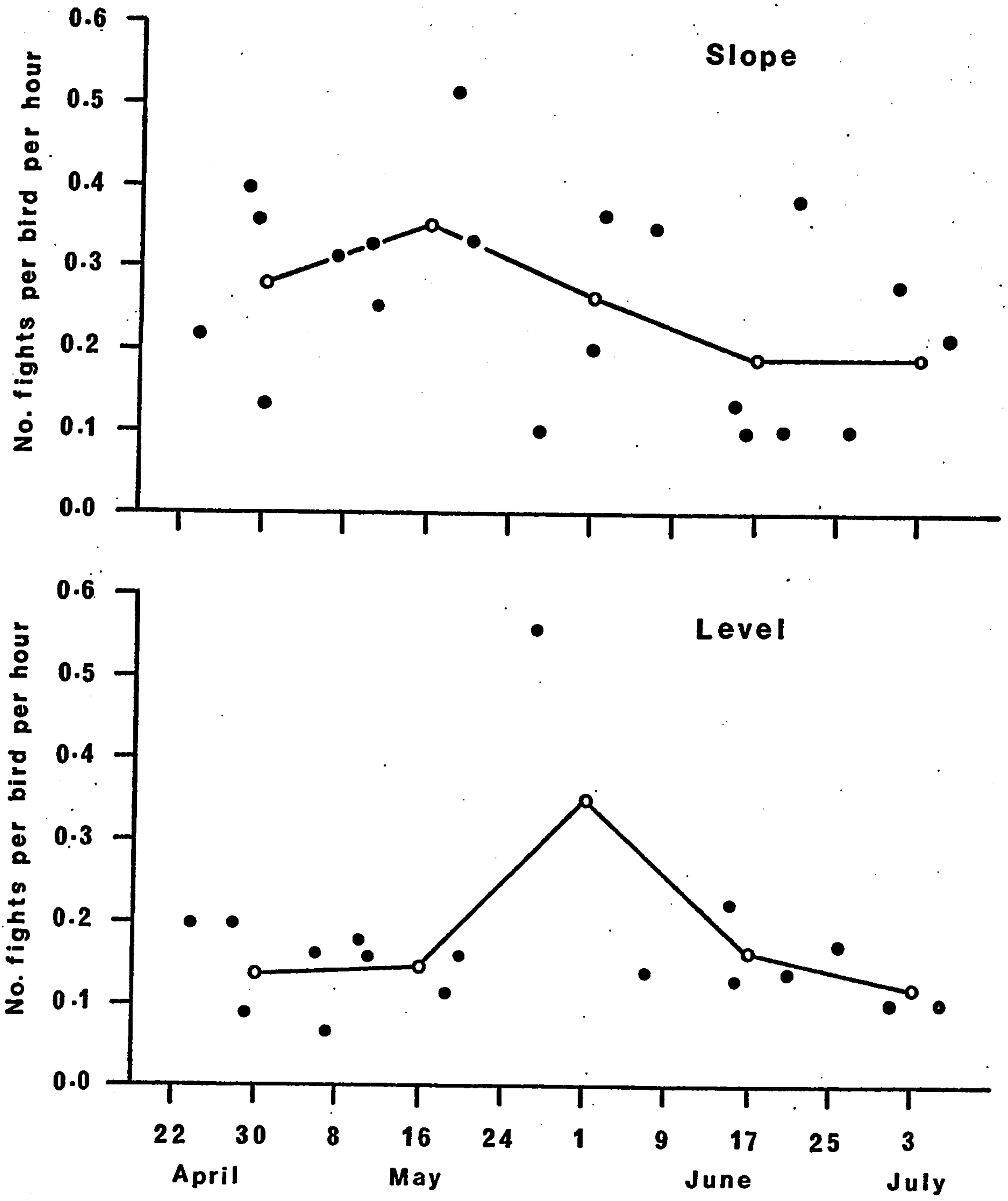


Figure 8. Comparison of frequency changes in fighting on slope and level habitat on the Main Colony between April and July 1969. (Open circles represent 16-day averages.)

S

Table 7. Measurements of eggs laid on s
Great Island.

Measurement	Slope (N = 90)			Lev
	$\bar{x}$	s	range	$\bar{x}$
Length (mm)	62.93	2.26	57.8 - 68.2	62.99
Breadth (mm)	44.54	1.20	40.7 - 46.8	44.62
Volume (cc)	61.05	4.30	51.3 - 69.4	61.43
Weight (g)	65.51	4.59	55.2 - 78.1	65.12
Shape Index	70.29	5.78	63.5 - 78.7	70.89

eggs laid on slope and level habitat at

Level (N = 60)				
$\bar{x}$	s	range	P	t
62.99	1.87	58.3 - 67.4	> 0.50	0.18
44.62	1.03	42.1 - 46.8	> 0.50	0.44
61.43	3.57	54.1 - 69.8	> 0.50	0.59
65.12	3.55	57.7 - 72.6	> 0.50	0.59
70.89	2.52	64.9 - 75.6	> 0.30	0.88

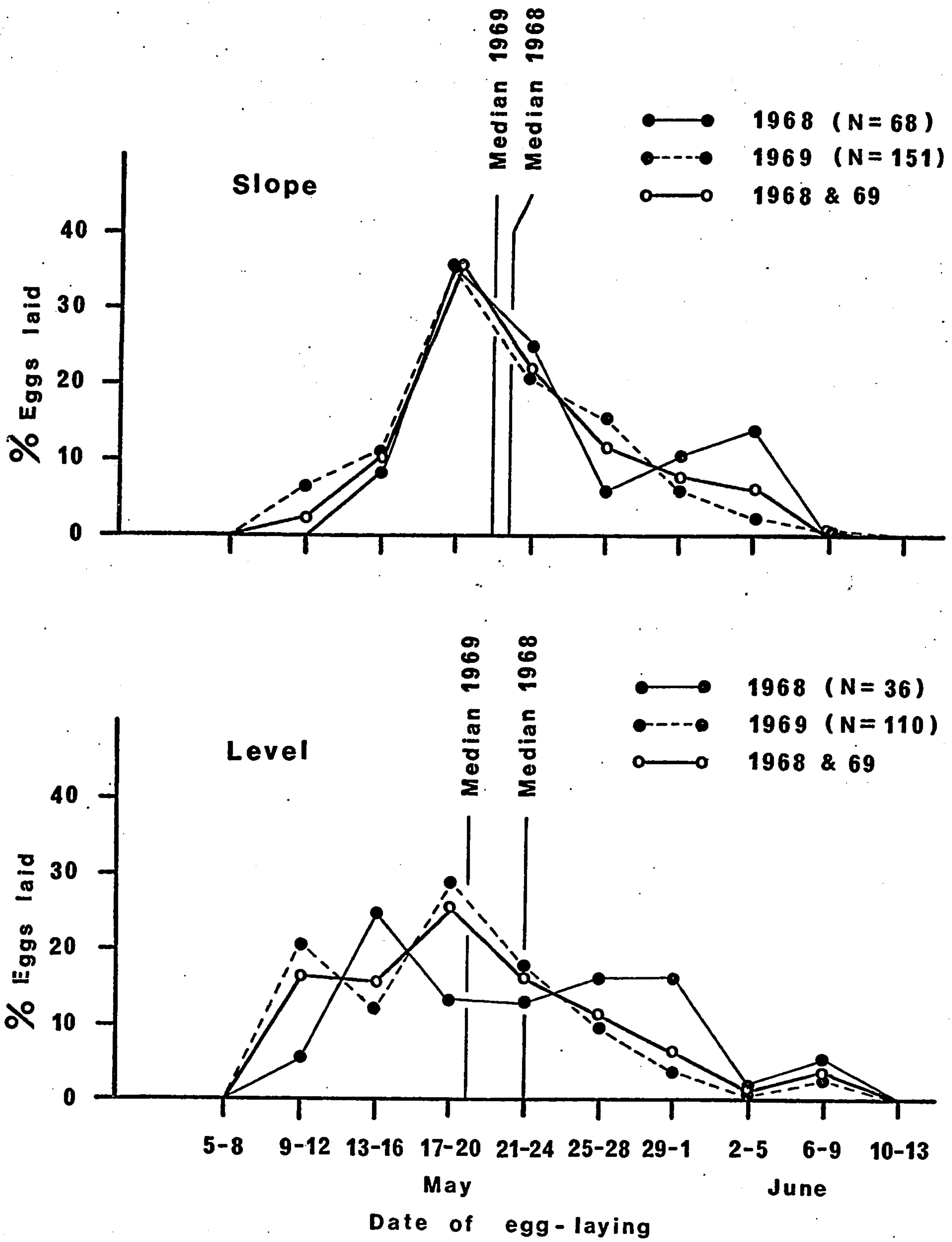


Figure 9. Frequency distribution of egg-laying on slope and level habitat at Great Island.

9

is the variation in synchronization and frequency distribution of laying. A chi-square test (2 x 8 contingency table) shows that the frequency distribution pattern (1968 and 1969 data combined) on the two habitats are significantly different ($P < 0.001$, $X^2 = 29.39$, df = 7). The percentage of eggs laid early (9 - 12 May) in the egg-laying period by birds on level habitat was higher than the percentage laid by birds on slope habitat ($P < 0.001$, $X^2 = 13.00$, df = 1). The percentage of eggs laid late (6 - 9 June) on level habitat was also higher than the percentage laid on slope habitat ($P < 0.02$, $X^2 = 6.08$, df = 1). The result is that laying was more concentrated, in time, in the slope group. Furthermore, the 1968 and 1969 egg-laying patterns for the first half of the egg-laying period (9 - 20 May) within each habitat are more similar on slope than on level habitat (2 x 3 contingency table: slope = $P > 0.30$, $X^2 = 1.90$, df = 2; level = $P < 0.02$, $X^2 = 8.84$, df = 2). Variation in the second half of the egg-laying period (21 May - 10 June) is more difficult to interpret because of the unknown significance of replacement laying and so is not analyzed statistically. Thus time of laying is more precise and synchronous from year to year amongst birds on slope habitat.

4. Breeding Success

Hatching success

Hatching success was significantly higher in nests on slope habitat than level habitat in both years (Table 8). The figures also show that many eggs disappeared from burrows, and than many remained but did not hatch. Most of the hatching failure can be attributed to

Table 8. **Comparison of hatching success on slope and level habitat at Great Island.**

Year	Nest habitat	Nest no.	Hatched No.	Hatched %	Infertile No.	Infertile %	Disappeared No.	Disappeared %
1968	Slope	90	58	64.4	3	3.3	29	32.3
	Level	60	28*	46.6	6	10.0	26	43.4
1969	Slope	200	151	75.5	4	2.0	45	22.5
	Level	202	110**	54.4	26	12.9	66	32.7
Totals	Slope	290	209	72.0	7	2.5	74	25.5
	Level	262	138	52.6	32	12.3	92	35.1

* $P < 0.05$, $X^2 = 4.65$

** $P < 0.001$, $X^2 = 19.54$

disappearance of the eggs.

There was no significant difference in egg infertility (slope: $P > 0.30$, $X^2 = 0.46$; level: $P > 0.50$, $X^2 = 0.35$) or egg disappearance (slope: $P > 0.05$, $X^2 = 3.08$; level: $P > 0.10$, $X^2 = 2.30$) on either habitat between years. However, the data do indicate that the yearly difference in hatching success within the habitats, though not significant (slope: $P > 0.05$, $X^2 = 3.76$; level: $P > 0.20$, $X^2 = 1.12$), resulted more from changes in frequency of egg disappearance during incubation than infertile eggs.

Infertile eggs were more frequent on level habitat than slope habitat (1968 and 1969 data combined: $P < 0.001$, $X^2 = 20.13$), although the difference in 1968 does not reach the 5% level of significance ($P > 0.05$, $X^2 = 2.84$). Similarly, total egg disappearance was higher on level habitat than slope habitat ($P < 0.02$, $X^2 = 6.02$), but the difference in 1968 was not significant ($P > 0.10$, $X^2 = 1.91$).

Fledging success

The survival of chicks to fledging was higher on slope habitat in both years (Table 9). The chi-square value for the 1968 data falls below the level required for significance when the Yates correction for continuity is applied ($P > 0.05$, $X^2 = 2.96$), perhaps as a consequence of the small sample size. However, the difference in fledging success in 1969 was highly significant ($P < 0.001$, $X^2 = 14.04$).

Fledging success was higher in 1969 than in 1968 on both habitats (slope: $P < 0.01$, $X^2 = 9.90$; level: $P < 0.05$, $X^2 = 4.62$). The proportion of chicks found dead inside their burrow remained the

Table 9. Comparison of fledging success on slope and level habitat at Great Island.

Year	Nest habitat	Nest no.	Fledged No.	Fledged %	Found dead No.	Found dead %	Disappeared No.	Disappeared %
1968	Slope	58	25 *	43.2	2	3.4	31	53.4
	Level	28	6	21.4	5	17.8	17	60.8
1969	Slope	151	101 **	66.9	11	7.3	39	25.8
	Level	110	48	43.6	23	21.0	39	35.4

* $P > 0.05$, $X_c^2 = 2.96$

** $P < 0.001$, $X^2 = 14.04$

same for each habitat between years (slope: $P > 0.30$, $X^2 = 1.05$; level: $P > 0.70$, $X^2 = 0.11$), but was significantly higher on level habitats in both years (1968: $P < 0.05$, $X^2 = 5.24$; 1969: $P < 0.01$, $X^2 = 10.42$). Chicks disappeared more frequently in 1968 than in 1969 on both habitats (slope: $P < 0.01$, $X^2 = 9.90$; level: $P < 0.05$, $X^2 = 4.62$). The proportion of chicks that did disappear was higher on level habitat each year, although the differences were not significant (1968: $P > 0.75$, $X^2 = 0.04$; 1969: $P > 0.05$, $X^2 = 2.81$).

Most chicks that did not fledge either died or disappeared early in the fledging period on both habitats (Table 10). Combining annual totals, 39% of all chick mortality occurred in the first eight days of life and 56% by day sixteen.

Fledging success was also strongly related to time of hatching (Table 11). The difference in fledging success totals (1968 and 1969 data combined) between chicks which hatched from eggs early (21 - 30 June) and late (post-30 June) is highly significant ($P < 0.01$, $X^2 = 6.74$) Mean fledging success is still lower ($P < 0.05$, $X^2 = 4.20$) for chicks hatched between 1 - 10 July than those hatched early, although an exception occurred in the 1969 level group. However, success for birds hatched between 1 - 10 July is significantly higher ($P < 0.01$, $X^2 = 8.57$) than for those hatched later (post-10 July). Therefore, poorest success is achieved by chicks hatched extremely late (post-10 July) in the breeding season, where the difference from birds hatched early (21 - 30 June) is greatest ($P < 0.001$, $X^2 = 16.72$). Thus in both years it was found that the earlier a chick hatches, the

Table 10. Mortality of puffin nestlings
fate code: FD = found dead;

	1968								
	SLOPE (N = 33)				LEVEL (N = 22)				
Age (days)	FD	D	N	%	FD	D	N	%	FD
1-8	1	13	14	(42.4)	4	9	13	(59.1)	3
9-16	0	6	6	(18.2)	0	2	2	(9.1)	1
17-24	0	3	3	(9.1)	1	4	5	(22.7)	0
25-32	0	5	5	(15.2)	0	0	0	(0)	3
33-40	1	2	3	(9.1)	0	2	2	(9.1)	0
41-48	0	2	2	(6.0)	0	0	0	(0)	1
> 48	0	0	0	(0)	0	0	0	(0)	3
TOTALS	2	31	33		5	17	22		11

uffin nestlings at Great Island. (N.B., Chick
= found dead; DP = disappeared prematurely)

	1969							
22)	SLOPE (N = 50)				LEVEL (N = 62)			
%	FD	D	N	%	FD	D	N	%
(59.1)	3	13	16	(32.0)	8	15	23	(37.0)
(9.1)	1	10	11	(22.0)	4	4	8	(12.9)
(22.7)	0	2	2	(4.0)	2	7	9	(14.5)
(0)	3	3	6	(12.0)	0	6	6	(9.7)
(9.1)	0	3	3	(6.0)	3	3	6	(9.7)
(0)	1	6	7	(14.0)	1	4	5	(8.1)
(0)	3	2	5	(10.0)	5	0	5	(8.1)
	11	39	50		23	39	62	

Table 11. Fledging success in relation
Great Island. (N.B., N = n
F = no. chicks fledged; %F
fledged)

Year	Nest habitat	(A) 21-30 June N	(A) 21-30 June F	(A) 21-30 June %F	(B) 1-10 July N	(B) 1-10 July F
1968	Slope	29	16	55.1	21	7
	Level	14	4	28.5	13	2
1969	Slope	82	65	79.2	60	34
	Level	69	30	43.4	34	18
	TOTALS*	194	115	59.3	128	61

* A : C - $P < 0.001$ $X^2 = 16.72$

A : B - $P < 0.05$ $X^2 = 4.20$

A: (B+C) - $P < 0.01$ $X^2 = 6.74$

B : C - $P < 0.01$ $X^2 = 8.57$

in relation to hatching date at
(N.B., N = no. chicks hatched;
ledged; %F = percent of chicks

(B) 1-10 July			(C) > 10 July		
N	F	%F	N	F	%F
21	7	33.3	8	2	25.0
13	2	15.4	1	0	0
60	34	56.7	9	2	22.3
34	18	52.9	7	0	0
128	61	47.7	25	4	16.0

greater the chance of survival to fledging.

When the 1968 and 1969 data are treated separately, the trends described from the totals are still present, but not quite as pronounced. More birds which hatched early fledged than those hatched later (post-30 June) in both years (1968: $P < 0.05$, $X^2 = 4.08$; 1969: $P < 0.05$, $X^2 = 4.96$). In 1968, success was always higher in the earlier period when comparing any of the individual groups (e.g., 21-30 June > 1-10 July; 1-10 July > post-10 July; etc.), but none of the differences were statistically significant ($P > 0.05$), perhaps due to the small sample size. In 1969, fledging success did not differ between birds hatched early and those hatched from 1-10 July ($P > 0.20$, $X^2 = 1.39$), although significantly fewer of the chicks hatched late fledged when the early group is compared with either the data from the chicks hatched late grouped together (post-30 June) ($P < 0.05$, $X^2 = 4.96$) or just the post-10 July chicks alone ($P < 0.01$, $X^2 = 6.74$). Chicks hatched very late in the season (post-10 July) also survived less frequently than those which hatched between 1-10 July ($P < 0.01$, $X^2 = 10.03$).

Fledging success was higher for birds on slope habitat in all three hatching periods in both years, but only the differences in the early period is significant ($P < 0.001$, $X^2 = 20.57$).

Breeding success

The difference in total breeding success (egg and chick survival data combined) between nest-sites on slope and level habitat is highly significant (Table 12). During both years breeding success

Table 12. Comparison of breeding success on slope and level habitat at Great Island.

Year	Nest habitat	No. nests	No. fledglings		% success
1968	Slope	90	25	*	27.7
	Level	60	6		10.0
1969	Slope	200	101	**	50.5
	Level	202	48		23.8

* $P < 0.01$, $X^2 = 6.93$

** $P < 0.001$, $X^2 = 30.79$

at nests on slope habitat was at least twice that at nests on level habitat. There was also a marked difference in breeding success within each habitat between years; the proportion of nests on slope and level habitat that produced fledglings was higher in 1969 than 1968 (slope: $P < 0.001$, $X^2 = 13.04$; level: $P < 0.05$, $X^2 = 5.35$).

5. Fledging Condition

Bodyweight at fledging

The mean bodyweight of fledglings on slope habitat was significantly higher than that of fledglings on level habitat in both years (Table 13). Variation between years was small, particularly on slope habitat.

Table 14 shows the relationship between bodyweight and date of hatching for the 1969 fledglings; the 1968 data have not been analyzed due to the small sample size. Mean fledging weight was highest for chicks that hatched early (21-30 June) in both nesting habitats although the difference on level habitat is not statistically significant ($P > 0.05$). Amongst chicks hatched early (21-30 June), those on slope habitat were heavier than those on level habitat ($P < 0.05$, $t = 2.09$). Fledglings that hatched late (1-10 July) in nests on slope habitat weighed more than those on level habitat, but the difference is not significant ($P > 0.20$, $t = 0.86$), possibly due to the small sample size of fledglings on level habitat.

Aside from difference in means, the standard deviations (Table 13) indicate that birds on slope habitat are less variable in bodyweight at fledging than those on level habitat in both 1968 and 1969,

Table 13. Comparison of bodyweight and winglength of fledglings reared on slope and level habitat at Great Island.

Year	Nest habitat	Nest No.	Bodyweight (g)				Winglength (mm)			
			$\bar{x}$		s	range	$\bar{x}$		s	range
1968	Slope	25	261.4	*	32.27	173-305	143.6	*	7.98	129-154
	Level	6	247.5		35.04	178-282	143.6		4.02	139-148
1969	Slope	101	261.8	**	35.87	159-323	140.5	**	6.21	127-153
	Level	47	248.2		47.00	137-330	140.6		6.56	130-154

* Bodyweight: $P > 0.30$, $t = 0.91$; Winglength: $P > 0.50$, $t = 0.01$

** Bodyweight: $P < 0.001$, $t = 5.66$; Winglength: $P > 0.50$, $t = 0.12$

Table 14. Fledging weight (g) of young at Great
in 1969.

	Hatching Per			
	(E) Early: 21-30 June			
Nest habitat	N	$\bar{x}$	s	range
Slope (S)	65	268.6	31.72	183-323
Level (L)	30	251.3	45.72	137-330

ES-LS : $P < 0.05$, $t = 2.10$

EL-LL : $P > 0.20$, $t = 0.63$

ES-EL : $P < 0.05$, $t = 2.09$

LS-LL : $P > 0.20$, $t = 0.86$

ung at Great Island in relation to hatching date

Hatching Period				
	(L) Late: 1-10 July			
range	N	$\bar{x}$	s	range
183-323	34	252.9	39.84	159-311
137-330	17	242.9	35.46	161-302

although only the difference in variation in 1969 was statistically significant (1968: $P > 0.05$, $F = 1.31$; 1969: $P < 0.01$, $F = 1.90$).

Winglength at fledging

Differences in winglength at departure between fledglings on slope and level habitat were small (Table 13) and not statistically significant in either year ($P > 0.05$). Similarly, the variation between habitats was not significant (1968: $P > 0.05$, $F = 3.94$; 1969: $P > 0.05$, $F = 1.12$).

Age at fledging

Differences in the average length of the fledging period for young on the two habitats were not significant ($P > 0.05$) within each year, but differed between years (Table 15). Thus in both habitats the average length of time spent as a chick in the burrow was greater in 1968 than in 1969, although the difference was not significant in level habitat ($P > 0.20$, $t = 1.07$), perhaps due to the relatively small sample size for 1968. Fledging age was also more variable on slope than level habitat in 1968 ($P < 0.05$, $F = 6.59$), but was similar in 1969 ($P > 0.05$, $F = 1.10$).

Table 16 shows the importance of hatching date in relation to the length of the fledging period for young on slope and level habitat in 1969 (N.B., 1968 data are not analyzed due to the small sample size). On slope habitat, chicks that hatched early (21-30 June) in the season had a shorter mean fledging period ($P < 0.001$, $t = 4.66$) than chicks hatched late (1-10 July). The mean difference between chicks hatched early and late in level nests was not significant ($P > 0.40$, $t = 0.76$).

Table 15. Comparison of age at fledging of birds reared on slope and level habitat at Great Island.

Year	Nest habitat	Nest no.	Fledging age (days)			
			$\bar{x}$		s	range
1968	Slope	25	59.7	*	10.38	45 - 83
	Level	6	55.5	* **	3.82	49 - 60
1969	Slope	101	52.3	** *	7.76	39 - 73
	Level	48	52.2	*	7.37	43 - 74

* 1968: $P > 0.30$, $t = 0.95$; 1969: $P > 0.50$, $t = 0.06$

** 1968 vs 1969: Slope - $P < 0.001$, $t = 4.00$; Level - $P > 0.20$, $t = 1.07$

Table 16. Fledging age (days) of young at Great Is
date in 1969.

Nest habitat	(E) Early: 21-30 June				
	N	$\bar{x}$	s	range	
Slope (S)	65	49.9	6.01	40 - 71	3
Level (L)	30	52.8	7.46	43 - 74	1

ES-LS : $P < 0.001$, $t = 4.66$

EL-LL : $P > 0.40$, $t = 0.76$

ES-EL : $P < 0.05$, $t = 2.00$

LS-LL : $P < 0.02$, $t = 2.46$

ng at Great Island in relation to hatching

	(L) Late: 1-10 July			
range	N	$\bar{x}$	s	range
0 - 71	34	56.8	8.92	39 - 73
3 - 74	18	51.1	7.05	44 - 66

Furthermore, the mean fledging age of birds hatched early on slope habitat was less than those hatched early on level habitat ($P < 0.05$, $t = 2.00$), whereas the opposite occurred in chicks hatched late, those on level habitat fledged at a younger age ($P < 0.02$, $t = 2.46$).

To summarize, fledging condition varies according to the habitat and time period in which the chick is raised. Young which hatch early on slope habitat fledge with the greatest bodyweight, those which hatch late on level habitat fledge with the least bodyweight. Similarly, young which hatch early on slope habitat have the shortest fledging period, but those which hatch late on slope habitat also have the longest fledging period. Winglength at fledging is similar in all young, regardless of nest habitat and hatching date.

6. Food for the Chick

Meal size

Table 17 shows the average meal size delivered to nestlings on slope and level habitat in 1968 and 1969. The meal size represents the total amount of food (in grams) brought by parents during a single visit to the nest, regardless of the number and diversity of prey organisms contained in the meal. The food types brought to chicks on slope and level habitat were the same. All the specimen meals consisted of fish.

The mean weight of meals did not differ significantly in the two habitats ($P > 0.50$, $t = 0.35$). Variation in meal size was also similar ($P > 0.05$, $F = 1.25$).

Table 17. Meal size (g) of puffin nestli

Year	MEAL SIZE (			
	Slope chicks			
	N	$\bar{x}$	s	range
1968	30	14.2	5.47	2 - 25
1969	125	12.0	5.12	3 - 33
Total	155	12.4*	5.33	2 - 33

* $P > 0.50$, $t = 0.35$

puffin nestlings at Great Island.

MEAL SIZE (g)				
	Level chicks			
range	N	$\bar{x}$	s	range
2 - 25	19	11.9	5.11	1 - 20
3 - 33	75	12.9	6.16	2 - 28
2 - 33	94	12.7*	5.98	1 - 28

Feeding rate

Feeding rates on the Main Colony were measured by observing 17 nests on slope and 15 nests on level habitat during the entire daylight period (0530 to 2100 hours) for three consecutive days (31 July to 2 August 1969). Each nest contained a chick at approximately the same stage of development. Table 18 gives the results, which show that nestlings on slope habitat received on average more meals, and hence more food, each day than chicks on level habitat ($P < 0.01$, $t = 3.15$).

Twinning experiment

Fledging success at 10 nests on slope habitat of twins, matched for age at time of twinning by weight and feather development (age: c. 9-10 days), is given in Table 19. No set of twins was reared by parents to fledging. Usually one twin gained weight while the other lost. Eventually the unsuccessful chick either disappeared or was found dead inside the burrow. For example, at Nest 2 both chicks gained weight early after twinning, but subsequently only the original chick continued to gain and the introduced chick disappeared prematurely; in Nest 5, however, the introduced chick immediately increased in weight while the original chick decreased until it was found dead ten days after twinning (Figure 10).

Single-parented chick experiment

None of the 12 chicks (starting age: c. 9-35 days) on slope habitat being fed by only a single parent, after one parent (either sex) was collected (day 0 = c. 20 July 1968), fledged (Table 20).

Table 18. Mean number of meals per day of 17 slope and 15 level puffin nestlings at Great Island from 31 July to 2 August 1969.

Nest habitat	No. nests	No. meals/day/chick			
		$\bar{x}$		s	range
Slope	17	3.6	*	1.08	1.6 - 6.3
Level	15	2.4		1.19	0 - 4.6

* $P < 0.01$, $t = 3.15$

Table 19. Fledging succes of twins at ten nests on slope habitat at Great Island in 1968. (N.B., Chick fate code: F = fledged; FD = found dead; DP = disappeared prematurely).

	CHICK FATE									
Nest Twin	1	2	3	4	5	6	7	8	9	10
Original	DP	DP	DP	DP	DP	F	FD	F	FD	DP
Introduced	F	DP	DP	DP	DP	DP	F	DP	F	DP
No. young fledged	1	-	-	-	-	1	1	1	1	-

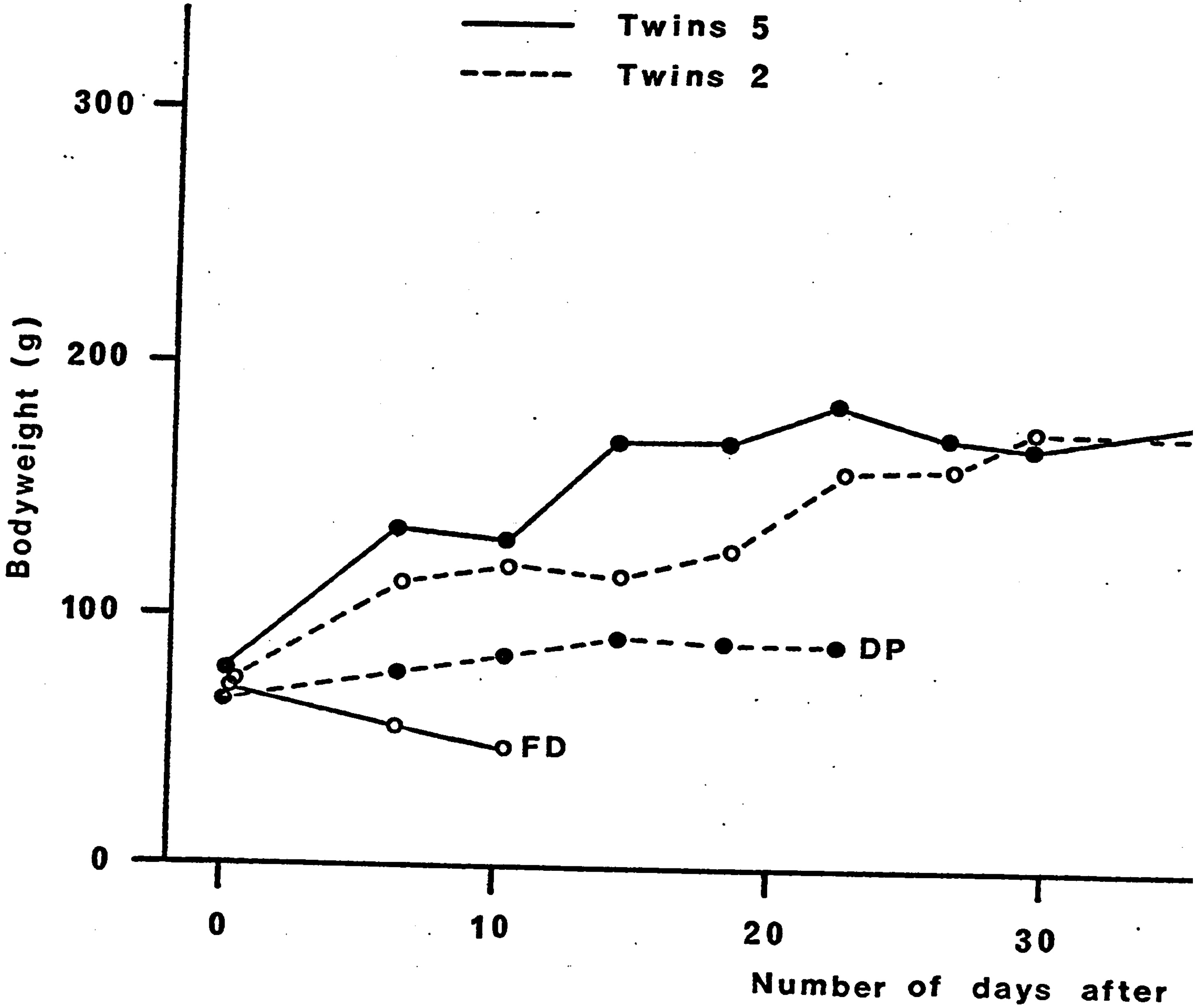
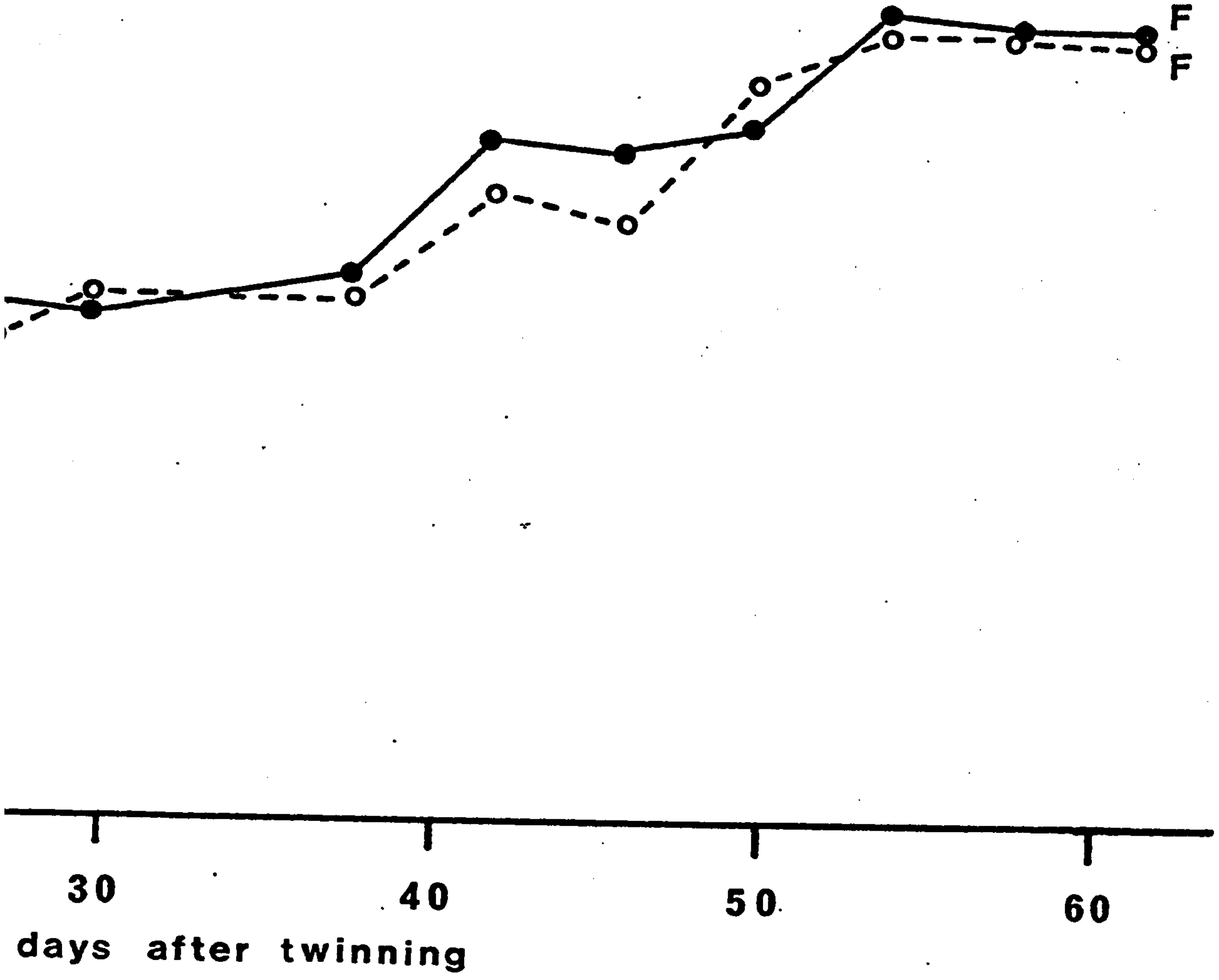


Figure 10. Growth curves of bodyweight for two sets at Great Island in 1968. (N.B., ● = i chick fate code: F = fledged, FD = fou prematurely.)



for two sets of twinned chicks on slope habitat
N.B., ● = introduced chick, o = original chick;
d, FD = found dead, DP = disappeared

Table 20. Fledging success of single-parented chicks at 12 nests on slope habitat at Great Island in 1968.

Starting bodyweight (g)	No.	No. found dead	No. disappeared prematurely	No. fledged
< 75	2	0	2	-
176-200	4	1	3	-
201-225	6	3	3	-
Totals	12	4	8	0
Percent	100.0	33.3	66.7	0.0

They either died in their burrow or disappeared prematurely.

Figure 11 compares the growth curves of four of the experimental chicks with curves of similar aged chicks being reared by two adults during the identical time period on the same habitat. Two of the single-parented chicks decreased in weight until they were found dead and two disappeared from their burrow at a premature stage of development. All four "control" chicks fledged in good condition, although two experienced declines in bodyweight early in the experiment.

7. Summary of Puffin Breeding Performance at Great Island

Puffins nest at a higher density on slope habitat, close to the cliff edge, than level habitat. The distribution patterns of adults standing on the colony does not match nest distribution, too few birds occurring in level areas and too many along the crest of the slope. In spring, both habitats are occupied simultaneously and nest-site tenacity is equally strong in them. During settlement, the frequency of fighting is higher and the peak reached earlier on slope habitat. In addition, bodyweights of males are heavier on slope than level habitat. Measurements of eggs from both habitats are the same. Egg-laying dates are also similar, but annual variation is greater on level than slope habitat, as is variation within a single year. Hatching success is higher on slope habitat, due mainly to a lower incidence of egg disappearance during incubation. Likewise, fledging success is greater on slope habitat. Thus, breeding success is higher on slope habitat, but success does vary within a habitat between years.

Fledging condition of chicks varies according to the habitat and

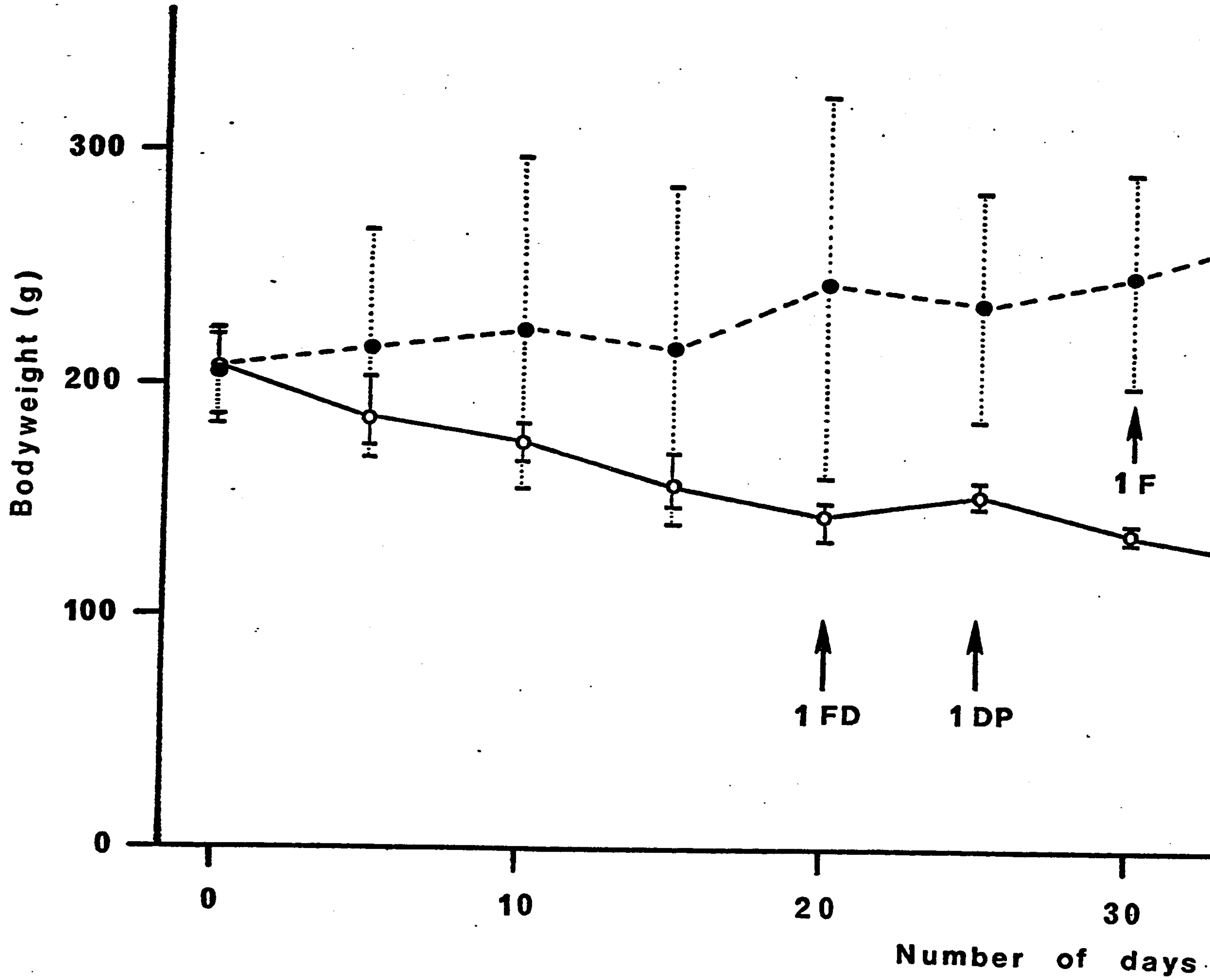
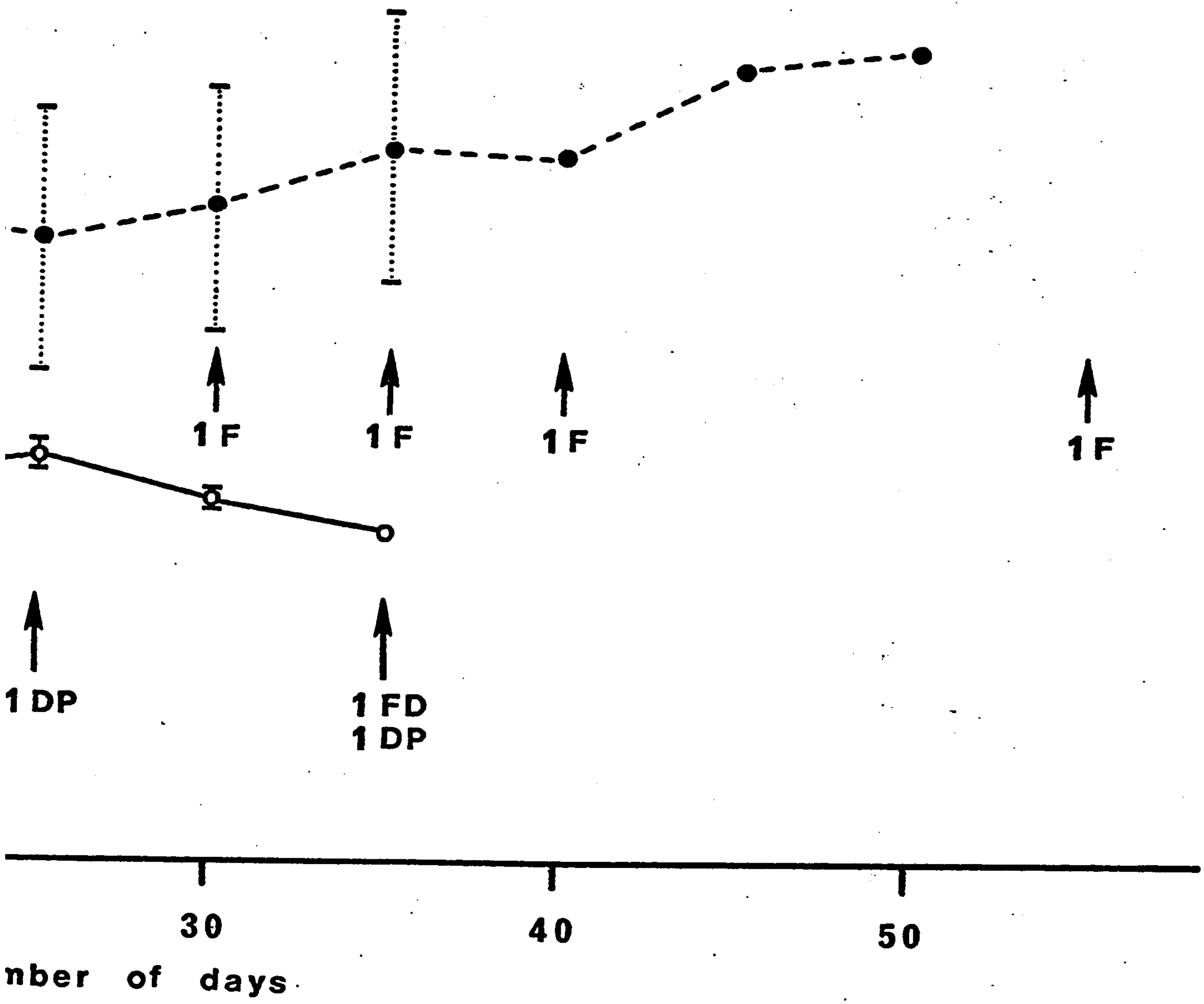


Figure 11. Mean growth curves of bodyweight of chicks (o————o) and examples of chicks (N = 4 from amongst the habitat study area nests period (day 0 = c. 20 July) at Great Islan of bodyweights for that number of days. 50 and 55. (N.B., chick fate code: F = disappeared prematurely.)



eight of chicks (N = 4) being reared by one parent
f chicks (N = 4) being reared by two parents (●--------●)
udy area nests on slope habitat during the same time
at Great Island in 1968. Vertical bars represent range
ber of days. Last 'control' chick fledged between day
ate code: F = fledged, FD = found dead, DP =

time period in which they were raised. On average, weight at fledging is greater and less variable on slope habitat; within both habitats, highest weights are among chicks which hatch earliest from eggs. Winglength at fledging is similar in all young, regardless of nest habitat and hatching date. The length of time spent in the burrow as a nestling varies between years on both habitats. Birds which hatch from eggs early in the season (21-30 June) fledge at a younger age than birds which hatch later (post-30 June) on slope habitat but not level habitat; birds which hatch early on slope habitat fledge quicker than those which hatch early on level habitat, whereas birds which hatch late on slope habitat fledge slower than those which hatch late on level habitat.

Meal size delivered to chicks by parents is the same on the two habitats, but frequency of feeding is greater on slope than level habitat. Breeding pairs on slope habitat are unable to raise two young to fledging. Similarly, one adult cannot rear a single chick.

B. Gull-Puffin Interactions

1. The Egg Stage

Egg displacement

Gulls cause puffins to leave the burrow in a hurry either directly (e.g., response to gull cries) or indirectly (e.g., response to puffin panic-flights), with displacement of the egg to the burrow entrance (where is can be secured by a gull) as an occasional consequence. To determine the frequency of egg displacement on the two habitats my field assistant and I made walks over slope and level nesting habitat on various parts of Great Island and recorded the position of the egg in burrows from which incubating birds were observed leaving in response to the disturbance created by our approach (e.g., gull cries). The results are given in Table 21. The frequency of egg displacement towards the burrow entrance was similar in the two habitats ($P = 0.50$, $X^2 = 0.46$).

Panic-flight rate

The number of panic-flights over the slope and level parts of the Main Colony were recorded through most of the incubation period (19 May - 26 June 1969) in observation periods of 60 minutes duration. During 1,200 observation minutes (600 minutes/habitat), the number of panic-flights was six from slope and 33 from level habitat. This considerably greater panic-flight rate from the level area of the colony is highly significant ($P < 0.001$, $t = 5.51$, $df = 9$).

An important point is that panic-flights were usually initiated by gull activity (e.g., landing, take-off, alarm cry) on level habitat, whereas on the slope it was most often a consequence of the commotion caused by the mass overhead exodus of birds from the level habitat, already in panic-flight from their nesting area, out towards the sea.

2. The Chick Stage

Gull robbing (cleptoparasitism)

The data were grouped into slope (Strips 1 and 2) and level (Strips 3 - 6) categories for the purpose of analyzing the relationship between gull interference and nesting habitat; the level region

Table 21. Egg displacement by departure of incubating puffins at Great Island.

Nest habitat	No. departures	Egg position			
		in nest chamber		in burrow tunnel	
		No.	%	No.	%
Slope	117	101	86.3	16*	13.7
Level	100	83	83.0	17	17.0

* $P = 0.50$, $X^2 = 0.46$

was subdivided to compare differences within this larger area.

Table 22 shows a strong association between the incidence of gull robbery and position of the nest-site within the colony. The proportion of meals lost to gulls by parents with young on level habitat (Strips 3-6) was significantly higher ($P < 0.001$, $X^2 = 32.00$) than on slope habitat (Strips 1 and 2). Furthermore, the further inland from the edge of the slope, the greater the loss to gulls; birds nesting on level Strips 5-6 were robbed more frequently than birds on level Strips 3-4 ($P < 0.05$, $X^2 = 4.26$). The data also indicate that the frequency of attack on arriving meal-carrying puffins is markedly higher on the level parts of the colony ($P < 0.001$, $X^2 = 66.09$, df = 1).

Adult mobility and characteristics of the nesting habitat

The influence of habitat on the mobility of adult puffins was measured in mid-August 1969 by releasing captive birds at various locations on the Main Colony and recording with a stop watch the time interval from release to flight. Figure 12 clearly indicates that the time required to become airborne is strikingly shorter for birds released on slope habitat (Strips 1-2). In fact, in 59 of the 69 birds released on slope habitat the time to gain flight was within one second of release whereas only five of 69 birds released on level ground (Strips 4-6) took flight immediately. Thus, the proportion of birds taking flight immediately after release to those showing movement on the ground (i.e., running) towards the sea is significantly higher on slope habitat ($P < 0.001$, $X^2 = 84.96$, df. = 1).

Table 22. Delivery success of meal
parts of the Main Colony
3 - 6: level) in 1968 a
brackets are percentages

	1 - 2	3 -
	(A)	(B
No. landings	601	412
No. landings attacked by gulls	113 (18.8)	141 (
No. landings robbed by gulls	27 (4.4)	46 (

No. landings robbed by gulls/No. landings:

A : B - $P < 0.001$, $X^2 = 16.27$

A : C - $P < 0.001$, $X^2 = 38.52$

A : (B + C) - $P < 0.001$, $X^2 = 32.00$

B : C - $P < 0.05$, $X^2 = 4.26$

success of meal-carrying puffins on different the Main Colony (Strips 1 - 2: slope; Strips level) in 1968 and 1969. (N.B., Figures in are percentages of total number of landings).

STRIPS			
2	3 - 4	5 - 6	3 - 6
)	(B)	(C)	(B + C)
	412	363	775
(18.8)	141 (34.2)	162 (44.6)	303 (39.0)
(4.4)	46 (11.1)	59 (16.2)	105 (13.5)

s:

27

52

0

5

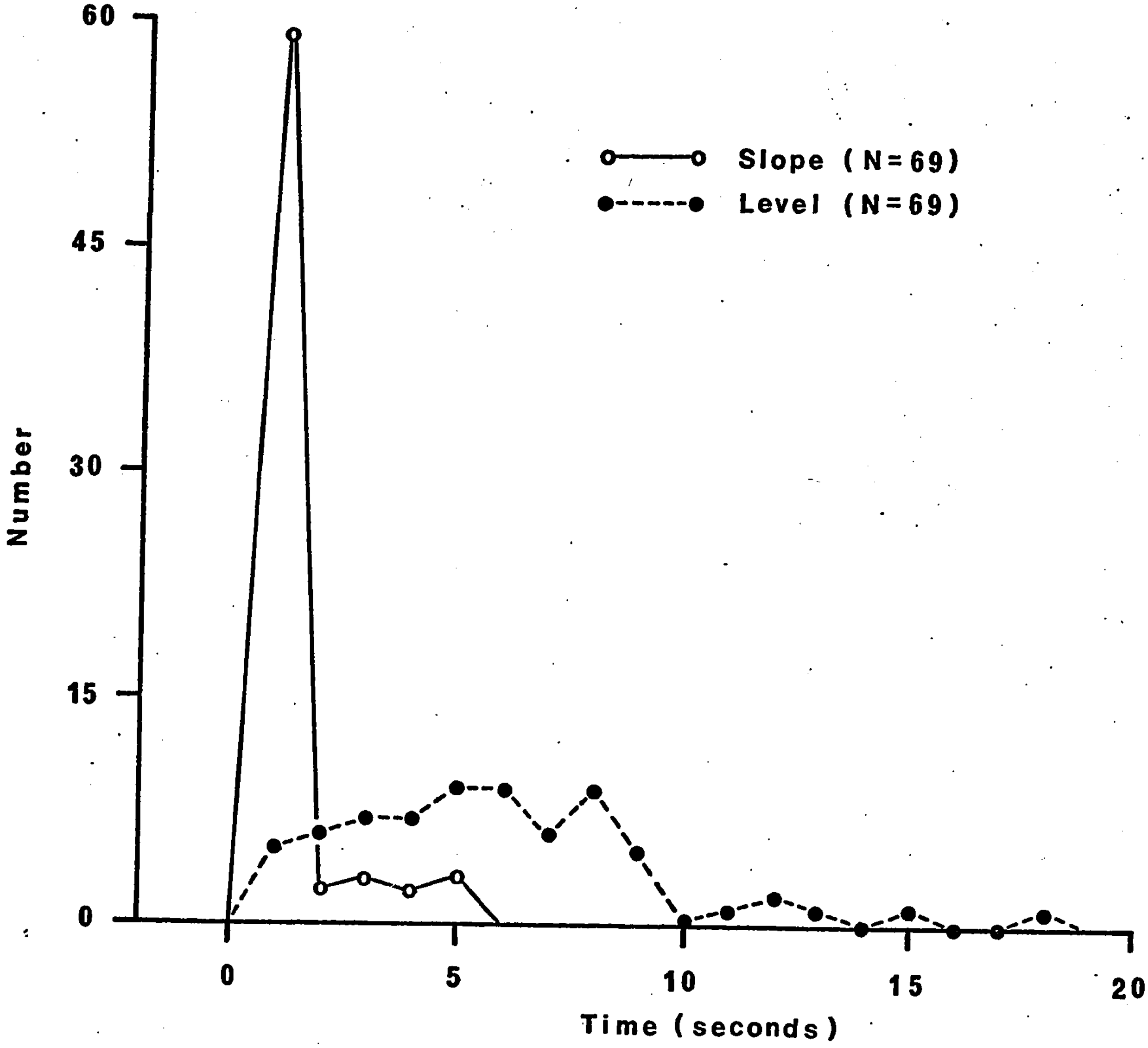


Figure 12. Distribution of time interval required to become airborne by adults released on slope and level habitat of the Main Colony.

12

Chick movement in burrows in relation to food supply

The proportion of time spent in various parts of the artificial burrow by four chicks is shown in Table 23. Time spent outside the nest chamber in the burrow tunnel (1-24" from burrow entrance) was significantly higher during the four day starvation period than in the four day feeding period ($P < 0.001$, $X^2 = 34.35$). Furthermore, of the time spent in the burrow tunnel, the chicks occurred more frequently in the section closest to the burrow entrance (0-12") when not fed than when fed ($P < 0.001$, $X^2 = 16.74$). Therefore, when rarely fed and presumably hungry, the chicks spent more time outside the nest chamber near the burrow entrance.

It is worth noting that the chicks, when fed regularly, moved close to the burrow entrance only to defecate, whereas during the starvation period, they often "loafed" near the entrance and occasionally actually stood outside at the mouth of the burrow for a few seconds before re-entering. During one of these outside exploratory trips, a chick that had not been fed for three days was seized by a Herring Gull fledgling, which flew off with it and presumably killed it.

3. Egg Survival, Breeding Success and Fledging Condition With (Great Island) and Without (Funk and Small Island) Gull Interference

Egg survival

The survival of eggs at Funk Island and Small Island during a period of 33 days is compared with survival at Great Island for a similar period in Table 24. Survival was significantly higher at

Table 23. Chick movement in artificial burrows in relation to food supply (N.B., reduced observation time in the 'No feedings' period caused by gull predation of one chick before the completion of the experiment).

Feeding schedule	Total no. min observed	(A) Burrow tunnel 0 - 12" No. min	(A) %	(B) Burrow tunnel 13 - 24" No. min	(B) %	(C) Nest chamber 25 - 36" No. min	(C) %
Regular feedings (75-100 g/day)	2880	14	(0.5)	52	(1.8)	2814	(97.7)
No feedings	2567	70	(2.7)	66	(2.6)	2431	(94.7)

(A + B): C - $P < 0.001$, $X^2 = 34.35$

A : B - $P < 0.001$, $X^2=16.74$

Table 24. Comparison of puffin egg survival at colonies with (Great Island) and without (Funk and Small Island) gull interference in 1969. (N.B., Great Island: 5 June - 9 July; Funk and Small Islands: 17 June - 19 July 1969).

Colony	Habitat	Total	With eggs or chicks		Empty		%
		N	N	%	N	%	survival
Funk	Level	106	98	92.4	8	7.6	92.4
Small	Level	147	144	98.0	3	2.0	98.0
Great	Slope	200	156 **	78.0	44	22.0	78.0
	Level	202	136	67.4	66	32.6	67.4
Funk and Small	Level	253	242	95.7	11	4.3	95.7
Great	Slope and Level	402	292 *	72.7	110	27.3	72.7

* $P < 0.001$, $X^2 = 54.61$

** $P < 0.001$, $X^2 = 32.62$

Funk and Small Island when compared with either the combined slope and level Great Island data ($P < 0.001$, $X^2 = 54.61$) or the slope data alone ($P < 0.001$, $X^2 = 32.62$).

Breeding success

Breeding success results at 253 nests on Funk and Small Island are given in Table 25. The estimated number of nests from which fledglings were produced was very high (90.5%).

Comparing the breeding data from the two puffin nesting situations (Table 26) it is apparent that breeding success was significantly higher at Funk Island and Small Island where gulls were scarce ($P < 0.001$, $X^2 = 181.75$).

Fledging condition

The average condition of young just before fledging in both breeding environments are presented in Table 27. Chicks at Funk and Small Island were much heavier close to fledging than those at Great Island ($P < 0.001$, $t = 19.94$), although winglengths were similar ($P > 0.50$, $t = 0.24$).

Bodyweight at fledging was less variable at Funk and Small Island than at Great Island ($P < 0.01$, $F = 3.94$), but variation in winglength did not differ significantly ($P > 0.05$, $F = 1.14$). Perhaps the most striking fact is that mean bodyweight at Funk and Small Island was higher than the maximum recorded for any single chick at Great Island. Altogether, young close to fledging displayed a higher bodyweight at areas without gull interference.

Table 25. Breeding success of puffins at Funk and Small Island in 1969.

Colony	No. eggs	No. fledglings	% success
Funk Island	106	92	86.8
Small Island	147	137	93.2
Total	253	229	90.5

Table 26. Comparison of breeding success at colonies with (Great Island) and without (Funk and Small Island) gull interference in 1969.

Colony	No. eggs	No. fledglings	% success
Great Island	402	149 *	37.1
Funk and Small Island	253	229	90.5

* $P < 0.001$, $X^2 = 181.75$

Table 27. Comparison of fledging condition at colonies with (Great Island) and without (Funk and Small Island) gull interference in 1969. (N.B., Great Island data - birds on slope habitat only).

Colony	Nest no.	Bodyweight (g)			Winglength (mm)		
		$\bar{x}$	s	range	$\bar{x}$	s	range
Great Island	101	261.8	35.87	159-323	140.5	6.21	127-153
		*			**		
Funk and Small Island	91	351.3	24.24	285-425	141.5	6.63	129-153

* $P < 0.001$, $t = 19.94$

** $P > 0.50$, $t = 0.24$

V. CONCLUSIONS

At Great Island, puffins nest above the cliffs in higher density on slope habitat close to the cliff edge than on adjacent level ground further from the cliff edge. Observations of the process of settlement on the island and establishment of nest-sites in spring show that there is a more or less simultaneous occupation of the total nesting area of the two habitats, with more birds going to the slope than to the level. It is possible that the mechanism described by Svärdson (1949) is also operative, that is first arrivals establish themselves in one habitat and then, when the density has reached a high level, subsequent arrivals settle in an adjacent habitat. If this does occur it must happen rapidly, and displacement must mainly involve those birds which have not bred before, because birds which have already bred exhibit a high degree of nest-site tenacity in each habitat.

Males which settle on slope habitat are heavier at this time than those on level habitat. If weight is correlated with age, this might mean that males on slope habitat are older on the average than those on level habitat. The absence of a reliable aging technique (see Lockley 1953; Salomonsen 1944; Williamson 1948) prevents this from being demonstrated or refuted, but three pieces of evidence favour refutation. First winglength, which might also be correlated with age, is not significantly different between birds in the two habitats. Second, there were no statistically demonstrable differences in some egg dimensions which might be expected to vary with age of bird since several other seabirds are known to lay progressively larger eggs as they increase in age (e.g., Coulson 1963; Coulson _et al_. 1969; Nelson 1966; Richdale 1955, 1957; Serventy 1967). Third, the high degree of nest-site tenacity displayed by birds which have already bred indicates that if there is an interchange of birds between habitats, its frequency was too low to be detected. Alternatively, the difference in mean bodyweight between males on slope and level habitat can be attributed to differences in the physiological condition of the arriving birds (e.g., fat deposits). An explanation for this would require knowledge of the birds feeding, activity, and distribution prior to their arrival on the island.

The frequency of fighting during settlement and laying was greater amongst birds on slope than on level habitat, and the time taken to reach peak frequency of fighting was shorter on slope habitat. Neither of these features is surprising in view of the greater density of birds on slope habitat. Although egg-laying dates were similar on the two habitats, the peak laying period was more concentrated on slope habitat, suggesting a greater degree of synchronization which cannot be attributed to time of arrival, since this was approximately the same in the two habitats, but which might be related to the greater density on slope habitat (Coulson and White 1960; Darling 1938).

From this point of the breeding cycle onwards, there occurred marked differences in breeding performance of birds in the two habitats. Hatching success, and then fledging success, were distinctly higher on slope habitat. Overall breeding success was twice as high on slope habitat as on level habitat.

The most important contributor to mortality of both eggs and chicks was gull predation, either presumed or observed; where not actually observed this was manifested as disappearance of the egg, during incubation, or chick before fledging, the only known reason for which is removal by gulls. This conclusion is based on numerous observations of adult gulls successfully taking puffin eggs and nestlings from burrows. Eggs found by gulls were either immediately pecked open and the contents eaten or carried off to another location to be eaten or presented to their young. When a chick was caught, it was usually held and struck repeatedly against the ground and then swallowed whole by the gull, often to be regurgitated later as food for gull chicks, or carried and given to the young immediately.

The higher disappearance of eggs from nests on level habitat during incubation appears to be related to differences in the exposure of the eggs to predatory gulls. Experiments showed that the frequency of eggs displaced from the nest chamber towards the burrow entrance by incubating birds responding to surface disturbance (e.g., gull cries) by rapid departure was the same in the two habitats, but that the frequency of panic-flights (the mass departure of birds following a disturbance) was much higher on level habitat than on slope habitat. Thus the likelihood of an egg being exposed to gulls is greater on level habitat than on slope habitat. Furthermore, it is possible that the higher proportion of those eggs on level habitat which did not disappear, but failed to hatch because they were addled or infertile, is also related to this difference in surface disturbance and brooding behaviour, because the other likely determinants, the characteristics of the egg and the nest, are similar in the two habitats.

The higher frequency of panic-flights on level habitat seems to be associated with differences in nervousness amongst the birds themselves. If panic-flights are a consequence of the nervousness caused by the nesting area (Cullen and Ashmole 1963; Tinbergen 1931), it is to be expected that birds on inland level areas would panic more because of their poorer chances of escape from predators than those on maritime slope (see page 67). This may also explain why adult distribution was concentrated along the crest of the slope on the Main Colony (Strip 3), rather than matching the distribution of nest-sites; presumably it is because take-off is quicker on slope than on level ground. The fact that the largest proportion of the surplus bird numbers on Strip 3 apparently came from the level Strips 5 and 6 (indicated by X^2 values, Table 3) fits this suggestion. A further consequence of this "psychological" effect of habitat is that the time interval between panic and return to the nest-site by birds appeared to be greater on level habitat, and so, exposure of any eggs displaced to the burrow entrance may be higher than on slope habitat where return to the colony is rapid.

Just as the disappearance of the egg from the nest (the main cause of egg loss) was attributed to gull predation, so was most pre-fledging chick mortality. The larger number of chicks that disappeared before fledging from nests on level habitat may also be related to differences in exposure to gulls. Experimental chicks (captive chicks in artificial burrows) spent more time near the burrow entrance when starved than when fed regularly. Thus it is possible that chicks on level habitat spent more time near the burrow entrance, where exposure to gull predation is highest, than chicks on slope habitat, because of a poorer food supply. However, the higher number of chicks found dead inside their burrows on level habitat than on slope habitat is more difficult to explain. A small number of carcasses had body wounds, which suggests death from an injury inflicted during an unsuccessful gull attack, but in most cases there was no obvious body damage. The difference indicates that in addition to gull predation, as reflected by chick disappearance, chick survival in level habitat was further reduced by some other critical factor, while in nests on slope habitat most chick mortality was the direct result of predation. Most chicks found dead were young (39% less than 9 days old). Insufficient food, intermittant brooding prior to the establishment of thermoregulation (c. 7 days, Rol'nik 1948) and accidental trampling by adults during panic-flights are possible causes of these deaths. The food factor is likely to have been important, if only because of the large amount of direct and indirect evidence (presented below), that it influences overall breeding success on Great Island.

If a slower rate of provisioning chicks with food on level habitat is responsible for the difference in numbers of chicks that disappeared prematurely between the two habitats, it may be due to differences in the gathering of food by adults at sea or in the delivering of food by adults to the young on land. Evidence for the former would be extremely difficult to obtain. All that can be said is that all birds appear to feed in the same general location, judging from the initial flight direction of birds departing from the island, and that the distribution and abundance of the chief food item for chicks at Great Island (Capelin, *Mallotus villosus*) is similar over vast areas of the east coast of Newfoundland (Pitt 1958; Templeman 1948).

Alternatively, a difference in rate of provisioning chicks might be due to the effects of gulls upon adult puffins at the colony, since gulls persecute food-carrying puffins more on level habitat than on slope. In fact meal size (weight of fish per meal) given to chicks was the same in the two habitats,but the rate at which meals were delivered to the chicks was higher on slope habitat than level habitat. The rates of feeding are based upon observations on only three days, towards the end of the fledging period, and so must be accepted for what they are, no more than an indication that throughout the fledging period chicks are provisioned at a faster rate on slope than on level habitat. Parents nesting on level habitat were both attacked and robbed more frequently than those on slope habitat. The difference in vulnerability to gull attack appears to be related to the greater exposure of the level-nesting birds as they fly over the slope to the level area of the colony, to their greater difficulty in landing precisely at their burrow entrance because of the angle of the ground, which influences the risk of being seized by an attacking gull, and to their inability to lift off level ground to escape an attack (they must run back to the crest of the slope in order to fly off). Thus, a landing on level habitat is a final commitment, whereas a bird landing on a slope may just "bounce" back into the air if the burrow entrance has been missed or a gull attack is imminent.

In addition to the higher loss of meals to gulls from birds nesting on level habitat, the time between arrival at the island and actual landing at the nest-site is probably greater. The concentration and flight patterns of the birds prevented this from being quantified, but the pressure exerted by a higher gull attack rate combined with a significantly lower chance of escape if attacked, clearly makes it crucial for birds with chicks on level habitat to land only when conditions are near perfect (i.e., flight speed and direction to burrow, position of gulls, etc.) to ensure a swift entry into the burrow entrance. Therefore, on average, more time and energy is probably expended by parents in reaching a nest-site on level habitat, one obvious consequence of which is a reduction in time for other activities (e.g., feeding, chick provisioning, resting, etc.).

The physiological condition of the young at time of fledging, as judged from bodyweights just before fledging, was distinctly poorer and more variable in birds raised on level habitat than in those on slope habitat. Since for reasons of similar microclimate, the energy demands of chicks are likely to be similar in the two habitats, the difference in bodyweights of fledglings must be attributed to differences in food supply (i.e., energy) or else length of residence in the burrow.

The comparison of chicks hatching early and late within a season, and comparisons of chicks between seasons shows that in both years and in both habitats the chicks which hatched from eggs early in the season survived better and fledged at a higher bodyweight than did those which hatched late. Since the energetic requirements of chicks of a given bodyweight are not likely to vary appreciably as the season progresses, this strongly suggests that the rate of provisioning the chicks was greater in the early part of the season than later on, perhaps because of a diminishing supply of fish available for parents to capture (Ashmole 1963; Ashmole and Tovar S. 1968; Harris 1966; Lack 1954, 1966, 1968; Nelson 1966; Perrins 1966). What can be called "early" chicks fledged at a younger age than "late" chicks on slope habitat, and quicker than "early" chicks on level habitat, which shows indirectly that growth rate must have been most rapid in "early" chicks on slope habitat. On the other hand "late" chicks on slope habitat took longer to fledge than "late" chicks on level habitat. This suggests that "late" chicks on slope habitat can compensate for any change in food quality or quantity delivered to them by their parents by extending the time spent in the burrow before fledging, whereas "late" chicks on level habitat cannot. The reason for this is unknown. Perhaps the behaviour of the parents (e.g., response to "food-begging" stimuli of chicks or feeding conditions at sea) differs in the two habitats.

Thus the slower rate of food provisioning on level habitat appears to be due to gull interference, either directly by clepto-parasitism or indirectly owing to the large amount of time spent avoiding gulls while en route to the burrow.

However, before the biological signficance of gull robbing can be assessed, regardless of how severe, it must be demonstrated that the observed interference is sufficient to disrupt the balance or equilibrium of the puffin's feeding ability (i.e., great enough to impair the survival of the young). There is some evidence which indirectly suggests that food supply is an important determinant of pre-fledging survival and that two parents experience difficulty in rearing a single chick at Great Island. First, twinning experiments showed that the amount of food collected by both parents is insufficient to feed two chicks on slope habitat, invariably one twin gained weight while the other lost. The unsuccessful chick eventually died or disappeared prematurely. To what extent sibling aggression influences the eventual outcome is unknown, but obviously food was not provided by the parents at a rate which would satisfy one chick and would allow any additional food to be eaten by the less competitive or aggressive twin. Similarly, the increased strain placed on single parents (either sex) to raise one chick alone following the loss of its mate was too burdensome, as all experimental single-parented chicks lost weight and either died or disappeared prematurely. These results seem to indicate that the amount of food which two parents are capable of gathering just meets that required by a single chick and that the difference in food lost to gulls is enough to alter the survival of chicks before fledging and their condition at fledging. Furthermore, this evidence supports the relationship between food supply and exposure of chicks to gull predation described earlier (see page 82).

To sum up, these observations strongly suggest that the difference in breeding performance of birds nesting in slope and level habitat is due to the direct and indirect effects of food shortage and gull interference.

If this conclusion is correct, it is to be expected that on islands where gull interference is zero but food supply per bird is the same as that on Great Island, breeding performance per bird would be distinctly higher. The brief studies on Funk and Small Island show this expectation to be correct. There is no interference from gulls on either island, and food conditions may be presumed to be similar to those at Great Island because capelin abundance is relatively uniform along the east coast of Newfoundland (Pitt 1958; Templeman 1948). From topographic characteristics, one might expect breeding success on both these islands to resemble success for nests on level habitat at Great Island. However, data for egg survival, breeding success, and fledging condition all indicate that puffin breeding performance at Funk and Small Island far surpasses that recorded on either slope or level habitat at Great Island.

The figures for egg survival are known precisely and show that egg losses were higher at Great Island where gulls exploit puffins than at Funk and Small Island where they do not. The distance between islands prevented the dates of the study period from coinciding exactly (Great Island: 5 June - 9 July 1969; Funk and Small Island: 17 June - 19 July 1969), but the length of the period in which the nest groups were exposed was virtually identical (Great Island: 35 days; Funk and Small Island: 33 days), making the comparison almost absolute.

Breeding success was significantly lower on Great Island than at Funk and Small Island. However, the values calculated for Funk and Small Island were partly estimated, as some chicks had apparently already fledged prior to the last inspection, while chicks still present were assumed to survive to fledging. Nevertheless, I consider these sources of error to be minor; first, because all empty nests which were classified as successful displayed obvious signs of lengthy chick occupation (e.g., heavy defecation stains, etc.), and second, the majority of chicks still in burrows were fully feathered with actual fledging imminent. Thus, breeding success as used here means the number of chicks estimated to have fledged plus those which survived to the last inspection.

Chicks estimated to be within a few days of fledging at Funk and Small Island were strikingly heavier than Great Island chicks at the same stage of development, although winglengths were similar. In fact, the mean bodyweight of Funk Island and Small Island chicks close to departure was higher than the maximum weight reached by any single chick examined during three years of study at Great Island. The bias created by the lack of precise fledging dates at the Funk and Small colonies is unimportant because of the large weight differences involved and the fact that measurements used for chicks at Great Island preceded actual fledging by only one to four days. This suggests that in the absence of gull interference chicks can attain bodyweights much higher than when gulls are present.

These findings are consistent with data from colonies elsewhere. At Lovunden Island in Norway (Myrberget 1962a) breeding success (86.7%) and mean fledging bodyweight (c. 280 g) are higher than at Great Island, as were fledging weights (352-400 g) at the Ainov Islands in Russia (Korneyeva 1967). All three populations belong to the same subspecies (F. a. arctica, Kozlova 1957; Myrberget 1963; Salomonsen 1944) and interference from avian predators (gulls, jaegers, crows, ravens) is apparently insignificant at both Lovunden (Myrberget 1962a) and the Ainov Islands (Skokova 1967).

If summer food shortage and gull interference are important determinants of puffin breeding success, it is also to be expected that breeding success would be higher in years of good food supply, climate, etc. The difference in breeding success between 1968 and 1969 supports this prediction. In the "normal" summer (temperature and precipitation) of 1969, 50.5 percent of nests on slope habitat and 23.8 percent on level habitat fledged young, whereas in the extremely wet and cold summer of 1968, only 27.7 percent of nests on slope and 10.0 percent on level were successful. Furthermore, age at fledging was greater in 1968 in both habitats, which is also probably attributable to weather differences (directly or indirectly), although bodyweight at fledging was similar. This indicates that chicks can compensate for adverse conditions (i.e., insufficient energy supply) by lengthening the fledging period (Lack 1948, 1968), a view which Harris (1969a) uses to explain the long and flexible fledging period of Audubon's Shearwater (Puffinus lherminiera). Excluding direct mortality of eggs and young (e.g., due to chilling, waterlogging, etc.), inclement weather can affect puffin breeding performance in two ways. First, by altering the normal summer distribution and abundance patterns of prey organisms (e.g., low water temperature can significantly reduce inshore capelin spawning, Templeman 1948; also see Lack 1954, 1966: 4; and Dusi and Dusi 1968) and second, by disrupting factors related to gull feeding ecology (e.g., abundance of alternate food supply, increased energy requirements, etc.), which in turn would result in an increase in puffin exploitation. Irrespective of the way in which below normal weather conditions affect puffins (directly or indirectly) the result will be the same - a decrease in breeding success.

Another factor influencing breeding success of puffins at Great Island is the timing of the breeding cycle. As mentioned earlier, early hatched chicks on both slope and level habitat survived better and fledged at a higher bodyweight than those hatched late. I concluded that this difference is most probably related to a diminishing food supply available for parents to capture and deliver to chicks as the season progresses. If this is correct, it seems likely that breeding as early as possible would be strongly selected for, especially if fledging condition influences post-fledging survival. Perrins (1966) has shown for Manx Shearwaters (Puffinus puffinus) that chicks fledging early survive better than those fledging later, even though their bodyweights at departure did not differ significantly; Harris (1966) attributes the higher mortality of chicks fledging late to differences in food supply experienced by chicks immediately after departure from the colony or during migration. If there is a similar high premium placed upon early fledging puffins, selection presumably acts against birds breeding late; the factor limiting early breeding is probably the amount of food required for the female to form an egg (Harris 1969; Lack 1966, 1968; Perrins 1966, 1970). Therefore it is possible that food supply is the proximate factor regulating the onset, duration and completion of breeding within the puffin population at Great Island.

To summarize, puffin breeding success at Great Island is higher on slope habitat than adjacent level habitat because adults are less vulnerable to gull disturbance during incubation and gull robbery when feeding their chick. Thus breeding failures result largely from the interactions of food shortage and gull interference.

VI. DISCUSSION

This study has demonstrated that puffin nest density at Great Island, Newfoundland, is inversely related to distance from the cliff edge. The biological significance of this correlation appears to be that the area close to the cliff edge, where the angle of slope is steep, is the most suitable for breeding; breeding success is significantly higher here than on adjacent level habitat. The reasons for the difference in breeding success are, firstly, eggs and chicks are more exposed to gull predation on level habitat, and secondly, parents are more vulnerable to robbery by gulls when taking food to chicks on level areas than when taking food to chicks on slope habitat. Thus, during the breeding season, natural selection acts most strongly against birds nesting on level habitat away from the cliff edge. The following discussion will therefore consider the ecological and evolutionary implications of these conclusions to puffin populations.

1. Population Dynamics

The balance in numbers of puffins breeding in the two habitats depends on the density of the population. In the initial stages of the development of a breeding colony individuals will select areas within the potential range of nesting habitat according to fixed environmental cues (Klopfer 1962; Klopfer and Hailman 1965; Lack 1933, 1937; Lack and Venables 1939). As numbers increase, birds are forced by intraspecific social pressure into other areas of the optimal habitat (i.e., where total productivity per bird is greatest) until it is full, the upper limit presumably being set by a fixed minimum amount of space (volume) required to excavate a burrow and/or behavioural characteristics associated with burrow defence (e.g., individual area, Burckhardt 1944; individual distance, Conder 1948). Further increases result in suboptimal contiguous habitat being used until this is also full. At this point in population growth, adults unable to secure a nest-site amongst those available do not breed and form a surplus around the periphery of the colony (e.g., Coulson and White 1956; Coulson 1968; Svärdson 1949; Wynne-Edwards 1962). Once both habitats are occupied the size of the breeding population stabilizes, with any vacancies being filled by members of the non-breeding surplus.

The simplest way in which equilibrium could be maintained is for birds to breed in the habitat in which they were reared, and for longevity, breeding success, etc. to be the same in the two habitats. In essence, there would be two populations in separate and adjacent habitats, rather than one population in two habitats. This situation would be of considerable theoretical interest (see e.g., Levene 1953; Ludwig 1950; Van Valen 1965). However, it is known that breeding success is not the same in the two habitats, a condition which tends to disturb the equilibrium towards a higher proportion of bird breeding in slope habitat. Unchecked, this disturbance would lead to the complete elimination of birds breeding on level habitat. It may be compensated in two ways. First, by greater mortality among slope-reared birds after fledging than among level-reared birds. Second, by a movement of slope-reared birds into level habitat to breed.

If there is a differential death rate among adults, which might occur before first breeding, after first breeding or in both periods, it would have to occur in autumn and winter because mortality of adults at the colony during the breeding season is negligible. For instance, it is likely that the condition of the young at fledging is critical since much post-fledging mortality of seabirds is caused by the inability of birds to acquire quickly enough the necessary skills of feeding in early independent life (Ashmole and Tovar S. 1968; Harris 1966; Lack 1968: 246; Nelson 1966; Orians 1969; Recher and Recher 1969). However, mean bodyweight of birds close to fledging was lower among those on level habitat than those on slope habitat, which indicates that immediate post-fledging mortality would be greatest among birds reared on <u>level</u> habitat, not <u>slope</u> habitat. Moreover, birds which breed on level habitat might be expected to die more quickly than birds which breed on slope habitat, in view of the energy demands of reproduction (apparently not equal in the two habitats) and in view of the bodyweight soon after the time of arrival at the colony in spring (if bodyweight is indicative of past success in feeding and storing food).

Therefore, there is no evidence that the greater reproductive output of birds which breed on slope habitat is compensated by greater mortality among those which were reared and those which breed there. This must mean that if equilibrium is maintained, it is achieved by more slope-reared birds breeding on level habitat than level-reared birds breeding on slope habitat, the result being a net flow of birds from slope to level habitat for breeding purposes. The flow may be even greater than presently suspected if birds which breed on slope habitat live longer on the average, and therefore breed more times, than birds which breed on level habitat.

Since mean breeding success is lower in level habitat, movement into this habitat seems to be poor strategy for slope-reared birds. However, settlement in level habitat would still be advantageous to slope-reared birds under the following three conditions. First, if the probability of breeding successfully on level habitat is distinctly higher than zero. Second, if the birds lack morphological and/or behavioural traits necessary to enable them to establish themselves on slope habitat, and are unlikely to obtain the traits in the future. Third, if all slope habitat is "full" when these birds are ready to breed for the first time (Coulson 1968; Gadgil and Bossert 1970, for further consideration of the question of when and where it is best for animals to breed for the first time). Assuming that breeding success can be achieved on level habitat, although less well than on slope habitat, the best strategy for a bird fitting the second condition is obvious - to settle on level habitat, no alternative breeding location being possible. Under the third condition deferment of first breeding may be the preferred strategy because it appears that choice of site to breed first determines the individuals position within the colony for the duration of their reproductive life. However, if breeding is repeatedly delayed in an attempt to secure a nest-site on slope habitat, the associated reproductive advantage will eventually be negated because of the relatively fewer times the bird will have remaining in which to breed. Thus, the best strategy may still be to nest and rear offspring on the poorer-quality level habitat, rather than delaying first breeding until a nest-site becomes available on the superior-quality slope habitat.

It also follows that when a space becomes vacant in the total nesting habitat it is more likely to be filled by a slope-reared bird because there are more of these than level-reared birds in the pool of potential breeders; due to differential breeding success, the ratio of slope-reared birds to level-reared birds in the pool of potential breeders is greater than the ratio of slope-breeders to level-breeders. Therefore, the existence of birds breeding in level habitat is probably dependent upon production in slope habitat, and breeding in level habitat in addition to slope habitat is also a means of maximizing total production of the population (Brown 1969).

Equilibrium of the population has been assumed to this point. However, the stability of numbers of individuals constituting the breeding population can be upset by population increase in one direction and increase of gulls in the other. Non-equilibrium due to puffin population increase would lead to greater nesting on level habitat. Non-equilibrium due to gull increase (see Amadon 1958; Kadlec and Drury 1968) is likely to lead to a decreased amount of nesting, and certainly breeding success (Bruyns 1958), in level habitat. Only a long term study could determine if the puffin population at Great Island is at equilibrium or not.

2. Natural Selection

If breeding systems evolve as a result of the interplay of different selective pressures, the net result should be the pattern most advantageous for the production of progeny to the next breeding generation by individuals of the species (Gadgil and Bossert 1970; Lack 1968). Several adaptive strategies are common among many long-lived seabirds. For example, age at first breeding (deferred maturity) and small clutch sizes of younger birds appear to be related to food-gathering ability (Orians 1969; Recher and Recher 1969) because they breed less successfully than older birds (e.g., Coulson and White 1958; Richdale 1957; Sladen _et al_. 1966; Tickell 1968; etc.); restriction of breeding to isolated nesting sites inaccessible to predatory mammals (Braestrup 1941; Lack 1968; Løvenskiold 1954); selection of nest-site at which to breed (e.g., Brown 1967; Coulson 1968; Kruuk 1964; Patterson 1965; Snow and Snow 1967; etc.); and breeding when environmental conditions are most favourable for rearing young (e.g., Ashmole 1962; Bédard 1969b; Beck 1970; Harris 1966, 1969; Nelson 1969; Perrins 1966, 1970; Salomonsen 1955). Most of these adaptations apply to puffins, but from the conclusions given earlier choice of nesting habitat at first breeding and timing of the breeding cycle appear to be most critical to reproductive success and so, the discussion will consider only these two factors.

Given the characteristics of the population dynamics outlined above, the choice of where to breed is relatively unimportant if only one nest space becomes available, but highly important if many are available. Many birds breed where they have bred before because, it is thought, their chances of success are higher than if they attempt to shift even to a topographically more favourable site (see Coulson 1968; Patterson 1965; Penney 1968). Since puffins show a strong habitat and nest-site tenacity it appears that individuals may breed under only one set of nesting conditions throughout their reproductive life and that the position within the colony is determined early. Consequently, the choice of site to breed first is of great importance to puffins because of the difference in breeding success (i.e., probability of successfully rearing a chick to fledging) on slope and level habitat. There is no direct evidence that birds reared on one habitat breed on another, but it is highly likely (see above, also Brown 1969). Thus, selection will favour those birds which: (a) discriminate between the two habitats, and (b) choose and succeed in settling on slope habitat. The first criterion may be a universal attribute of the population, fixed and therefore not susceptible to selection, but the second criterion is clearly susceptible to selection.

The attributes of birds which are likely to pre-dispose them to successful establishment on slope habitat are those pertaining to the aggressive behaviour exhibited in the context of securing and defending a nest-site (Collias 1944; Svärdson 1949; Tinbergen 1957).

In addition, body size appears to be important (Miller 1967, 1969). Thus it is to be expected that selection favours large and aggressive males (at the age of first breeding) because these are able to establish themselves on that habitat which (in the presence of gull interference) confers the highest probability of breeding success. The data necessary to make the comparison between birds breeding for the first time on slope and level habitats were not obtained, but there is one prediction which can be tested for all breeders. It is that birds breeding on slope habitat should be larger, as measured by bodyweight, than those on level habitat during the spring settlement period. This prediction is true (see page 35). Furthermore, bodyweight at the time of arrival at the colony is considered to be indicative of past success in feeding and storing food. Therefore, response to selection in the breeding season is determined in males at least partly by environmental factors operating in a different environment, perhaps the one in which the birds spend the winter.

How female choice of nesting habitat is made is unknown. However, since body measurements of females breeding on slope and level habitat showed no significant differences it seems unlikely that position within the colony is determined through aggression. A more likely alternative is that females make a choice among the available site-holding unmated males according to the same criteria used by males for selecting nest-sites (see page 95).

Given the differences in habitat quality (measured by mean breeding success) a model can be constructed which relates the use of nesting habitat by puffins to the presence and absence of gull interference (i.e., predation of eggs and young, and clepto-parasitism), and is shown in Figure 13. Distance from the cliff edge is the topographic variable most closely correlated with nest density and has therefore been used in the model. Angle of slope, which is also strongly correlated with nest density, could be used separately or in combination with distance. The model is based upon the assumptions that all other environmental factors (e.g., topography, food availability, etc.) are the same at the colonies being compared and that both populations are stable (i.e., at equilibrium).

In the absence of gull interference, selection pressure due to the effects of gulls is zero. Thus, breeding success and nest density should be high and similar throughout the nesting space, with the upper limit of population size being set by the abundance of nest-sites (Figure 13: S_o).

In the presence of gull interference selection strongly favours nesting on steep slopes close to the cliff edge where breeding success is highest. Since the probability of breeding success decreases as the individual moves away from the cliff, the area containing suitable nest-sites (i.e., those where the probability of breeding successfully is higher than zero) is reduced, and so, both colony size and number of breeding pairs per unit area on level ground inland from the cliff should be distinctly smaller. Nesting inland on level habitat may also be limited by direct

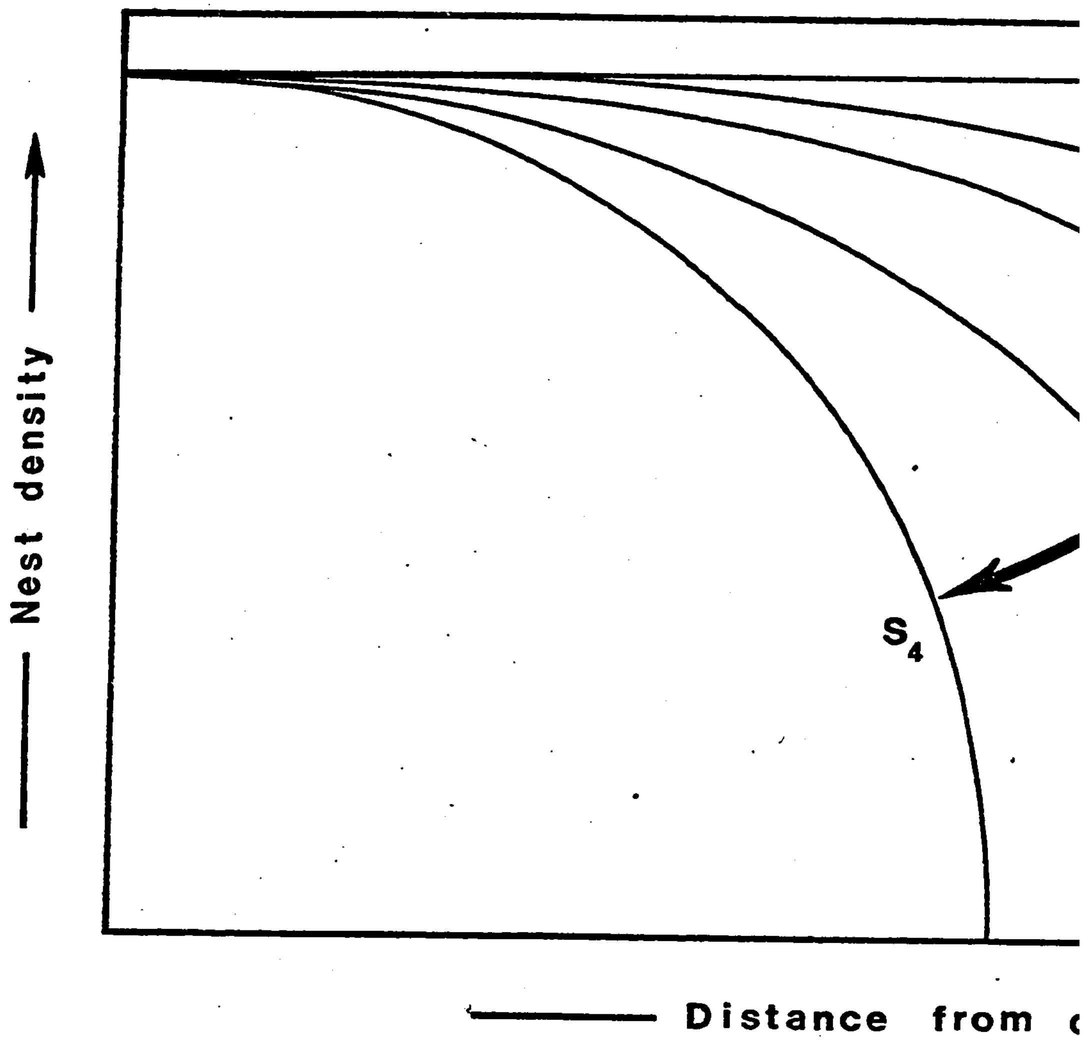
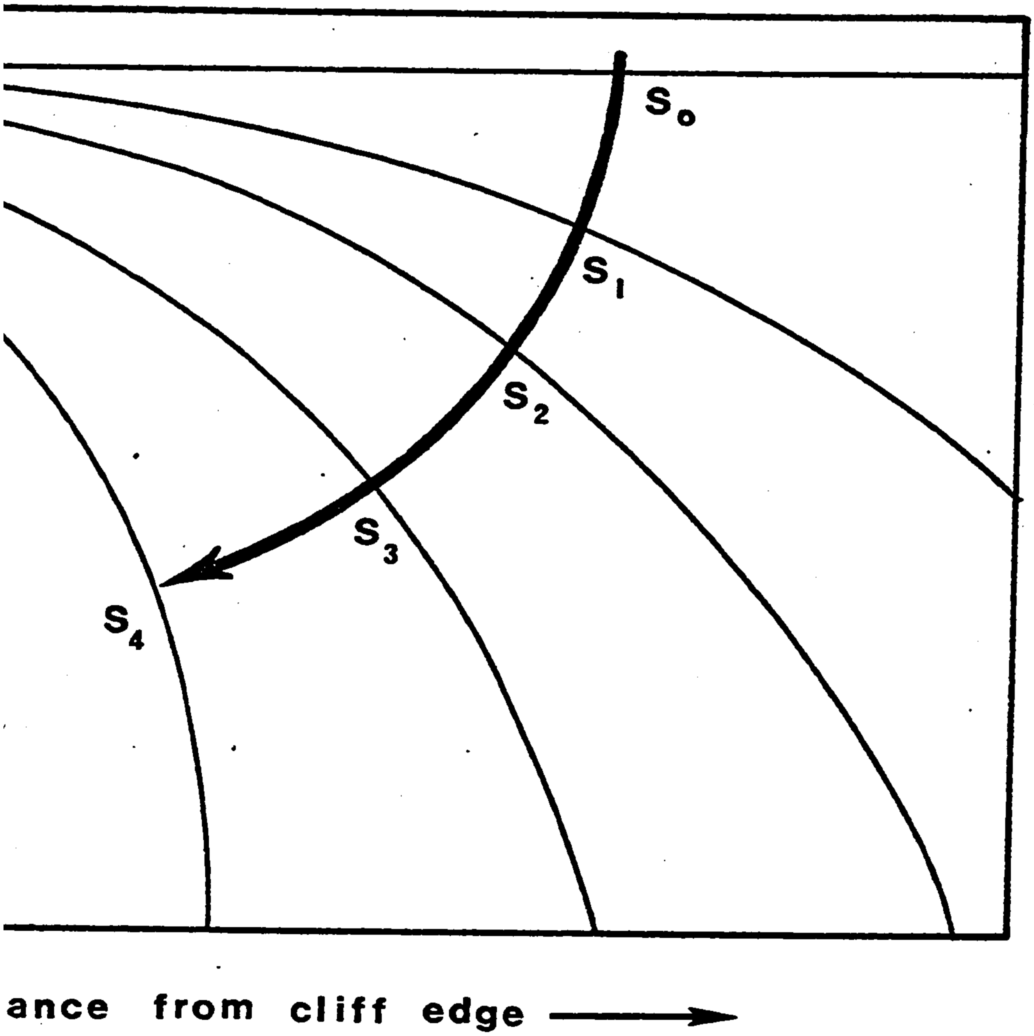


Figure 13. A model of nest density of puffins in
under conditions of different levels o
($S_o \longrightarrow S_4$). The arrow shows the
mediated by the effects of gulls upon
puffins.



f puffins in relation to a topographic variable
rent levels of interference from gulls
ow shows the direction of selection, which is
f gulls upon breeding performance of the

predation of adults by gulls (Aspden 1928; Coward 1936; Harris 1965; Lockley 1934, 1953). Therefore, the use of contiguous level habitat for nesting is counteracted by selective pressure due to gull interference; selection intensity will differ under conditions of different levels of interference from gulls (Figure 13: $S_o \longrightarrow S_4$).

It is desirable to assess the degree of generality of the model. This can be done by repeating the study at colonies in other regions. In addition, predictions can be made and tested by collecting the relevant data at other colonies. Two such predictions are presented:

1. <u>Differences in mean bodyweight and variation of breeding males in spring along the habitat gradient should be less at colonies where gull interference is absent</u>.

Since competition for nest-sites on maritime slope habitat in the presence of gull interference is very high, birds occupying these regions of the nesting space might be expected to show a higher bodyweight and lower variation than those nesting away from the cliff (Levins 1962, 1963, 1964; Van Valen 1965). The difference in mean bodyweight between breeders on slope and level habitat was significant at Great Island, but variation of bodyweights was similar, possibly due to the small sample size and/or the relatively small amount of level habitat being used by puffins for nesting. Nevertheless, the critical test of comparing these differences against those of a "gull-free" colony has not been made.

2. Utilization of level habitat adjacent to the maritime slope should be greater at colonies where gull interference is absent. The presence of surplus non-breeding adults is usually attributed to the lack of nest-sites at the colony (Coulson 1968; Huntington 1963; Rowan 1952, 1965) However, at Great Island there is seemingly suitable habitat inland from the cliff edge on which non-breeding adults could breed (judged by environmental variables such as soil depth, texture, etc.), but do not. The effect of gulls on puffin nest distribution may be assessed by comparing density levels on level habitat at colonies with and without gull interference (similar in age and topography) or, where possible, by removal experiments at gull-occupied colonies (see Young 1970).

Other predictions about breeding patterns of puffins with and without gull interference can be made (e.g., proportion of breeders to non-breeders, etc.), but the two presented above are the easiest to test and should provide the most useful results.

Theoretically, the above model and predictions assume the interference factor to be gulls only, but they may still apply where other species are cleptoparasitic on the puffins, such as Stercorarids. However, only detailed comparative studies of breeding efficiency at colonies with and without interference from cohabiting species will provide the necessary data to evaluate the importance of cleptoparasitism and food shortages to the long term evolutionary history of puffin populations.

SUMMARY

1. The study was primarily concerned with breeding success of puffins (*Fratercula arctica*) in different habitats on Great Island, on the southeast coast of the Avalon Peninsula, Newfoundland. Preliminary observations were made in 1967 and detailed comparisons of birds on slope and level habitat in 1968 and 1969.

2. A multiple regression analysis showed that puffin burrow density was negatively correlated with distance from the cliff edge, and positively correlated with angle of slope. Thus, puffins nest at a higher density on slope habitat, close to the cliff, than on level habitat. The distribution pattern of adults standing on the colony did not match the nest distribution; too few birds occurred on level areas and too many along the crest of the slope.

3. In spring, both habitats were occupied simultaneously and nest-site tenacity was equally strong in them. During settlement, the frequency of fighting was higher and the peak reached earlier on slope habitat. Males were heavier on slope than level habitat just after peak egg-laying, although winglengths were similar. Females were similar on the two habitats.

4. Measurements of eggs from both habitats were the same. Egg-

laying dates were also similar, but annual variation was greater on level than slope habitat, as was variation within a single year.

5. Hatching success was higher on slope habitat, due mainly to a lower incidence of egg disappearance during incubation; the frequency of infertile eggs was also greater on level habitat. Fledging success was higher on slope habitat, and higher on both habitats in 1969. Frequency of chick deaths in the nest and disappearance before fledging was higher on level habitat in both years. Fledging success was higher for early-hatched chicks in both habitats. Total breeding success was higher on slope habitat, and higher in both habitats in 1969.

6. Fledging condition of chicks varied according to the habitat and time period in which they were raised. On average, bodyweight at fledging was heavier and less variable for birds on slope habitat; early-hatched chicks were heaviest in both habitats. There was no difference in winglength of young at fledging.

7. Early-hatched chicks on slope habitat fledged quickest (also quicker than early-hatched chicks on level habitat); late-hatched birds on slope fledged slower than late-hatched birds on level habitat. Age at fledging was greater in 1968 than 1969 on both habitats.

8. Meal size delivered to chicks by parents was the same on the two

habitats, but frequency of feeding was greater on slope than level habitat.

9. Breeding pairs on slope habitat were unable to raise two chicks (artificial twins) to fledging; similarly, one adult could not rear a single chick.

10. Adults feeding chicks on level habitat were attacked and robbed more frequently by gulls than birds on slope habitat. This was attributed to the fact that escape (take-off) from an attack is quicker on slope than on level ground.

11. Experiments were performed to determine causes of the differential egg and chick loss before fledging in the two habitats. It was found that during incubation the proportion of eggs displaced to the burrow entrance by incubating birds when leaving the burrow in a hurry was the same, but that there was a higher rate of panic-flights on level habitat. It was also demonstrated that chicks when starved spend more time at the burrow entrance than when fed regularly.

12. It is concluded that the difference in breeding success on the two habitats was due to a higher exposure of eggs and chicks to gull predation on level habitat. The primary causes for this differential exposure was that adults on slope habitat were less vulnerable to gull disturbance during incubation and gull robbery when feeding their chicks. Thus breeding failures resulted from the interactions of food shortage and gull interference.

13. This conclusion was tested by comparing breeding performance of birds at Great Island with birds at two islands where gull interference was absent. Egg and chick survival was greater under "gull-free" conditions. In addition, bodyweights at fledging were higher and less variable at the colonies without gull interference than at Great Island.

14. The ways in which selection acts upon puffins at the breeding colony are considered. A model relating puffin nest distribution and habitat features is presented, and predictions which might be tested are outlined.

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