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BREEDING SUCCESS OF THE COMMON PUFFIN (*FRATERCULA ARCTICA* L.) ON DIFFERENT HABITATS AT GREAT ISLAND, NEWFOUNDLAND¹

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ABSTRACT

Factors contributing to breeding success of puffins were studied on Great Island, Newfoundland, in 1968 and 1969. Puffin burrow density was negatively correlated with distance from the cliff edge and positively correlated with angle of slope. These correlations are biologically significant in that close to the cliff edge, where the angle of slope was steep, breeding success was significantly higher than on adjacent level habitat. 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 was reached earlier on slope habitat. Males were heavier on slope than on level habitat just after peak egg laying, although wing lengths were similar. Females were similar on the two habitats. Measurements of eggs from both habitats were the same. Egg-laying dates were also similar, but annual variation was greater on level than on slope habitat, as was variation within a single year.

Hatching success was higher on slope habitat, mainly because the incidence of egg disappearance was lower during incubation; also the frequency of infertile eggs was 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. Fledging condition of chicks varied according to the habitat and time period in which they were raised. On the average, body weight at fledging was greater and less variable for birds on slope habitat; early-hatched chicks were heaviest in both habitats. Wing length of young at fledging did not differ. 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 in 1969 on both

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habitats. 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. Breeding pairs on slope habitat were unable to raise two chicks (artificial twins) to fledging; similarly, one adult could not rear a single chick. Adults feeding chicks on level habitat were attacked and robbed more frequently by gulls than birds on slope habitat, probably because escape (take-off) from an attack was quicker on slope than on level ground.

Experiments performed to determine causes of the differential egg and chick loss before fledging in the two habitats showed 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 the rate of panic flights was higher on level habitat. Also, chicks when starved spent more time at the burrow entrance than when fed regularly. 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 cause 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. 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, body weights at fledging were higher and less variable at the colonies without gull interference than at Great Island. The ways in which natural 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.

INTRODUCTION

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 nonrandom 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 factors limiting the distribution of a species have been considered by many biologists (e.g., Shelford 1911, Elton 1927, 1933, Lack 1933, 1934, 1940, Miller 1942, Thorpe 1945, Svårdson 1949, Andrewartha and Birch 1954, MacArthur 1958, Hinde 1959, Klopfer 1962, Hilden 1965, Klopfer and Hailman 1965, Fretwell and Lucas 1969). They have found two classes of environmental agents acting in a limiting fashion: (1) biological interactions between individuals, species, populations, or any group; and (2) 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.

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., MacArthur 1958, Sturman 1968, Bédard 1969). Often

abundance has been related to particular features of the environment 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 Fretwell 1968, 1969, Dow 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) and the degree of productivity attained in it.

Thus to adequately describe the relationship between a species and the habitat it 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, Southwood, and Cross 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 is small. Breeding success in relation to position in a colony has been found to vary in a predictable way (e.g., Coulson and White 1956, 1958, 1960. Richdale 1957, Snow 1960, Tuck 1960, Patterson 1965, Nelson 1966, Sladen, Wood, and Emison 1966, Brown 1967, Coulson 1968), 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 reasons: (1) the nesting habitat has been described throughout its geographic breeding range, and thus the associated environmental characteristics can be ascertained in general; (2) puffins are relatively free from competitive interactions with other species for their nesting habitat; and (3) 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 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 appeared to be greatest on sloping ground ($>30^\circ$) and least on level ground ($<15^\circ$), slope and level ground were the two habitats considered in the study of breeding success.

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

Thus the results are presented in two parts. The first compares breeding performance and charac-

teristics of puffins nesting on slope and level habitats. The second presents observational and experimental data that aid in evaluating the causal relationship between gull interference and puffin breeding success in the two habitats. Lastly, the biological significance of the results is considered in relation to puffins at Great Island and to evolutionary theory.

Summary of puffin breeding biology

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

Descriptions of the nesting habitat of the puffin throughout its geographical range are abundant (North American mainland: Bent 1919, Austin 1932, Todd 1963; Newfoundland: Lucas 1888, Peters and Burleigh 1951, Tuck 1967; Greenland: Salomonsen 1950; Iceland: Lack 1934, Gudmundsson 1953; Faeroes: Salomonsen 1935, Williamson 1948, Nørrevang 1960; British Isles: Lockley 1934, 1953, Perry 1946; Norway: Collett 1921, Løvenskiold 1947, Myrberget 1959a, 1961, 1962a; Murmansk region east to Novaya Zemlya: Belopol'skii 1957, Uspenski 1958, Kartaschew 1960, Korneyeva 1967, Skokova 1967; 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 Lockley (1934, 1953), Perry (1946), Salomonsen (1950), Belopol'skii (1957), Kozlova (1957), Myrberget (1959b, 1962a, b), Kartaschew (1960), and Bannerman (1963). At Great Island 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 Salomonsen (1944) and Lockley (1953)) do not appear until late May or early June. Nest-site establishment is accomplished by territorial agonistic behavior among males. Courtship and copulation take place at sea close to the island. Single-egg clutches 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 Sep-

tember. Except for the latest breeders, both breeding and nonbreeding puffins depart in late August. The wintering range of Newfoundland puffin populations is unknown, but Tuck (1967) suggests that it is the Grand Banks.

DESCRIPTION OF THE STUDY AREA

Location and seabird fauna

Field work 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 (Fig. 1). The precise location of Great Island is $47^{\circ}11'N$, $52^{\circ}46'W$, approximately 1.5 miles from the coastal settlement of Bauline East. In addition, three trips were made to Funk Island ($49^{\circ}46'N$, $53^{\circ}11'W$) and Small Island ($49^{\circ}35'N$, $53^{\circ}46'W$) in 1969 (Fig. 1).

At least 100,000 pairs of puffins breed on Great Island. Nests are situated above the cliffs; most of them are within 50 m 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 (*Cephus grylle*). Except for the gulls and petrels, there is little overlap in breeding habitats between these species and puffins. Approximately 1,500 pairs of Herring Gulls and 40 pairs of Great Black-backed Gulls nest on Great Island; both populations appear to be increasing (Dr. W. Threlfall, *personal communication*).

Great Island

Topography.—Great Island is approximately 0.85 mile long and 0.46 mile broad at its widest point and runs southeast-northwest along the greater dimension (Fig. 1). The island has a rocky coastline of precipitous cliffs that reach their greatest height along the north-facing shore (Fig. 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 gives 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.—Six major habitat types can be recognized on the basis of the physical characteristics of the terrain and vegetative cover. Conifers and shrubs account for 51% of the surface area, grass-hummocked slope and level 19%, *Rubus*-grass meadow 13%, exposed peat 9%, bare bedrock on the top of the island 6%, and eroded meadow 2% (Fig. 2).

The characteristic physical features of the peripheral area of the island are shown in Fig. 3. The maritime slope (Fig. 3A) is covered mostly by grass hummocks (*Bromus* sp.), but sometimes it has undergone 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*). Contiguous grass level areas (Fig. 3B) are also covered by grass hummocks.

The dominant plant of the meadow region (Fig. 3C), which extends from the grass or peat slope to the trees, is wild red raspberry (*Rubus* sp.), and a thick undergrowth is composed 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- to 4-ft-high reed grass (*Calamagrostis in expansa*), fireweed (*Epilobium angustifolium*), wood fern (*Dryopteris clintoniana*), clintonia (*Clintonia borealis*), and to a lesser extent bunchberry (*Cornus canadensis*).

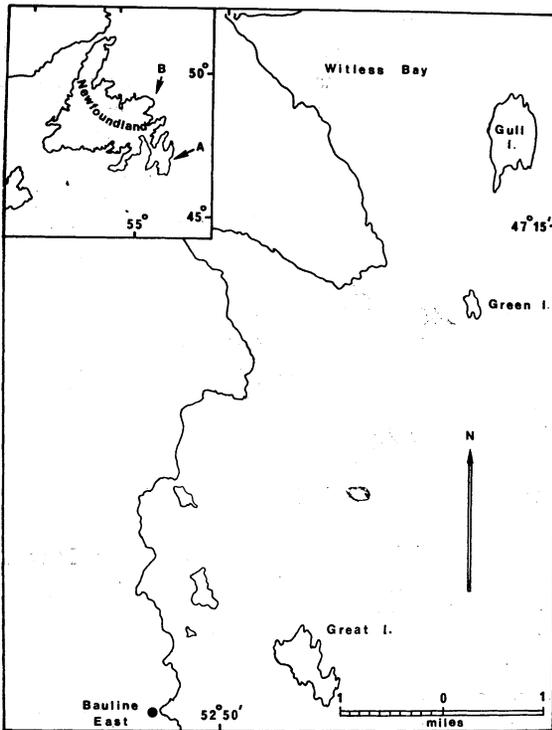


FIG. 1. The Witless Bay islands, Newfoundland. Inset map shows the general location of the Witless Bay islands (A) and Funk and Small Islands (B) off the coast of Newfoundland.

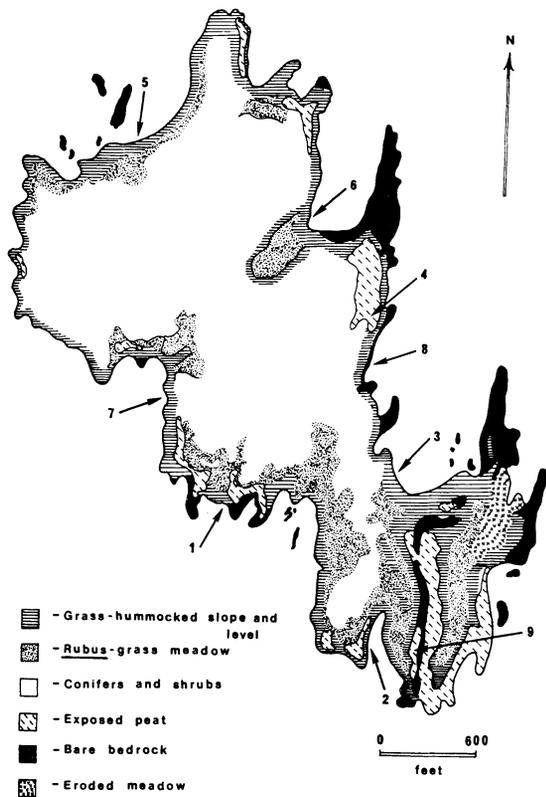


FIG. 2. Sketch map of Great Island, showing principal habitats and location of main study areas: (1) Main Colony, (2-5) nests on slope habitat, (6-9) nests on level habitat. Areas 2, 3, 4, 6, 7, 8, and 9 were studied in 1968; areas 2, 5, 6, 7, and 8 were studied in 1969.

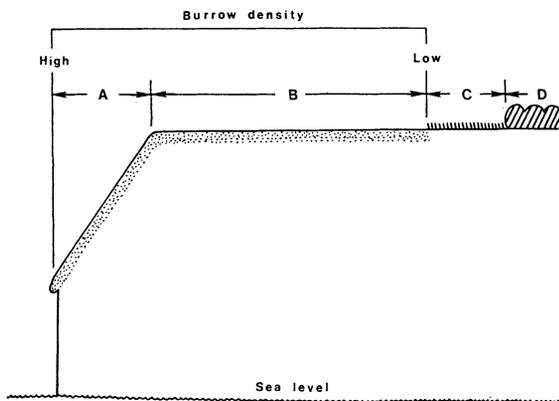


FIG. 3. Comparison of puffin burrow density with habitat on a schematic section through the periphery of Great Island. Habitats: A—maritime grass slope; B—grass level; C—*Rubus*-grass meadow; D—balsam fir and black spruce forest.

sis), goldenrod (*Solidago* spp.), and false Solomons-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 fansy, yarrow (*Achillea millefol-*

ium), 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.

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 north-northeast direction. It is 0.5 mile long, 0.25 mile wide, and approximately 46 ft high at its highest point. At the center of the south end of the island on level ground, 500-1,000 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 ft. 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 (Lucas 1888, Gilliard 1937a, b, Peters and Burleigh 1951, Garrity 1960, Tuck 1960, Russell 1965a, b). The gull population is small (about 15 pairs in 1969) and does not appear to interact with puffins or other species on the island (Tuck 1960:210, and personal observation).

Small Island.—Small Island is the second outermost island of the six that comprise the Wadham Islands group located 10 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 area 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 20-30 ft 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*).

Summer climate

The summer temperature 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. A comparison of the monthly averages and extremes of temperature and precipitation for the months April to September 1967-69 (breeding seasons studied) recorded at the St. John's Airport Weather

Office shows that seasonal patterns of temperature and precipitation differ greatly between years. However, based on the standard normals for 1942–60, the 1969 summer weather most closely approximated the average, whereas 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 were above normal, and the mean temperature for August was the lowest on record.

METHODS AND MATERIALS

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

The measurements of the puffin's breeding biology collected at Great Island during this study separate clearly into two parts: measurements taken at one area of the island, designated the Main Colony, and measurements recorded at various locations around the island (Fig. 2). The analysis of the breeding habitat (nest density and habitat characteristics), attendance (bird census), behavior (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 Fig. 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 is 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 sections with the experimental results.

Main Colony

The total area of this colony was divided into a grid of 6-m squares by one-half-inch polypropylene rope just before egg-laying began in 1968 (Fig. 4). The grid was 60 m long by 36 m 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 the maritime grass slope with the remaining strips on level ground.

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 (Fig. 4) and measuring in each 9-m² subquadrat the following

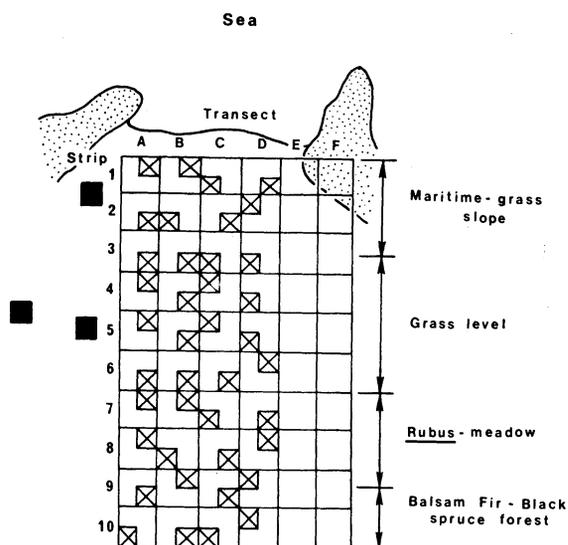


FIG. 4. Grid system (60 m by 36 m) and habitat distribution on the Main Colony. Subdivisions of the quadrats (blocks marked with X) were samples used in the habitat analysis. Shaded squares are permanent observation blinds, and stippled areas at the front of the colony are exposed rock cliffs.

characteristics: puffin burrow number (Y), percentage total vegetative cover (X_1), percentage grass hummock cover (X_2), percentage 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 2 ft long and unconnected to adjoining burrows were used to determine Y . All mean values (X_4 , X_5 , X_6) were obtained from 10 random measurements.³ The measurements were limited to transects A to D because of their vegetative and topographic similarity (a semipermanent 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 correlation is handicapped because 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. More likely 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 regres-

³ Soil depth was determined by plunging a thin, graded iron rod into the soil. The diameter and height of grass hummocks were measured with a metal tape ruler. Angle of slope was measured with a slope gauge at four places within the subquadrat, and then the average of the values obtained was calculated.

sion analysis performed by computer (see Grant 1969).

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

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

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 : $b'_i = b_i(s_i/s_y)$. The value R^2 was then derived from the equation:

$$R^2_{y . 1 \dots k} = r_{y1}b'_1 + r_{y2}b'_2 + \dots + r_{yk}b'_k.$$

Census

Attendance at the colony was recorded by counting the number of birds standing on each quadrat of the grid each day (ca. 1200–1400 hr) through the breeding season in 1968 and 1969 from a permanent blind located above the colony (Fig. 4). These census figures were used to determine variation in attendance at the colony, bird distribution, habitat occupation and utilization, etc.

Behavior

Quantitative observation of behavioral 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) was observed at regular intervals (ca. 4–5 days) through the breeding season in 1969 from two lower permanent blinds (Fig. 4), 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 an observer (myself and field assistant) in each of the two lower blinds (Fig. 4). All watches were conducted in midafternoon (1400–1600 hr) for 60 consecutive minutes and commenced only after at least 20 min had elapsed from time of entering the blind.

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 4-hr 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 6 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.

Collection of adults

The morphological and physiological condition of breeding adults nesting on slope and level habitat was compared early in the breeding season. Birds incubating an egg were collected weekly between May 26 and July 9, 1968, and just after the peak of egg-laying on June 2 and 8, 1969. This time was selected 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.

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 Richdale 1955, 1957, Coulson 1963, Nelson 1966, Serventy 1967, Coulson, Potts, and Horobin 1969, and Fisher 1969 for similar work on other seabirds). Fertile eggs were collected between May 28 and June 3, 1968, and length, breadth, and weight were measured. From these measurements a shape index and volume were derived according to the method described by Coulson (1963).

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 (Fig. 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.

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 Fig. 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. This source of error probably is not significant, however, because no obvious replacement clutches were detected from hatching dates. From late June onwards regular checks were made at 4-day intervals, weather permitting, until the egg disappeared, chick disappeared, or chick fledged. Towards the end of the fledging period chicks were checked at 2-day intervals. This procedure was adopted to reduce nest desertion and avoid causing premature departure of young that has hampered other studies when a daily inspection was used during this period (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 (June 21–30) and late (post-June 30) periods 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 June 17 (Funk) and 18 (Small) in 1969. They were re-examined on July 18 (Funk) and 19 (Small) to determine egg survival, and again on August 29 (Funk) and 30 (Small) for chick survival and fledging.

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 4-day intervals until primary wing length exceeded 120 mm, from which time the chick was measured every 2 days until it fledged. Data used for fledging condition (i.e., body weight and wing length just prior to

fledging) are in most cases those taken from the chick 1 or 2 days before actual fledging (time of deserting the nest); rarely, chick measurements were known only within 4 days of fledging.

Funk Island and Small Island.—All the 166 young still in study nests on the final visit to Funk Island (August 29) and Small Island (August 30) were weighed, their wing lengths were measured, and they were 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.

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

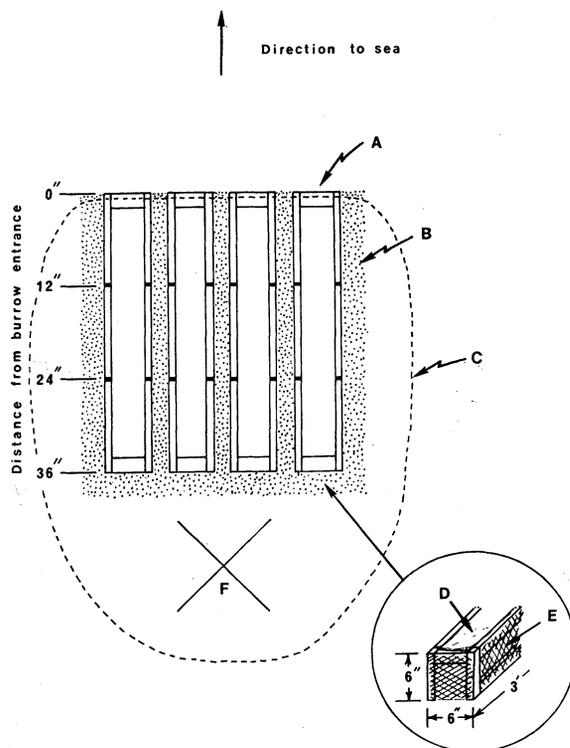


FIG. 5. Design of the artificial burrows, showing: A—open burrow entrance; B—soil; C—perimeter of tent enclosure; D—one-way-view aluminum foil roof; E—wire screening; F—observer's position inside tent. Inset shows end of one artificial burrow with soil removed.

burrow with the chick. Partially eaten loads, recognizable by the chick's swollen gullet, are not included in this analysis.

Chick movements in relation to food supply

The construction and arrangement of artificial burrows used in the chick-activity experiment are shown in Fig. 5. Each burrow consisted of a rectangular wood frame of 2- by 1-inch strapping 3 ft 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 was placed into each of the four experimental burrows. Acclimation was apparently rapid, as the chicks ate fish thrown in to them from the burrow entrance on their first day of captivity. Nevertheless, to ensure adjustment to the new burrow environment and feeding method, the activity measurements were not started until 7 days after capture.

The movements of the four chicks were observed through the burrow roofs from inside the darkened tent enclosure for 3 hr (1400–1700 hr) for 8 consecutive days (August 22–29, 1969). On the first 4 days (control period) the chicks were fed 75–100 g of fish per day, but no food was given to them during the second half (starvation period) of the experiment. Position of the chicks in their separate ar-

TABLE 1. Puffin burrow density and habitat characteristics in 40 quadrats on the Main Colony grid

Quadrat (transect-strip)	Burrow number per 9 m ² (Y)	Total vegetative cover (%) (X ₁)	Grass hummock cover (%) (X ₂)	Other vegetative cover (%) (X ₃)	Mean soil depth (cm) (X ₄)	Mean grass hummock diameter (cm) (X ₅)	Mean grass hummock height (cm) (X ₆)	Grass hummock number (X ₇)	Angle of slope (°) (X ₈)	Distance from cliff edge (m) (X ₉)
A 1	16	45	45	0	39.2	34.3	24.7	27	38	3
2	15	65	65	0	47.0	36.9	16.3	28	36	12
3	10	40	40	0	24.3	32.9	14.1	13	14	18
4	7	20	20	0	30.0	26.6	11.0	17	16	21
5	11	45	40	5	47.6	31.7	13.1	21	6	27
6	7	90	80	10	47.6	27.2	13.3	43	9	36
7	4	100	80	20	45.6	30.2	16.1	39	7	39
8	0	100	15	85	27.8	25.2	19.5	22	8	45
9	0	100	0	100	41.9	28.2	16.7	4	8	54
10	0	100	20	80	36.8	30.2	22.6	12	5	60
B 1	15	40	40	0	34.9	27.9	21.6	24	31	3
2	21	60	60	0	45.2	33.2	22.1	33	37	12
3	12	95	95	0	32.9	26.8	18.2	34	24	18
4	8	70	50	20	26.6	36.4	14.6	16	11	24
5	9	80	80	0	32.7	28.3	11.9	28	10	30
6	6	100	80	20	38.1	25.6	27.0	46	5	36
7	0	100	60	40	31.4	28.3	16.3	36	5	39
8	0	100	70	30	32.7	29.4	22.5	27	2	48
9	0	100	35	65	38.1	22.5	17.4	10	8	51
10	0	100	0	100	43.4			0	3	60
C 1	16	60	60	0	37.1	35.2	25.6	28	35	6
2	25	60	60	0	47.1	31.7	28.6	35	35	12
3	13	85	85	0	34.0	25.8	17.4	31	23	18
4	13	100	90	10	43.6	30.8	13.8	38	12	21
5	11	25	20	5	30.8	30.8	16.4	28	9	27
6	3	100	85	15	34.6	22.7	11.3	39	6	33
7	0	100	30	70	37.7	25.3	15.2	29	8	42
8	0	100	75	25	45.5	27.6	17.4	19	5	48
9	0	100	15	85	51.4	25.0	11.4	9	8	54
10	0	100	0	100	43.5			0	5	60
D 1	18	40	40	0	32.1	28.0	22.7	30	36	6
2	19	40	40	0	35.4	31.2	24.9	33	37	9
3	8	90	90	0	30.2	35.4	15.0	33	11	18
4	12	80	80	0	33.9	31.8	17.9	30	9	24
5	10	80	80	0	40.2	23.6	14.6	33	11	30
6	3	95	75	20	33.5	31.1	15.7	25	7	36
7	0	100	65	35	40.3	27.7	15.6	41	10	42
8	0	100	80	20	40.3	26.7	17.8	25	12	45
9	0	100	50	50	43.1	26.4	19.8	14	13	51
10	0	100	50	50	42.0	29.2	17.9	22	3	57

TABLE 2. Multiple regression analysis^a of puffin nest density (Y) in relation to three significant variables—soil depth (X_4), angle of slope (X_8), and distance from cliff edge (X_9)—in 40 quadrats on the Main Colony

Independent variables	Standard partial regression coefficients (b_i')			Multiple correlation coefficients (R)			Total R	Total $R^2 \times 100$	Multiple linear regression equations
	X_4	X_8	X_9	X_4	X_8	X_9			
X_9	—	—	0.38	—	—	0.8099	0.8099	65.6	$Y = 7.3 - 0.38(X_9 - 31.87)$
X_9, X_4	0.25	—	0.40	0.0054	—	0.8755	0.8809	77.6	$\hat{Y} = 7.3 - 0.40(X_9 - 31.87) + 0.25(X_4 - 80.12)$
X_9, X_4, X_8	0.20	0.11	0.34	0.0044	0.1498	0.7442	0.8984	80.7	$\hat{Y} = 7.3 - 0.34(X_9 - 31.87) + 0.20(X_4 - 80.12) + 0.11(X_8 - 14.45)$

^aSignificant independent variables are entered into the multiple linear regression equation in decreasing order of their b_i' values.

tificial burrows was recorded each minute throughout the daily watches.

Statistical analysis

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

COMPARATIVE BREEDING PERFORMANCE OF PUFFINS AT GREAT ISLAND

Nest and adult distribution

Nest distribution.—The values for the nine independent and one dependent variables, which have been derived from the data collected in the 40 quadrats in the Main Colony grid (see methods), are given in Table 1. The results of a multiple linear regression analysis on these data show that 65.5% 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%. 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 strips 1–6 (transects A–D) of the Main Colony grid on May 5, 1968, was compared with the expected number of birds based on known nest-density figures for the same 24 quadrats (Table 3). It is obvious that the ratio between the absolute values for the number of birds and number of nests

TABLE 3. Comparison of observed and expected frequencies in distribution of adult puffins (based on nest density) over part of the Main Colony (strips 1–6, transects A–D) on May 5, 1968

Strip	Number of nests/36 m ²	Number of birds		X^2 (1 df)
		Observed values	Expected values	
1	65	140	167.0	4.36
2	80	203	205.6	0.03
3	43	230	110.5	129.81
4	40	107	102.8	0.17
5	41	58	105.3	21.30
6	19	2	48.8	45.62
Total	288	740	740.0	201.29 (df = 5)

is meaningless, as the former is the total number of birds present and the latter is the total number of nests for only the four subquadrats surveyed in each strip of the census area (see methods for habitat analysis), which represents only one-quarter of the puffin nesting habitat in each strip. For these reasons, it is the difference between the observed and expected frequencies of birds to nests which is being tested.

A chi-squared test (1×6 contingency table) showed the differences between the observed and expected distributions of birds to be highly significant ($P < 0.001$, $\chi^2 = 201.29$). Adult puffins ap-

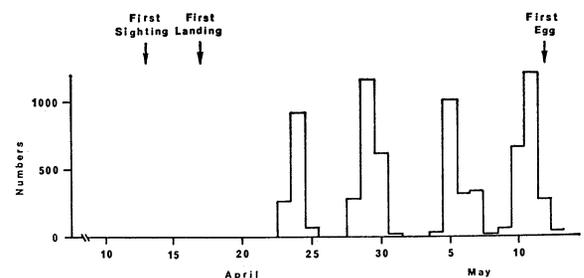


FIG. 6. Attendance at the Main Colony during the prelaying period (April 9–May 12) in 1969.

TABLE 4. Numbers of adult puffins on each strip of the Main Colony grid during the prelaying period (April 9–May 12) in 1969 (on days not shown total attendance was less than 10 birds)

Habitat	Strip	April			April			May				May			
		23	24	25	28	29	30	4	5	6	7	9	10	11	12
Slope	1	64	118(12.9) ^a	28	68	131(11.4)	157	18	166(16.6)	80	112	30	102	143(11.9)	42
	2	105	205(22.5)	36	73	254(21.9)	213	16	260(26.0)	90	113	20	139	260(21.6)	100
Slope and level	3	80	187(20.5)	5	77	292(25.2)	197	—	285(28.0)	67	78	12	178	301(25.0)	88
Level	4	13	167(18.4)	—	42	193(16.6)	27	—	146(14.6)	47	20	—	118	194(16.1)	33
	5	1	164(18.0)	—	24	205(17.6)	7	—	112(11.2)	28	—	—	88	201(16.7)	9
	6	—	63(6.9)	—	5	81(7.0)	1	—	31(3.1)	3	—	—	41	96(8.0)	1
	7	—	6(0.8)	—	—	4(0.3)	—	—	1(0.1)	—	—	—	5	9(0.7)	—
Total attendance		263	910	69	286	1,160	602	34	1,001	310	323	62	671	1,202	273

^aValues in parentheses are percentages of total attendance for each peak day.

TABLE 5. Comparison of body weight (g) and wing length (mm) of breeding puffins nesting on slope and level habitat at Great Island

Date and measurement	Item					
	N	\bar{x}	s	Range	t	P
Males						
May 26–July 9, 1968						
Body weight						
Slope	18	491.6	30.11	432–524	2.56	<0.02
Level	21	468.3	25.06	429–513		
Wing length						
Slope	18	172.4	5.68	166–180	0.88	>0.30
Level	21	173.6	4.65	164–182		
June 2–8, 1969						
Body weight						
Slope	29	497.9	34.35	434–562	3.37	<0.01
Level	23	463.7	30.52	384–530		
Wing length						
Slope	29	173.1	3.60	168–181	0.39	>0.50
Level	23	172.7	4.22	163–181		
Females						
May 26–July 9, 1968						
Body weight						
Slope	29	439.9	31.63	386–511	1.55	>0.10
Level	28	451.4	25.88	402–498		
Wing length						
Slope	29	168.9	3.57	161–176	1.33	>0.10
Level	28	171.0	7.99	163–179		
June 2–8, 1969						
Body weight						
Slope	21	442.9	21.67	407–485	0.79	>0.40
Level	56	438.1	27.77	372–510		
Wing length						
Slope	21	170.2	3.14	167–179	0.49	>0.50
Level	56	170.6	3.58	163–180		

peared more frequently in strip 3 ($P < 0.001$, $\chi^2 = 129.81$) than expected and less frequently in strip 1 ($P < 0.05$, $\chi^2 = 4.36$), strip 5 ($P < 0.001$, $\chi^2 = 21.30$), and strip 6 ($P < 0.001$, $\chi^2 = 45.62$.) 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.

Although this analysis is based on puffin distribu-

tion on only one day just prior to the egg-laying period, numerous unquantified observations indicate that this pattern is the normal one throughout the breeding season.

Prelying 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 (Fig. 6). 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 concentration of 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 (Table 4). The differences in distribution between the first full visit (April 24) and the last one prior to the commencement of egg laying are small and are therefore not analyzed statistically.

Morphology of breeding birds.—Body weight and wing length of breeding adults were measured early in the breeding cycle (Table 5). The average body weight of males from nests on slope habitat was higher than that of birds from nests on level habitat in both years (1968: $P < 0.02$; 1969: $P < 0.01$), although the difference in variation was not significant (1968: $P > 0.10$, $F = 1.31$; 1969: $P > 0.10$, $F = 1.09$). Differences in wing length were not significant. Body weight and wing length of females were similar in the two habitats.

Nest-site tenacity.—Puffins at Great Island displayed a high degree of nest-site tenacity. Data from breeding birds in the Main Colony in 1969, where they had been banded and color coded the previous season (captured brooding an egg or chick), show that birds not only return to the same local area (island and colony), but also nest in the identical habitat situation (Table 6). All color-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 color-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 behavior. The male puffin defended a small area at the burrow entrance against intruders by threat (physical presence, head flicking, billgaping) and physical combat (fighting with beak and claws). Frequency of fighting (number of fights per bird per hour) in the Main Colony changed during the settlement, egg-laying, and incubation periods on both the slope and level areas (Fig. 7). In 1969 fighting was more frequent on slope habitat than level habitat during the

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

Nest habitat	Strip	Number of birds color banded-1968	Number of birds returned to nest site 1969	Percentage return
Slope	2	28	22	78.6
Level	4 and 6	33	25	75.7
Total	2, 4 and 6	61	47	77.0

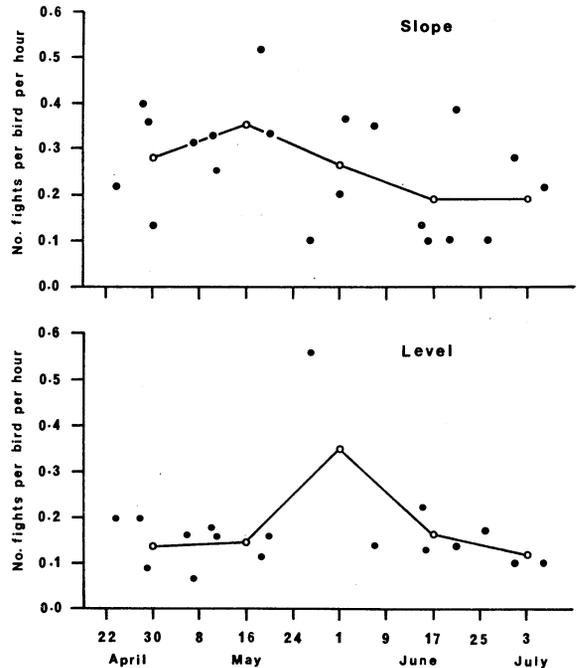


FIG. 7. Frequency of puffin fighting on slope and level habitat on the Main Colony between April and July 1969. Open circles represent 16-day averages.

April 22–May 11 prelaying period ($P < 0.01$, $t = 3.58$, $df = 12$). However, the most intense fighting between the start and peak of egg laying occurred earlier on the slope than level habitat. Numbers of fights tended to be lower over the entire colony during the incubation period, although much fighting was sometimes observed on slope habitat after egg laying had terminated.

Egg-laying period

Morphology of eggs laid on slope and level habitats.—Mean values for the morphological data of fertile eggs removed from nests on slope ($N = 90$ eggs) and level ($N = 60$ eggs) habitats are: length (mm) and breadth (mm): slope = 62.93 by 44.54, level = 62.99 by 44.62; volume (cc): slope = 61.05, level = 61.43; weight (g): slope = 65.51, level = 65.12; and shape index: slope = 70.29, level = 70.89.

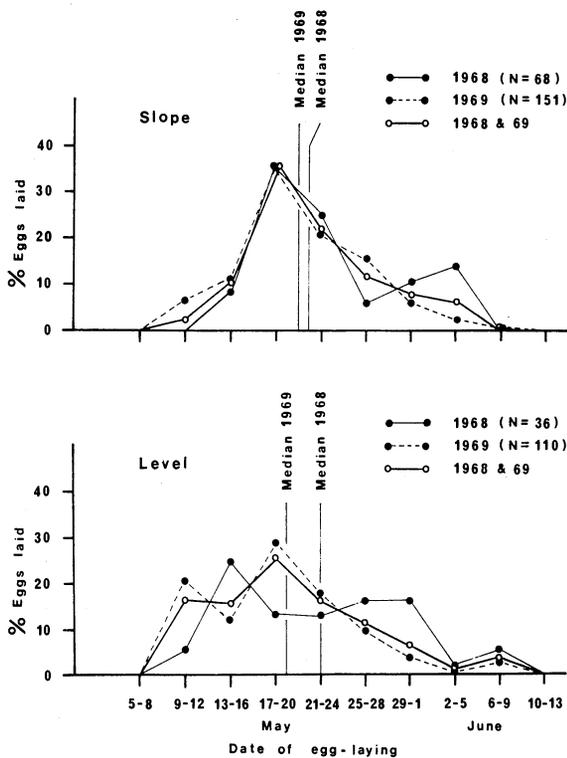


FIG. 8. Frequency distribution of egg laying on slope and level habitat at Great Island.

The differences in egg size and shape between the two groups are small and are not statistically significant.

Time of egg laying on slope and level habitats.—The characteristics of the egg-laying regime of birds on slope and level habitats are shown in Fig. 8. In both groups the median laying dates are very similar; there is no statistically demonstrable 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 is the variation in synchronization and frequency distribution of laying. A chi-squared test (2×8 contingency table) shows that the frequency distribu-

tion pattern (1968 and 1969 data combined) on the two habitats is significantly different ($P < 0.001$, $\chi^2 = 29.39$, $df = 7$). The percentage of eggs laid early (May 9–12) in the egg-laying period by birds on level habitat was higher than the percentage laid by birds on slope habitat ($P < 0.001$, $\chi^2 = 13.00$, $df = 1$). The percentage of eggs laid late (June 6–9) on level habitat was also higher than the percentage laid on slope habitat ($P < 0.02$, $\chi^2 = 6.08$, $df = 1$). 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 (May 9–20) within each habitat are more similar on slope than on level habitat (2×3 contingency table: slope = $P > 0.30$, $\chi^2 = 1.90$, $df = 2$; level = $P < 0.02$, $\chi^2 = 8.84$, $df = 2$). Variation in the second half of the egg-laying period (May 21–June 10) is more difficult to interpret because of the unknown significance of replacement laying and therefore is not analyzed statistically. Thus time of laying is more precise and synchronous from year to year amongst birds on slope habitat.

Breeding success

Hatching success.—Hatching success was significantly higher in nests on slope habitat than level habitat in both years (Table 7). Many eggs disappeared from burrows, and many remained but did not hatch (i.e., “infertile” eggs). Most of the hatching failure can be attributed to disappearance of the eggs. There was no significant difference in egg infertility (slope: $P > 0.30$, $\chi^2 = 0.46$; level: $P > 0.50$, $\chi^2 = 0.35$) or egg disappearance (slope: $P > 0.05$, $\chi^2 = 3.08$; level: $P > 0.10$, $\chi^2 = 2.30$) on either habitat between years. However, the yearly difference in hatching success within the habitats, though not significant (slope: $P > 0.05$, $\chi^2 = 3.76$; level: $P > 0.20$, $\chi^2 = 1.12$), 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: $P < 0.001$, $\chi^2 =$

TABLE 7. Hatching success on slope and level habitat at Great Island

Year	Nest habitat	Number of eggs	Eggs hatched		Infertile eggs		Eggs disappeared	
			Number	Percentage	Number	Percentage	Number	Percentage
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
Total	Slope	290	209	72.0	7	2.5	74	25.5
	Level	262	138	52.6	32	12.3	92	35.1

* $P < 0.05$, $\chi^2 = 4.65$
 ** $P < 0.001$, $\chi^2 = 19.54$

TABLE 8. Fledging success on slope and level habitat at Great Island

Year	Nest habitat	Number of chicks	Chicks fledged		Chicks found dead		Chicks disappeared	
			Number	Percentage	Number	Percentage	Number	Percentage
1968	Slope	58	25 _j *	43.2	2	3.4	31	53.4
	Level	28	6 _j	21.4	5	17.8	17	60.8
1969	Slope	151	101 _j **	66.9	11	7.3	39	25.8
	Level	110	48 _j	43.6	23	21.0	39	35.4

* $P > 0.05$, $\chi^2_c = 2.96$
 ** $P < 0.001$, $\chi^2 = 14.04$

TABLE 9. Mortality of puffin nestlings on slope and level habitats at Great Island

Item	Age (days)							Total
	1-8	9-16	17-24	25-32	33-40	41-48	>48	
1968								
Slope								
Found dead	1	0	0	0	1	0	0	2
Disappeared prematurely	13	6	3	5	2	2	0	31
Total number	14	6	3	5	3	2	0	33
Percentage	42.4	18.2	9.1	15.2	9.1	6.0	0	
Level								
Found dead	4	0	1	0	0	0	0	5
Disappeared prematurely	9	2	4	0	2	0	0	17
Total number	13	2	5	0	2	0	0	22
Percentage	59.1	9.1	22.7	0	9.1	0	0	
1969								
Slope								
Found dead	3	1	0	3	0	1	3	11
Disappeared prematurely	13	10	2	3	3	6	2	39
Total number	16	11	2	6	3	7	5	50
Percentage	32.0	22.0	4.0	12.0	6.0	14.0	10.0	
Level								
Found dead	8	4	2	0	3	1	5	23
Disappeared prematurely	15	4	7	6	3	4	0	39
Total number	23	8	9	6	6	5	5	62
Percentage	37.0	12.9	14.5	9.7	9.7	8.1	8.1	

20.13), although the difference in 1968 does not reach the 5% level of significance ($P > 0.05$, $\chi^2 = 2.84$). Similarly, total egg disappearance was higher on level habitat than slope habitat ($P < 0.02$, $\chi^2 = 6.02$), but the difference in 1968 was not significant ($P > 0.10$, $\chi^2 = 1.91$).

Fledging success.—The survival of chicks to fledging was higher on slope habitat in both years (Table 8). The chi-squared value for the 1968 data falls below the level required for significance when the Yates correction for continuity is applied, perhaps as a consequence of the small sample size. However, the difference in fledging success in 1969 was highly significant.

Fledging success was higher in 1969 than in 1968 on both habitats (slope: $P < 0.01$, $\chi^2 = 9.90$; level: $P < 0.05$, $\chi^2 = 4.62$). The proportion of chicks found dead inside their burrow remained the same for each habitat between years (slope: $P > 0.30$, $\chi^2 = 1.05$; level: $P > 0.70$, $\chi^2 = 0.11$), but was significantly higher on level habitats in both years

(1968: $P < 0.05$, $\chi^2 = 5.24$; 1969: $P < 0.01$, $\chi^2 = 10.42$). Chicks disappeared more frequently in 1968 than in 1969 on both habitats (slope: $P < 0.01$, $\chi^2 = 9.90$; level: $P < 0.05$, $\chi^2 = 4.62$). The proportion of chicks that disappeared was higher on level habitat each year, although the differences were not significant (1968: $P > 0.75$, $\chi^2 = 0.04$; 1969: $P > 0.05$, $\chi^2 = 2.81$).

Most chicks that did not fledge either died or disappeared early in the nestling period on both habitats (Table 9). When annual totals are combined, 39% of all chick mortality occurred in the first 8 days of life and 56% by 16 days.

Fledging success was also strongly related to time of hatching (Table 10). The difference in fledging success totals (1968 and 1969 data combined) between chicks which hatched from eggs early (June 21-30) and late (after June 30) is highly significant. Mean fledging success is still lower ($P < 0.05$) for chicks hatched between July 1 and July 10 than those hatched early, although an exception occurred

TABLE 10. Fledging success in relation to hatching date at Great Island (N = number of chicks hatched; F = number of chicks fledged; %F = percentage of chicks fledged)

Year	Nest habitat	(A) June 21-30			(B) July 1-10			(C) After July 10		
		N	F	%F	N	F	%F	N	F	%F
1968	Slope	29	16	55.1	21	7	33.3	8	2	25.0
	Level	14	4	28.5	13	2	15.4	1	0	0
1969	Slope	82	65	79.2	60	34	56.7	9	2	22.3
	Level	69	30	43.4	34	18	52.9	7	0	0
Total ^a		194	115	59.3	128	61	47.7	25	4	16.0

^aA : C $P < 0.001$ $\chi^2 = 16.72$
 A : B $P < 0.05$ $\chi^2 = 4.20$
 A : (B + C) $P < 0.01$ $\chi^2 = 6.74$
 B : C $P < 0.01$ $\chi^2 = 8.57$

in the 1969 level group. However, success for birds hatched between July 1 and 10 is significantly higher than for those hatched later (after July 10). Therefore, poorest success is achieved by chicks hatched extremely late in the breeding season (after July 10), where the difference from birds hatched early (June 21-30) is greatest ($P < 0.001$). Thus in both years it was found that the earlier a chick hatches, the 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 are not quite as pronounced. More birds which hatched early fledged than those hatched later (after June 30) in both years (1968: $P < 0.05$, $\chi^2 = 4.08$; 1969: $P < 0.05$, $\chi^2 = 4.96$). In 1968 success was always higher in the earlier period when comparing any of the individual groups (e.g., June 21-30 > July 1-10; July 1-10 > after July 10; 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 July 1-10 ($P > 0.20$, $\chi^2 = 1.39$), 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 (after June 30) ($P < 0.05$, $\chi^2 = 4.96$) or just the post-July 10 chicks alone ($P < 0.01$, $\chi^2 = 6.74$). Chicks hatched very late in the season (after July 10) also survived less frequently than those which hatched between July 1 and 10 ($P < 0.01$, $\chi^2 = 10.03$).

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

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 11). During both years breeding success at nests on slope habitat was at

TABLE 11. Breeding success on slope and level habitat at Great Island

Year	Nest habitat	Number of eggs	Number of fledglings	Percentage success
1968	Slope	90	25	27.7
	Level	60	6	10.0
1969	Slope	200	101	50.5
	Level	202	48	23.8

* $P < 0.01$, $\chi^2 = 6.93$
 ** $P < 0.001$, $\chi^2 = 30.79$

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: $P < 0.001$, $\chi^2 = 13.04$; level: $P < 0.05$, $\chi^2 = 5.35$).

Fledging condition

Body weight at fledging.—The mean body weight of fledglings on slope habitat was significantly higher than that of fledglings on level habitat in both years (Table 12). Variation between years was small, particularly on slope habitat.

Table 13 shows the relationship between body weight and date of hatching for the 1969 fledglings; the 1968 data have not been analyzed because the sample was too small. Mean fledging weight was highest for chicks that hatched early (June 21-30) in both nesting habitats, although the difference on level habitat is not statistically significant ($P > 0.05$). Amongst chicks hatched early (June 21-30), those on slope habitat were significantly heavier than those on level habitat. Fledglings that hatched late (July 1-10) in nests on slope habitat weighed more than those on level habitat, but the difference is not significant, possibly because of the small sample size of fledglings on level habitat.

Aside from difference in means, the standard

TABLE 12. Comparison of body weight and wing length at fledging of young reared on slope and level habitat at Great Island

Year	Nest habitat	Number of nests	Body weight (g)			Wing length (mm)		
			\bar{x}	<i>s</i>	Range	\bar{x}	<i>s</i>	Range
1968	Slope	25	261.4*	32.27	173-305	143.6*	7.98	129-153
	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	127-154
	Level	47	248.2	47.00	137-330	140.6	6.56	130-154

*Body weight: $P > 0.30$, $t = 0.91$; Wing length: $P > 0.50$, $t = 0.01$ **Body weight: $P < 0.001$, $t = 5.66$; Wing length: $P > 0.50$, $t = 0.12$

TABLE 13. Body weight (g) at fledging of young at Great Island in relation to hatching date in 1969

Nest habitat	(E) Early hatching: June 21-30				(L) Late hatching: July 1-10			
	<i>N</i>	\bar{x}	<i>s</i>	Range	<i>N</i>	\bar{x}	<i>s</i>	Range
Slope (S)	65	268.6	31.72	183-323	34	252.9	39.84	159-311
Level (L)	30	251.3	45.72	137-330	17	242.9	35.46	161-302

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 : $P > 0.20$, $t = 0.86$

TABLE 14. Comparison of age at fledging of young reared on slope and level habitat at Great Island

Year	Nest habitat	Number of nests	Fledging age (days)		
			\bar{x}	<i>s</i>	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 - $P > 0.20$, $t = 1.07$

deviations (Table 12) indicate that birds on slope habitat are less variable in body weight at fledging than those on level habitat in both 1968 and 1969, although only the difference in variation in 1969 was statistically significant (1968: $P > 0.05$, $F = 1.31$; 1969: $P < 0.01$, $F = 1.90$).

Wing length at fledging.—Differences in wing length at departure between fledglings on slope and level habitat were small (Table 12) and not statistically significant in either year. 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 within each year, but differed between years (Table 14). 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,

perhaps because of the relatively small sample size for 1968. Fledging age was 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 15 shows the importance of hatching data in relation to the length of the fledging period for young on slope and level habitat in 1969 (1968 data are not analyzed because the sample was too small). On slope habitat, chicks that hatched early in the season (June 21-30) had a shorter mean fledging period ($P < 0.001$) than chicks hatched late (July 1-10). The mean difference between chicks hatched early and late in level nests was not significant. Furthermore, the mean fledging age of birds hatched early on slope habitat was less than those hatched early on level habitat ($P < 0.05$); the opposite occurred in chicks hatched late—those on level habitat fledged at a younger age ($P < 0.02$).

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

Food for the chick

Meal size.—The average meal size delivered to nestlings on slope and level habitat in 1968 and

TABLE 15. Fledging age (days) of young at Great Island in relation to hatching date in 1969

Nest habitat	(E) Early hatching: June 21-30				(L) Late hatching: July 1-10			
	N	\bar{x}	s	Range	N	\bar{x}	s	Range
Slope (S)	65	49.9	6.01	40-71	34	56.8	8.92	39-73
Level (L)	30	52.8	7.46	43-74	18	51.1	7.05	44-66

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 : $P < 0.02, t = 2.46$

TABLE 16. Meal size (g) of puffin nestlings at Great Island

Year	Slope				Level			
	N	\bar{x}	s	Range	N	\bar{x}	s	Range
1968	30	14.2	5.47	2-25	19	11.9	5.11	1-20
1969	125	12.0	5.12	3-33	75	12.9	6.16	2-28
Total	155	12.4*	5.33	2-23	94	12.7*	5.98	1-28

* $P > 0.50, t = 0.35$

1969 varied from 11.9 to 14.2 g (Table 16). The meal size represents the total amount of food 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. Variation in meal size was also similar ($P > 0.05, F = 1.25$).

Feeding rate.—Feeding rates on the Main Colony were measured by observing 17 nests on slope habitat and 15 nests on level habitat during the entire daylight period (0530 to 2100 hr) for 3 consecutive days (July 31 to August 2, 1969). Each nest contained a chick at approximately the same stage of development. Nestlings on slope habitat received, on the average, more meals, and hence more food, each day than chicks on level habitat ($P < 0.01$) (Table 17).

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: ca. 9-10 days), is given in Table 18. 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 10 days after twinning (Fig. 9).

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

Nest habitat	Number of nestlings	Number of 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 18. Fledging success of twins at 10 nests on slope habitat at Great Island in 1968 (F = fledged; FD = found dead; DP = disappeared prematurely)

Twin	Nest number									
	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
Number of young fledged	1	0	0	0	0	1	1	1	1	0

Single-parented chick experiment.—None of the 12 chicks (starting age: ca. 9-35 days) on slope habitat being fed by only a single parent, after one parent (either sex) was collected (day 0 = ca. July 20, 1968), fledged (Table 19). They either died in their burrow or disappeared prematurely.

Growth curves of four of the experimental chicks and curves of similar-aged chicks being reared by two adults during the identical time period on the same habitat are shown in Fig. 10. Two of the single-parented chicks decreased in weight until they were found dead, and two disappeared from their bur-

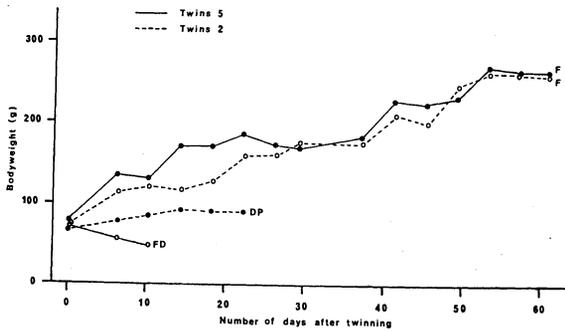


FIG. 9. Growth curves of body weight for two sets of twinned chicks on slope habitat at Great Island in 1968. Solid circles = introduced chick; open circles = original chick. F = fledged; FD = found dead; DP = disappeared prematurely.

TABLE 19. Fledging success of single-parented chicks at 12 nests on slope habitat at Great Island in 1968

Starting body weight (g)	N	Number of chicks found dead	Number of chicks disappeared prematurely	Number of chicks fledged
<75	2	0	2	0
176-200	4	1	3	0
201-225	6	3	3	0
Total	12	4	8	0
Percentage	100.0	33.3	66.7	0.0

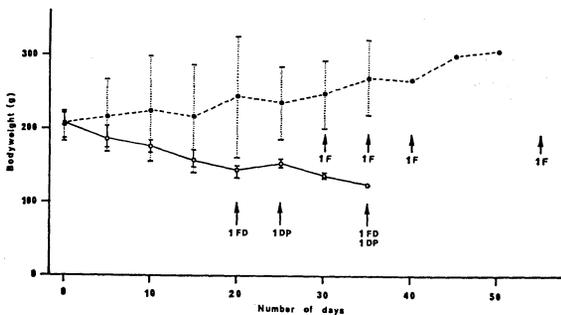


FIG. 10. Mean growth curves of body weight of chicks ($N=4$) being reared by one parent (o—o) and examples of chicks ($N=4$) being reared by two parents (●-●) from nests on slope habitat during the same time period (day 0 = ca. July 20) at Great Island in 1968. Vertical bars represent range of body weights for that number of days. Last "control" chick fledged between day 50 and 55. F = fledged; FD = found dead; DP = disappeared prematurely.

row at a premature stage of development. All four "control" chicks fledged in good condition, although two experienced declines in body weight early in the experiment.

Summary of puffin breeding performance at Great Island

Puffins nest at a higher density on slope habitat, close to the cliff, than level habitat. The distribution

pattern of adults standing on the colony does not match the nest distribution; too few birds occur 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, body weights of males are greater 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 varies within a habitat between years.

Fledging condition of chicks varies according to the habitat and time period in which they are raised. On the 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. Wing length 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 that hatch from eggs early in the season (June 21-30) fledge at a younger age than birds that hatch later (after June 30) on slope habitat but not level habitat; birds that hatch early on slope habitat fledge quicker than those that hatch early on level habitat, whereas birds that hatch late on slope habitat fledge slower than those that 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.

GULL-PUFFIN INTERACTIONS

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 it can be secured by a gull) as an occasional consequence. To determine the frequency of egg displacement on the two habitats we walked 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

TABLE 20. Egg displacement by departure of incubating puffins at Great Island

Nest habitat	Number of departures	Egg position			
		in nest chamber		in burrow tunnel	
		N	%	N	%
Slope	{117	101	86.3	16	13.7
Level	{100	83	83.0	17	17.0

* $P = 0.50$, $\chi^2 = 0.46$

given in Table 20. The frequency of egg displacement towards the burrow entrance was similar in the two habitats.

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 (May 19–June 26, 1969) in observation periods of 60 minutes' duration. During 1,200 observation minutes (600 min/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.

Chick stage

Robbery by gulls (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; data from the front part of strip 3 on slope habitat are not included. The level

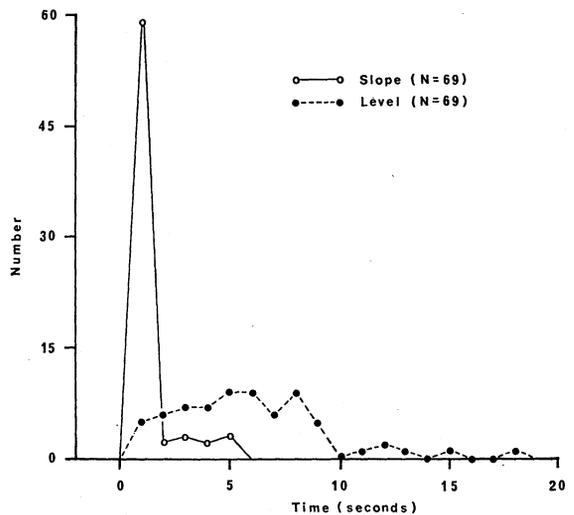


FIG. 11. Distribution of time interval required to become airborne by adult puffins released on slope and level habitat of the Main Colony.

region was subdivided to compare differences within this larger area.

There is a strong association between the incidence of gull robbery and position of the nest site within the colony (Table 21). The proportion of meals lost to gulls by parents with young on level habitat (strips 3–6) was significantly higher 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 ($P < 0.05$). Also the frequency of attack on arriving meal-carrying puffins is markedly higher on the level parts of the colony ($P < 0.001$, $\chi^2 = 66.09$, $df = 1$).

Adult mobility and characteristics of the nesting habitat.—The influence of habitat on the mobility of adult puffins was measured in mid-August 1969

TABLE 21. Delivery success of meal-carrying puffins on different parts of the Main Colony (strips 1–2, slope; strips 3–6, level) in 1968 and 1969

Item	Strips			
	1–2 (A)	3 ^a –4 (B)	5–6 (C)	3–6 (B + C)
Number of landings	601	412	363	775
Number of landings attacked by gulls	113 (18.8) ^b	141 (34.2)	162 (44.6)	303 (39.0)
Number of landings robbed by gulls	27 (4.4)	46 (11.1)	59 (16.2)	105 (13.5)

Number of landings robbed by gulls—number of landings:

- A:B $P < 0.001$, $\chi^2 = 16.27$
- A:C $P < 0.001$, $\chi^2 = 38.52$
- A:(B + C) $P < 0.001$, $\chi^2 = 32.00$
- B:C $P < 0.05$, $\chi^2 = 4.26$

^aData from the front part of strip 3 on slope habitat are not included.
^bFigures in parentheses are percentages of total number of landings.

TABLE 22. Chick movement in artificial burrows in relation to food supply

Feeding schedule	Total observation time (minutes)	Distance from burrow entrance				Nest chamber	
		Burrow tunnel		13-24 inches		25-36 inches	
		0-12 inches					
		Number of minutes	%	Number of minutes	%	Number of minutes	%
Regular feedings (75-100 g/day)	2,880	14	(0.5)	52	(1.8)	2814	(97.7)
No feedings	2,567*	70	(2.7)	66	(2.6)	2431	(94.7)

* $P < 0.001$, $X^2 = 16.74$

*Reduced observation time in the "No feedings" period was caused by gull predation of one chick before the completion of the experiment.

by releasing captive birds at various locations on the Main Colony and recording with a stop watch the time interval from release to flight. The time required to become airborne is strikingly shorter for birds released on slope habitat (strips 1-2) (Fig. 11). 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 ($P < 0.001$, $\chi^2 = 84.96$, $df = 1$).

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 22. Chicks spent most of the time inside the nest chamber under both feeding conditions (regular feeding = 97.7%; no feedings = 94.7%). However, of the time spent in the burrow tunnel, the chicks occurred more frequently in the section closest to the burrow entrance (0-12 inches) when not fed than when fed ($P < 0.001$). 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 3 days was seized by a Herring Gull fledgling, which flew off with it and presumably killed it.

Egg survival, breeding success, and fledging condition with (Great Island) and without (Funk and Small Islands) gull interference

Egg survival.—The survival of eggs at Funk Island and Small Island, where there was no gull in-

terference, was significantly higher for a period of 33 days when compared with either the combined slope and level Great Island data or the slope data alone (Table 23).

Breeding success.—The estimated number of nests from which fledglings were produced was very high (90.5%) on Funk and Small Islands (Table 24). On Great Island only 37.1% of 402 nests produced fledglings. It is apparent that breeding success was significantly higher at Funk Island and Small Islands where gulls were scarce.

Fledging condition.—The average condition of young just before fledging in both breeding environments is presented in Table 25. Chicks at Funk and Small Islands were much heavier close to fledging than those at Great Island ($P < 0.001$), although wing lengths were similar. Body weight at fledging was less variable at Funk and Small Islands than at Great Island ($P < 0.01$, $F = 3.94$), but variation in wing length did not differ significantly ($P > 0.05$, $F = 1.14$). Perhaps the most striking fact is that mean body weight at Funk and Small Islands was higher than the maximum recorded for any single chick at Great Island. Altogether, young close to fledging displayed a higher body weight at areas without gull interference.

DISCUSSION

General conclusions

At Great Island, puffins nest above the cliffs at 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 Svårdson (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 dis-

TABLE 23. Puffin egg survival at colonies with (Great Island) and without (Funk and Small Islands) gull interference in 1969 (Great Island: June 5–July 9; Funk and Small Islands: June 17–July 19)

Colony	Habitat	Number of nests with egg at start	Nest with egg or chick at end		Nests empty at end	
			N	%	N	%
Funk Island	Level	{106	98	92.4	8	7.6
Small Island	Level	{147	144	98.0	3	2.0
Great Island	Slope	{200	156	78.0	44	22.0
	Level	{202	136	67.4	66	32.6
Funk and Small Islands	Level	{253	242	95.7	11	4.3
Great Island	Slope and level	{402	292	72.7	110	27.3

* $P < 0.001$, $\chi^2 = 54.61$ ** $P < 0.001$, $\chi^2 = 32.62$

TABLE 24. Breeding success at puffin colonies with (Great Island) and without (Funk and Small Islands) gull interference in 1969

Colony	Number of eggs	Number of fledglings	Percentage success
Funk Island	106	92	86.8
Small Island	147	137	93.2
Funk and Small Islands	{253	229	90.5
Great Island	{402	149	37.1

* $P < 0.001$, $\chi^2 = 181.75$

placement 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 that 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 Salomonsen 1944, Williamson 1948, Lockley 1953) prevents this hypothesis from being demonstrated or refuted, but three pieces of evidence favor refutation. First, wing length, 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., Richdale 1955, 1957, Coulson 1963, Nelson 1966, Serventy 1967, Coulson et al. 1969). 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 body weight 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 among 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. This apparent greater degree of synchronization cannot be attributed to time of arrival, since this was approximately the same in the two habitats, but it might be related to the greater density on slope habitat (Darling 1938, Coulson and White 1960).

From this point in the breeding cycle onwards, marked differences occurred 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 it was carried away and given to their young immediately.

TABLE 25. Comparison of fledging condition at colonies with (Great Island) and without (Funk and Small Islands) gull interference in 1969

Colony	Number of nests	Body weight (g)			Wing length (mm)		
		\bar{x}	<i>s</i>	Range	\bar{x}	<i>s</i>	Range
Great Island ^a	101	261.8*	35.87	159-323	140.5**	6.21	127-153
Funk and Small Islands	91	351.3	24.24	285-425	141.5	6.63	129-153

* $P < 0.001$, $t = 19.94$ ** $P > 0.50$, $t = 0.24$ ^aBirds on slope habitat only.

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 behavior, 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 among the birds themselves. If panic flights are a consequence of the nervousness caused by the nesting area (Tinbergen 1931, Cullen and Ashmole 1963), 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. 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 χ^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 of their time near the burrow entrance when starved than when fed regularly. Thus it is possible that chicks on level habitat spend 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, whereas 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, intermittent brooding prior to the establishment of thermoregulation (ca. 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 (Templeman 1948, Pitt 1958).

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 3 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 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 the 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 body weights 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 body weights 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, show that in both years and in both habitats the chicks that hatched from eggs early in the season survived better and fledged at a higher body weight than did those that hatched late. Since the energetic requirements of chicks of a given body weight are not likely to vary appreciably as the season progresses, this strongly suggests that the ease with which the adults could provision 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 (Lack 1954, 1966, 1968, Ashmole 1963, Harris 1966, Nelson 1966, Perrins 1966, Ashmole and Tovar S. 1968). What can be called the "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 behavior 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 kleptoparasitism or indirectly owing to the large amount of time spent avoiding gulls while en route to the burrow.

However, before the biological significance 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 young). There is some evidence which indirectly suggests that food supply is an important determinant of prefledging 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 sufficient 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.

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 Islands 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 (Templeman 1948, Pitt 1958). From topographic characteristics, breeding success at both these islands might be expected 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 Islands 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 Islands where they do not. The distance between islands prevented the dates of the study period from coinciding exactly (Great Island: June 5–July 9, 1969; Funk and Small Islands: June 17–July 19, 1969), but the length of the period in which the nest groups were exposed was virtually identical (Great Island: 35 days; Funk and Small Islands: 33 days), making the comparison almost absolute.

Breeding success was significantly lower on Great Island than at Funk and Small Islands. The values

calculated for Funk and Small Islands were partly estimated, however, as some chicks had apparently already fledged prior to the last inspection, and chicks still present were assumed to survive to fledging. Nevertheless, these sources of error are probably minor for the following reasons: (1) all empty nests which were classified as successful displayed obvious signs of lengthy chick occupation (e.g., heavy defecation stains, etc.) and on Great Island extremely few chicks died after this stage had been reached; and (2) 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 Islands were strikingly heavier than Great Island chicks at the same stage of development, although wing lengths were similar. In fact, the mean body weight of Funk Island and Small Island chicks close to departure was higher than the maximum weight reached by any single chick examined during 3 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 1–4 days. This suggests that in the absence of gull interference chicks can attain body weights 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 body weight (ca. 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*, Salomonsen 1944, Kozlova 1957, Myrberget 1963) and interference from avian predators (gulls, jaegers, crows, ravens) is apparently insignificant at both Lovunden (Myrberget 1962a) and the Ainov Islands (Skokova 1967).

Weather conditions seem also to affect breeding success. In the "normal" summer (based on standard normals for temperature and precipitation) of 1969, 50.5% of nests on slope habitat and 23.8% on level habitat fledged young, whereas in the extremely wet and cold summer of 1968, only 27.7% of nests on slope and 10.0% 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 body weight 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 (1969) uses to explain the long and flexible fledging period of Audubon's Shearwater (*Puffinus l'herminieri*). 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, it can alter 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). Second, bad weather can disrupt 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 inclement 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. 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; 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 of 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 (Lack 1966, 1968, Harris 1969, 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.

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 (Lack 1933, 1937, Lack and Venables 1939, Klopfer 1962, Klop-

fer and Hailman 1965). As numbers increase, birds are forced by intraspecific social pressure into other areas of the slope habitat until it is full, the upper limit presumably being set by a fixed minimum amount of space (volume) required to excavate a burrow or behavioral characteristics associated with burrow defense, or both. Further increases result in the use of contiguous level habitat until this is also full. Once both habitats are occupied the size of the breeding population stabilizes, and any further increase in adult numbers results in the formation of a surplus stock, ready to fill any vacancies in the breeding population (e.g., Svårdson 1949, Coulson and White 1956, Wynne-Edwards 1962, Coulson 1968).

The simplest way in which overall population size 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. 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 birds 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 a greater mortality among slope-reared birds after fledging than among level-reared birds, or second, by a movement of slope-reared birds into level habitat to breed.

No direct evidence is at hand to suggest that a differential death rate exists among adults, either before first breeding, after first breeding, or in both periods. However, if a difference does exist, it is likely that mortality would be greatest among birds which are reared or breed on *level* habitat, not *slope* habitat, in view of: (1) the body weight of birds close to fledging (if condition at fledging is critical to the birds' ability to acquire quickly enough the necessary skills of feeding in early independent life (Nelson 1966, Lack 1968:246, Orians 1969)); (2) the body weight soon after the time of arrival at the colony in spring (if body weight is indicative of past success in feeding and storing food); and (3) the energy demands of reproduction (apparently not equal in the two habitats). Therefore, since the greater reproductive output of birds that breed on slope habitat is not compensated by greater mortality among those that were reared and those that 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 breed-

ing 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: (1) if the probability of breeding successfully in level habitat is distinctly higher than zero; (2) if these individuals lack morphological or behavioral traits, or both, necessary to enable them to establish themselves on slope habitat, and are unlikely to obtain the traits in the future; and (3) if all slope habitat is "full" when these birds are ready to breed for the first time (see Coulson (1968) and 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). 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, if dominance increases with age, it may be advantageous for a bird to defer first breeding, when the chance of obtaining a slope site will be high, especially since 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 lower quality level habitat, rather than delaying first breeding until a nest site becomes available on the higher 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 regardless of the actual numbers of either). Therefore, since it is likely that production of young in level habitat is not sufficient to balance the mortality of the birds breeding there, the existence and equilibrium 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. The stability of numbers of individuals constituting the breeding population can be upset, however, by either an increase or decrease in population size. Population increase due to factors favoring nesting success would lead to greater nesting on level habitat, whereas population decrease due to gull increase (see Amadon 1958 and 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.

Natural selection

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 favorable site (see Patterson 1965, Coulson 1968, 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 favor those birds that (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 predispose them to successful establishment on slope habitat are those pertaining to the aggressive behavior exhibited in the context of securing and defending a nest site (Collias 1944, Svårdson 1949, Tinbergen 1957). In addition, body size appears to be important (Miller 1967, 1969). Thus it is to be expected that selection favors 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 the fact that birds breeding

on slope habitat were larger, as measured by body weight, than those on level habitat during the spring settlement period is compatible with this hypothesis. Furthermore, body weight 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.

Given the differences in habitat quality (measured by mean breeding success), a hypothetical 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 kleptoparasitism), and is shown in Fig. 12. Distance from 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 three assumptions: (1) all other environmental factors (e.g., topography, food availability, etc.) are the same at the colonies being compared, (2) both populations are stable (i.e., at equilibrium), and (3) nest sites are limiting breeding population size.

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 sim-

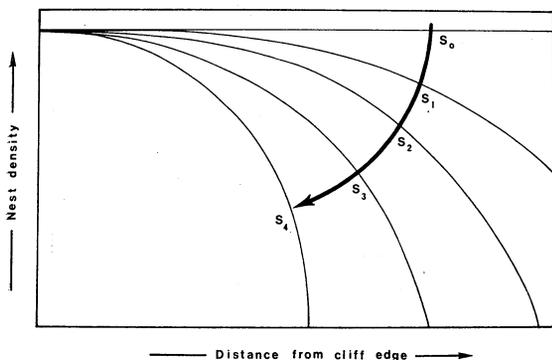


FIG. 12. A hypothetical model of nest density of puffins in relation to a topographic variable under conditions of different levels of interferences from gulls ($S_0 \rightarrow S_4$). The arrow shows the direction of selection, which is mediated by the effects of gulls upon breeding performance of the puffins.

ilar throughout the nesting space, with the upper limit of population size being set by the abundance of nest sites (Fig. 12: S_0).

In the *presence* of gull interference selection strongly favors 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 predation of adults by gulls (Aspden 1928, Lockley 1934, 1953, Coward 1936, Harris 1965), although this was not observed at Great Island. 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 (Fig. 12: $S_0 \rightarrow S_4$).

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) Differences in mean body weight and variation of breeding males in spring along the habitat gradient should be less at colonies where gull interference is absent.

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 body weight and lower variation than those nesting away from the cliff (Levins 1962, 1963, 1964; Van Valen 1965). The difference in mean body weight between breeders on slope and level habitat was significant at Great Island, but variation of body weights was similar, possibly due to the small sample size or the relatively small amount of level habitat being used by puffins for nesting, or both. 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 nonbreeding adults is usually attributed to the lack of nest sites at the colony (Rowan 1952, 1965, Huntington 1963, Coulson 1968). 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 nonbreeders, 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 puffin, such as stercorariids. 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.

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