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Abstract. Common Puffins (Fratercula arctica L.) in Newfoundland showed differences in breeding success, bodyweight at fledging, and utilisation of nesting habitat, associated with interference by gulls at the colony. Breeding success and mean fledging weights were highest at colonies without gulls. In the presence of gull interference breeding success and bodyweight at fledging were significantly higher at nests on maritime slopes close to the cliff edge, where the angle of slope is steep, than inland on adjacent level ground. These differences were due to differential exposure of eggs and chicks to gull predation, and of parents to robbing by gulls when taking food to chicks. This suggests that gull interference may be an important determinant of productivity and habitat utilisation in puffins and other colonial birds. Recommendations for future research on gull management and the effective utilisation of seabird sanctuaries are given.

Effect of gulls on breeding performance and nest distribution in Common Puffins

Disturbance by gulls of colonial birds during the breeding season has been often observed (1), but our knowledge of the selective pressures involved is meagre. Analysis of data from Common Puffin (Fratercula arctica L.) colonies with and without gull interference has demonstrated how gulls can affect breeding success (i.e.,% of eggs laid which produced fledged young) and dispersion of puffins (2).

Preliminary observations of puffin colonies at Great Island, Witless Bay, Newfoundland, during the summer of 1967, showed that puffin nest abundance varied and that interference by Great Black-backed Gulls (Larus marinus L.) and Herring Gulls (Larus argentatus Pont.) occurred during both the incubating and chick-rearing stages of the puffin's breeding cycle; gulls ate puffin eggs and chicks, and robbed parents taking food to chicks (i.e., cleptoparasitism or piracy). Later, a multiple regression analysis showed that puffin nest density was negatively correlated with distance from the cliff edge, and positively correlated with angle of slope (2). This suggested that close to the cliff edge, where the angle of slope is steep, breeding success is significantly higher than on adjacent level ground due to differential exposure of eggs and chicks to gull predation, and of parents to robbing by gulls when taking food to chicks. Thus, during the breeding season, natural selection would act more strongly against birds nesting on level habitat away from the cliff edge than against those nesting close to the cliff edge (the existence of a point inland from the cliff edge at which the probability of fledging young approaches or becomes zero can be assumed).

To test this hypothesis, the breeding history of some 600 nests in low-density and high-density areas was collected during 1968 and 1969 at Great Island; breeding performance was then associated with characteristics of the nest-site. Because nest abundance was found to be greatest on maritime sloping ground ($>30^{\circ}$) and least on level ground ($<15^{\circ}$), slope and level ground were considered as the two habitats for the purpose of studying breeding success.

In spring, both habitats were occupied simultaneously and nest-site tenacity was equally strong in them, as no birds changed position within the colony between years. During settlement (prior to egg-laying), the frequency of fighting was higher and the peak reached earlier on slope habitat, but laying dates of the single-egg clutch were similar. Males were heavier on slope than level habitat, just after peak egg-laying, although females were similar on the two habitats, and there was no significant difference between winglength of the males. Thus, males breeding on level habitat appear to be of a similar structural size to those occupying nests on maritime slopes, but differ in physiological condition, (e.g., fat deposits (3)), at time of arrival at the colony in spring, which may be indicative of past success in feeding and storing food (2).

Comparison of some aspects of the breeding performance of puffins in the two habitats show marked differences (Table 1). Hatching success (i.e., % of eggs laid which hatched) and fledging success (i.e., % of eggs hatched which produced fledged young) were higher on slope habitat, due mainly to a lower incidence of egg disappearance during incubation and disappearance of young before fledging. The only known reason for this mortality was gull predation, many examples of which were observed during the study. Slope-reared young were not only more successfully reared, but were also heavier just prior to fledging (c.2-4 days) than birds reared on level habitat, although winglengths and fledging periods were similar. Since the microclimate and length of residence in the burrow are similar, the difference in bodyweights of fledglings must be attributed to differences in food supply.

Experiments and observations were made to determine causes of the differential egg loss, chick loss before fledging, and condition just prior to fledging, in the two habitats (Table 2). It was found that the frequency of eggs displaced from the nest chamber towards the burrow entrance was the same in the two habitats (caused by rapid departure of incubating birds responding to surface disturbance, e.g., gull cries), but that the frequency of panic-flights (i.e., 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.

Just as the disappearance of the egg from the nest was attributed to gull predation, so was most pre-fledging chick mortality. Experimental chicks (captive chicks in artificial burrows) spent more time outside the nest chamber in the burrow tunnel (0-24" from burrow entrance) and more time in the section closest to the burrow entrance (0-12") when starved than when fed regularly (2). Thus it is possible that chicks on level habitat spent more time near the burrow entrance, where exposure to gull predation is highest, than chicks on slope habitat, because of a poorer food supply.

If a slower rate of provisioning chicks with food on level habitat is responsible for the differences 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 delivery of food 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 Müller) is similar over vast areas of the east coast of Newfoundland (4). 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 (i.e., 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 (Table 2). The rates of feeding are based upon observations on only three days and so must be accepted as no more than an indication that throughout the fledging period chicks are provisioned at a faster rate on slope than on level habitat. Table 2 also shows that parents nesting on level habitat were both attacked and robbed more frequently than those on slope habitats.

The difference in vulnerability to gull attack appears to be related to the greater exposure of the level nesting birds as they fly over the slope to the level area of the colony, to their greater difficulty in landing precisely at their burrow entrance because of the angle of the ground, which influences the risk of being seized by an attacking gull, and to their inability to lift off level ground to escape an attack (they must run back to the crest of the slope in order to fly off) (2). 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 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 (flight speed and direction to burrow, position of gulls) to ensure a swift entry into the burrow entrance. Therefore, on average, more time and energy is probably expended by parents in reaching a nest-site on level habitat, one obvious consequence of which is a reduction in time for other activities (e.g., feeding, chick provisioning, resting, etc.). Thus the slower rate of food provisioning on level habitat appears to be due to gull interference, either directly by cleptoparasitism, or indirectly owing to the large amount of time spent avoiding gulls while en route to the burrow.

If this conclusion is correct, it is to be expected that on islands with no gull interference but where the food supply per bird is the same as that on Great Island, breeding performance would be distinctly higher. This expectation was tested by examining breeding performance of puffins on Funk and Small Islands, two colonies also situated on the east coast of Newfoundland. 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 (4). Since nesting was confined to level habitat on both these islands one might expect breeding success 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 (Table 3). In addition to the fact that breeding success is lower among birds breeding in the presence of gull interference, a further decrease in their productivity might also occur if survival after fledging is related to bodyweight at time of fledging, as has been found in other birds (5).

These results are of considerable importance to the ecology of colonial birds. The conclusion that selective pressure due to the effects of gulls (predation and cleptoparasitism) limits the nesting space containing suitable nest-sites (i.e., those where the probability of breeding successfully is higher than zero), and alters the outcome of any breeding attempt by puffins clearly underlines the need for more investigations to evaluate the ultimate importance of this kind of interspecific relationship, especially since continued increase in gull populations (6) is likely to lead to a decreased amount of nesting, and certainly breeding success (7), by puffins. Moreover, while these findings implicate gulls only, they may still be expected to occur where other species are cleptoparasitic on puffins (8) or other food-hosts.

Proposal for Research on Gull Management

Much emphasis has been placed on chemical poisoning (pesticides), oil pollution, and climatic changes to explain the observed decline in many seabird populations, but little attention has been drawn to the possible adverse effects of successful opportunistic species which have "exploded" in numbers as a consequence of man's pollution of the environment. I have tried to show in this report how deleterious the gulls are to breeding populations of puffins and the threat they pose to all colonial species.

The northeast Herring Gull populations have increased by a factor of 15-30 in this century (9) and have experienced similar rapid increases in other areas of their range (10). It is impossible to give an accurate prediction of the population trend for future years, but it is reasonable to expect continued increases in gull numbers, especially since garbage and sewage from human populations (apparently the main causes of gull increases) are not likely to stabilise or decline in the near future. This means that the incidence of damage by gulls to other colonial seabirds (e.g., auks, terns), in the form of predation of eggs and young, cleptoparasitism, and physical displacement, will also continue to increase. Thus, it is imperative that seabird colonies be carefully managed, especially large breeding colonies, which account for a significant proportion of the productivity of the total breeding population.

The following discussion will consider the ecological implications of these conclusions and offer recommendations for future research on gull management and the effective utilisation of seabird sanctuaries.

Biology of Puffins

The adult mortality rate of puffins is not well known. In Russian populations it is believed to be close to 5 percent (11), whereas at Great Island, Newfoundland , only 77 percent of the breeding birds banded and colour-coded in 1968 returned the following season, which gives a mortality rate of 23 percent. Part of the high mortality rate for puffins at Great Island may have been caused by band loss, lack of detection, or change of nesting colony (no missing 1968 colour-banded birds were observed in other locations at Great Island), but the size of the difference suggests that at least some of it can be attributed to a real differential mortality rate between populations. If the mortality rate of adult puffins at Great Island is taken to be 10 percent, this means that a 10 percent recruitment of new breeders is needed annually to maintain the population. Thus, on average, each adult pair needs to raise two young in a breeding period of ten years. It is unlikely that birds nesting at Great Island will succeed in raising this number of young, since breeding success is low on slope habitat (43.4%) and even less on level habitat (20.6%). In order to maintain population equilibrium, survival to first breeding must be near to 50 percent for slope-reared young and virtually 100 percent for level-reared birds. The likelihood of this survival rate being realised is low (based on post-fledging survival rates of other seabirds), as is the probability of there being sufficient surplus slope-reared birds which move into level habitat to breed to offset the lower productivity of birds on level habitat. It seems more probable that the population will decline, which is likely to lead to a decreased amount of nesting on level habitat. Further non-equilibrium due to continued gull increases may be expected to limit puffins to certain nesting habitat (maritime slope) or maintain puffin numbers near a level below which gulls cannot secure sufficient food from puffins (predation of eggs and young, and cleptoparasitism) to satisfy their energy requirements forcing them to exploit other food supplies. One final factor which may temporarily compensate for low productivity at colonies with gull interference is a large immigration rate. However, if predation and cleptoparasitism by gulls on puffins is not a local phenomenon (available evidence suggests that it is not), then all large breeding colonies will eventually be exploited (assuming gull increases continue), and the higher breeding success of puffins at small colonies without gulls (e.g., Funk and Small Islands) will certainly not be sufficient to make up for these population declines. It is evident that detailed research on gull management is necessary to find effective control measures for preventing the deterioration and possible destruction of seabird populations in Canada.

Proposal for Gull Control

Attempts to reduce gull numbers over a large part of their range have been unsuccessful. In Holland and eastern United States, control programmes to significantly reduce the total Herring Gull population proved to be futile as local declines were offset by influxes of immigrant gulls. At best, these programmes contained total gull numbers over the whole area and caused declines in local populations. It is this last point which is important and perhaps indicates a feasible management programme. If large-scale reduction is not possible due to high immigration rates from areas where gulls are not controlled and therefore still increasing, then control should be exercised on a local level (where control measures have been shown to be effective (12)) at major colonies of threatened species to ensure high productivity and a sufficient supply of new individuals to the breeding population. Since small colonies of some persecuted species (e.g., puffins)exempt from gull interference experience high breeding success (although relatively unimportant when total production and numbers are considered), it seems evident that the most effective method of protecting endangered species from serious gull damage is to eradicate gulls at major colonies so that a highly productive central stock exists which would guarantee the "safety" of the species and help to offset population declines caused by gulls elsewhere.

Effective management of threatened colonial seabirds can be initiated as follows:

1. Identify threatened species (i.e., rare, interesting or endangered species whose productivity is, or is likely to be, adversely affected by gulls).
2. Determine major colonies of threatened species (i.e., colonies important to a species' total production).
3. Establish major colonies as federal sanctuaries or national wildlife areas.
4. Estimate degree of gull control required (e.g., removal of breeding population, reduction in breeding population, prevention of further gull increases).
5. Implement necessary control measures.

6. Determine annual population trends and effectiveness of control programmes.

Together these points will assist in evaluating the measures required for local control of gulls and perhaps provide the preliminary information necessary for the establishment of an effective national system of gull management to protect seabirds in Canada which are potentially threatened by the geometric increase in gull numbers presently taking place in North America.

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Table 1. Comparison of the breeding performance of puffins breeding on slope and level habitat at Great Island in the presence of gulls in 1968 and 1969.

	Slope		Level
No. of nests	290		262
Hatching success	209 (72.0%)	*	138 (52.6%)
Fledging success	126 (60.3%)	*	54 (39.1%)
Breeding success	126 (43.4%)	*	54 (20.6%)
Young at fledging	126		53/54[1]
$\bar{x}$ bodyweight, S.E. (g)	261.7 $\pm$ 3.15	*	248.1 $\pm$ 5.88
$\bar{x}$ winglength, S.E. (mm)	141.1 $\pm$ 0.56		141.0 $\pm$ 0.68
$\bar{x}$ age, S.E. (days)	53.7 $\pm$ 0.79		52.5 $\pm$ 0.97

* $P < 0.001$

[1] Means for bodyweight and winglength based on 53 chicks only as measurements for one chick just prior to fledging were not recorded; sample size for mean age at fledging = 54 chicks.

Table 2. Observations of puffins nesting on slope and level habitat associated with differential egg loss, chick loss before fledging, and condition just prior to fledging, at Great Island.

	Slope		Level
% eggs displaced by rapid departure of incubating bird	13.7 (N=117)		17.0 (N=100)
Panic-flight rate [1]	6	**	33
Food for the chick			
$\bar{x}$ meal size, S.E. (g)	12.4 ± 0.42 (N=155)		12.7 ± 0.62 (N=94)
$\bar{x}$ no. meals/day[2], S.E.	3.6 ± 0.26 (N=17)	*	2.4 ± 0.31 (N=15)
Interference by gulls of parents taking food to chicks			
% landings attacked	18.8 (N=601)	**	39.0 (N=775)
% landings robbed	4.4 (N=601)	**	13.5 (N=775)

* $P < 0.01$

** $P < 0.001$

[1] Based on 10 observation periods of 60 minutes duration (600 minutes/habitat) recorded simultaneously by two observers from equal areas ($36m^2$) of slope and level habitat containing at least 30 puffins on the surface, through most of the incubation period (19 May - 26 June 1969).

[2] Measured by observing 17 nests on slope and 15 nests on level habitat during the entire daylight period for three consecutive days (31 July - 2 August 1969). Each nest contained a chick at approximately the same stage of development.

Table 3. Comparison of breeding performance at colonies with (Great Island) and without (Funk and Small Islands) gull interference in 1969. (N.B., Great Island data - birds on slope habitat only).

	Great Island (Slope)		Funk and Small Islands (Level)
No. of nests	200		253
Egg survival[1]	156 (78.0%)	*	242 (95.7%)
Breeding success	101 (50.5%)	*	229 (90.5%)
Young at fledging	101		91[2]
$\bar{x}$ bodyweight, S.E. (g)	261.8 ± 3.58	*	351.3 ± 2.55
$\bar{x}$ winglength, S.E. (mm)	140.5 ± 0.62		141.5 ± 0.67

* $P < 0.001$

[1] Based on the survival of eggs for the same length and period of time: Great Island - 5 June to 9 July (35 days); Funk and Small Islands - 17 June to 19 July (33 days). The distance between islands prevented the dates of the study period from coinciding exactly.

[2] 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.