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POPULATION CENSUS OF BREEDING ATLANTIC PUFFINS AT GREAT ISLAND, NEWFOUNDLAND IN 1993-1994

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Summary

Breeding colonies of Atlantic Puffins (Fratercula arctica) in the northwest Atlantic were severely reduced or eliminated by hunting, egg collecting, habitat destruction, and the introduction of domestic animals throughout the 18th and 19th centuries. Federal protection commencing early this century reduced direct human exploitation but negative impacts of oil pollution, accidental entrapment in fishing gear, expanding gull populations, and the capelin fishery have renewed concern for the species. Today the majority of North American Atlantic Puffins breeds on three islands within the Witless Bay Seabird Ecological Reserve off the southeast coast of Newfoundland. Great Island is the largest of the three colonies in the reserve with previous population estimates of 148,000 breeding pairs in 1973 and 52,000 pairs in 1979. The apparent steep drop in population from 1973 to 1979 was an artifact of the survey methodology used in 1979 and cannot be interpreted as an indication of real population decline by itself. Furthermore, survey methodologies used in 1973 are unclear and so it is impossible to say how accurate that estimate is. Thus, because of the uncertainty of previous population estimates and the importance of Great Island as the largest Atlantic Puffin colony in North America, we decided to resurvey the colony in 1993-94 as part of a larger study of the breeding ecology of puffins on the island.

Three component measurements were used in the calculation of a breeding population estimate for Atlantic Puffins on Great Island: burrow density, burrow occupancy, and colony area. Population size is the product of these three variables. To rigorously sample the Great Island puffin colony, a series of 10 east-west, parallel transects, 100 m apart were marked with white PVC tubing. Burrow density and other habitat variables such as slope, and aspect were determined in 1994 in 240 2 x 2 m quadrats spaced 5 m apart along the transects, within the puffin colony. The proportion of burrows containing an egg (burrow occupancy) was determined during mid-incubation by sampling in 28 plots of five burrows each along transects in 1993. Data from eight similar plots in 1992 are included for comparison. Colony and habitat boundaries were measured along and between transects to the nearest 0.1 m. Measurements were taken along the ground and thus include surface contours. Colony areas were transferred to a map and horizontal surface area measured with a planimeter. Horizontal surface area was corrected for slope to obtain real areas.

The average density of Atlantic Puffin burrows on Great Island was 0.92 ± 0.04 burrows.m⁻². Birds nested over an area of 151,936 m² giving an estimate of 140,070 ± 6,245 burrows over the whole island. Burrow occupancy rate averaged 76.1 ± 3.4% in 1992 and 87.9 ± 3.1% in 1993. Therefore the breeding population of Atlantic Puffins on Great Island, based on the higher occupancy rate in 1993 was 123,066 ± 7,029 pairs. Use of the lower occupancy rate from 1992 resulted in an estimate of 107,000 pairs. Rounding off, we estimate the Great Island Atlantic Puffin population to number 123,000 ± 7000 pairs in 1993-94. Bias inherent in our methodology may make this a conservative estimate: the real figure could be higher.

Our 1993-94 estimate of the Great Island Atlantic Puffin population was over double the previous estimate of 52,000 pairs obtained in 1979. The difference was due to a lower occupancy rate in 1979, and larger colony area estimate in 1993-94. The occupancy rate in 1979 was much lower than in 1993 because in 1979 burrow occupancy was determined during the late chick stage. In so doing, burrows in which an egg or chick was lost without replacement before the census were not considered occupied, and as a result, observed occupancy rates in 1979 were biased downwards. In order to compare results we adjusted our census figures by using the proportion of burrows containing late-stage chicks in 1992 and 1993 as measures of occupancy rate. This yielded population estimates of 75,000 in 1992 and 93,000 pairs in 1993, both still higher than the 1979 estimate of 52,000 pairs. However, since puffin breeding success was low on nearby Gull Island in 1979, this could explain the difference in population estimates. We recommend that occupancy rates should be determined early in breeding season (i.e., during incubation), and that timing should be standardized so that comparisons between years, habitats or other factors are not confounded by differences in breeding success.

Between 1979 and 1994, the Great Island puffin colony expanded from 12.9 to 15.2 ha, mainly due to expansion into pockets of inland habitat, and more extensive nesting on inland slopes and in maritime level habitat. Given that burrow density was similar in 1979 and 1994, the increase in colony area strongly suggests that the breeding population of Atlantic Puffins on Great Island has expanded since 1979.

Data on the distribution of puffins amongst the three main islands in Witless Bay in 1979, and the 1993-94 estimate of colony size for Great Island allow an up-to-date estimate of the total Witless Bay population. In addition to the 123,000 pairs currently on Great Island, an estimated 22,000 pairs nest on Green Island, and 71,000 pairs nest on Gull Island, for a total population of 216,000 pairs. The Witless Bay population represents an estimated 57% of the total North American Atlantic Puffin population, of which 33% nest on Great Island. Clearly, conservation efforts aimed at the Witless Bay population of Atlantic Puffins are needed to ensure the continued health of this species in North America.

The report concludes with incidental information on other seabirds and mammals observed on Great Island in 1992-94.

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1. Introduction

Breeding colonies of Atlantic Puffins (*Fratercula arctica*) in the northwest Atlantic were severely reduced or eliminated by hunting, egg collecting, habitat destruction and the introduction of domestic animals throughout the 18th and 19th centuries (Drury 1973, Nettleship and Evans 1985). Most colonies were eliminated in the Gulf of Maine, Bay of Fundy, and along the north shore of the Gulf of St. Lawrence, and numbers were greatly reduced in Newfoundland and Labrador (Bent 1919). Reduction of human exploitation following enactment of the Migratory Birds Convention in 1917 allowed puffin populations to partially recover during the early and mid 20th century, although these protective measures did not apply to Newfoundland until 1949. Factors such as mortality from oil pollution, accidental entrapment in fishing nets, fisheries impacts on capelin (*Mallotus villosus*), the puffins' primary summer prey, and increasing numbers of kleptoparasitic and predatory Herring (*Larus argentatus*) and Great Black-backed (*L. marinus*) Gulls, have renewed concern for Atlantic Puffin populations since the 1970s (Brown and Nettleship 1984a,b, Evans and Nettleship 1985, Nettleship and Evans 1985, Nettleship 1991).

Today a significant proportion of North American Atlantic Puffins breeds on three islands (Gull, Green and Great) within the Witless Bay Seabird Ecological Reserve off the southeast coast of Newfoundland (Nettleship and Evans 1985). Observations of puffins nesting in Witless Bay date from the mid-19th century, but quantitative estimates were not attempted until 1967 when L.M. Tuck and D.N. Nettleship made preliminary estimates of 75,000 pairs on Gull, 20,000 pairs on Green and 100,000 pairs on Great Island (Nettleship and Evans 1985). Later surveys gave estimates of 60,000, 17,000 and 148,000 pairs in 1973 (Brown et al. 1975, Nettleship and Evans 1985, Montgomerie and Nettleship unpubl. data), and 30,000, 9,300 and 52,000 pairs in 1979 (Cairns and Verspoor 1980, Cairns et al. 1989) for Gull, Green and Great islands, respectively.

Although the 1979 estimates were lower than those made in 1973, several factors prevented conclusions that populations had really declined (Cairns and Verspoor 1980).

Methods used to determine the 1973 estimate were not documented and so it is impossible to assess its validity. Furthermore, the 1979 estimates had wide confidence limits and may have been biased in relation to the 1973 estimate due to differences in the definition of what constituted a "burrow" and "colony area". Finally, the 1979 survey was performed in the late-chick stage in late-July/August (Cairns and Verspoor 1980). At this time, burrows in which an egg or chick had been lost without replacement before the census would not have been considered occupied, thereby producing underestimated occupancy rates, and a lower population estimate.

Despite uncertainties or problems with previous estimates, there is some evidence that puffin populations have declined in the past on Great Island. Small sections of the colony showed reductions of 22-25% in the number of burrows recorded between 1973 and 1979 (Cairns and Verspoor 1980), and the number of adults in attendance early in the season declined 76% between 1974 and 1981 in the "main colony" study plot (Nettleship 1972, Nettleship et al. 1989).

In view of the importance of the Witless Bay area to Atlantic Puffin populations on a continental scale (Nettleship and Evans 1985), the fact that previous population estimates from the area were suspect due to lack of documentation or methodology (see Cairns and Verspoor 1980), and concern over possible declines in the past, we decided to conduct a census of the Atlantic Puffin population on Great Island in 1993-94. We confined our efforts to Great Island in particular for several reasons: (1) it is the largest colony in the northwest Atlantic, (2) most previous data indicating population declines pertained to that colony, and (3) limited resources allowed a thorough survey of only one major colony. We assume that conclusions drawn about the status of the Great Island population likely apply to populations on neighbouring Gull and Green Islands.

2. Methods

2.1. Study site

Great Island (47° 11'N, 52° 46'W) is part of the Witless Bay Seabird Ecological Reserve and lies approximately 2.4 km offshore of southeast insular Newfoundland (Fig. 1). The island is about 1200 m long and ranges from about 150 to 700 m wide. Eastward tilting of underlying strata results in topography aligned north to south with most slopes facing east and west, some facing north, and few facing south. Steep, grassy slopes above a precipitous, rocky shoreline change to level or gently sloping, perimeter grassy areas, grass-Rubus meadows, and finally to a central balsam fir (Abies balsamea)/black spruce (Picea mariana) forest (Fig. 2). North-south ridges create steep interior slopes covered with forest or grass. The island has been described in detail by Nettleship (1972). Forested area has contracted and perimeter grassy and meadow habitats have probably expanded since the. time of Nettleship's study (Nettleship 1972; J. Reddick, pers. comm.). Changes are 3 especially obvious on the southern end and along the eastern and northern sides of the island where dead snags are abundant. The activities of nesting birds, particularly puffins and Herring Gulls, likely contributed to habitat changes (see Harris 1984). 9

2.2. Sampling methods

Three component measurements were used in the calculation of a breeding population estimate for puffins on Great Island: burrow density, burrow occupancy, and colony area (Nettleship 1976). Numbers of nesting pairs could not be counted directly because puffins lay a single egg hidden in a burrow they excavate themselves, or, infrequently on Great Island, in a rock crevice. Burrows persist from year to year and not all burrows are used for nesting in a particular season. Thus, separate estimates were required for the number of burrows and for the proportion of burrows that were occupied by nesting birds (occupancy rate). Burrow occupancy was determined on 17-28 June 1993 as part of a larger study on

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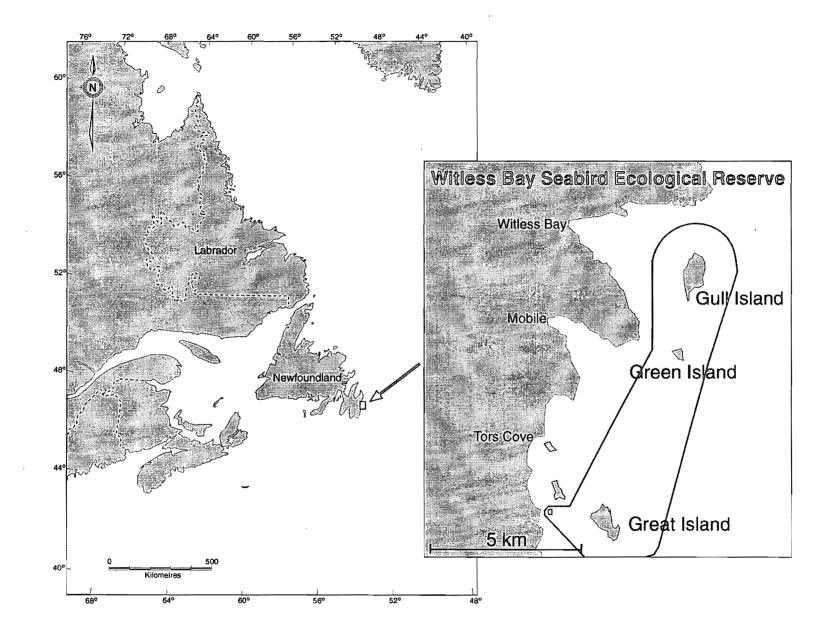


Figure 1. Site map including location of the Witless Bay Seabird Ecological Reserve and Great Island.

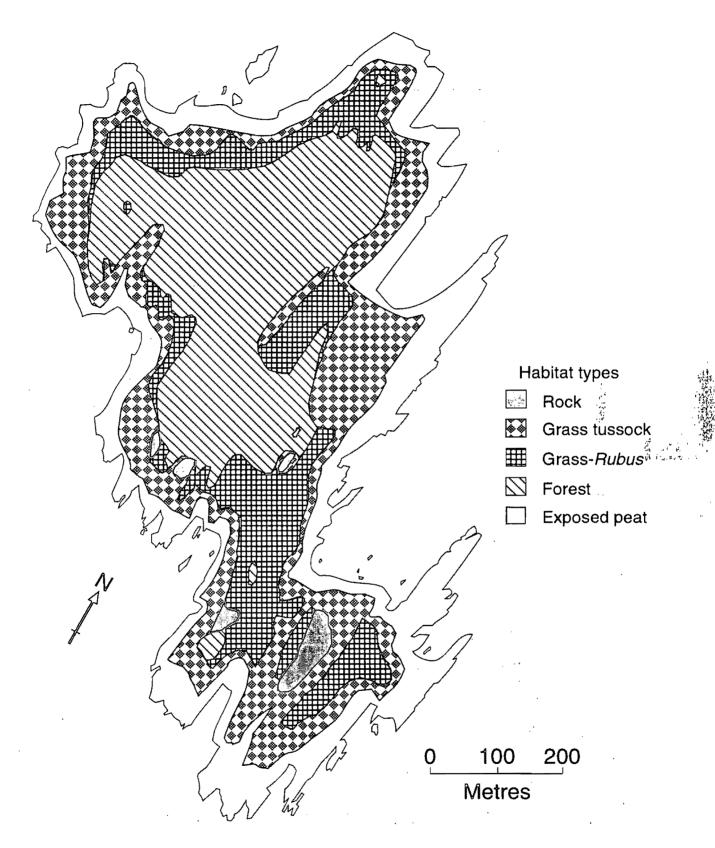


Figure 2. Distribution of vegetation types on Great Island in 1994

puffins in 1992-93 (Rodway 1994). Burrow density was determined and colony area mapped on 22 July to 8 August 1994.

2.2.1. Burrow density

Burrow density was estimated by calculating the average density of burrows in sample quadrats (N = 237). Quadrats were distributed using a stratified, centred start, systematic sampling scheme (Madow and Madow 1944, Madow 1949, 1953, Kingsley and Smith 1980) to insure adequate representation of different parts of the colony. Ten parallel transects, 100 m apart, were run east and west across the island from a centre line measured down the long axis of the island (Fig. 3). Centre lines and transects were marked with white, 1/2" PVC pipe placed every 25 m along centre lines and every 20 m along transects. Identification numbers were melted into the tops of PVC marker stakes at 100 m intervals or more frequently. Transect 1 was placed half a spacing distance, (i.e., 50 m) from the northern tip of the colony. Quadrats, 2 x 2 metres in size were established at 5 m intervals throughout the puffin colony along each transect. We used frequent, small quadrats to sample burrow density in preference to few, large strip transects, as used by Cairns and Verspoor (1980), because smaller, more frequent plots yield estimates with narrower confidence intervals (Savard and Smith 1985). Quadrat size was selected so that an average of at least one burrow occurred in each quadrat. All quadrats were laid out to the west of measured points to maintain constant spacing across the island, and extended 1 m either side of the transect line. For example, the quadrat at 2W-90 was placed at 90-92 m along transect 2-West, while the quadrat at 2E-90 was placed at 88-90 m along transect 2-East. Transect measurements began at zero at the centre line.

Number of burrows were counted, and slope and aspect were measured in each quadrat. Slope was measured to the nearest degree using a Silva Ranger compass and a protractor aligned with a plumb. The direction the slope faced was referred to as aspect and was estimated to the nearest degree by sighting directly down slope with the compass. The

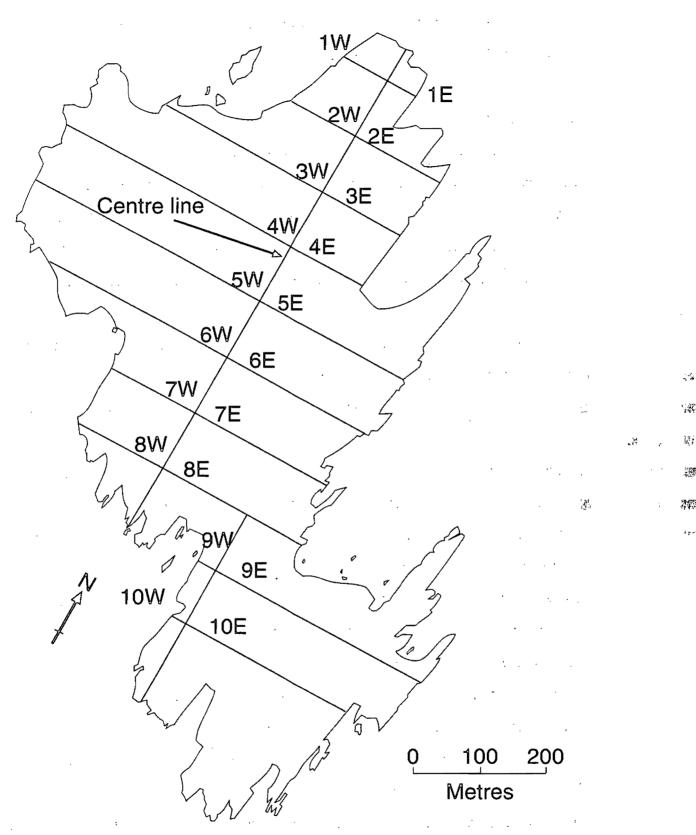


Figure 3. Location of permanently marked transects on Great Island

colony was arbitrarily divided into four locations: north, south, east and west. Transects 1E through 4E and the western portion of 5 E was at the north location, transects 1W through 8W and the western portion of 8E were in the west, transects 6E, 7E and eastern portions of 5E and 8E were in the east, and transects 9E, 9W, 10E, 10W were in south (see Fig. 3). Boundaries of vegetation types were measured to the nearest 0.1 m along transects (Appendix 1 and Fig. 2). Vegetation-type boundaries between transects were determined by careful exploration of the island, examination of photographs taken on the ground, and by measurements of boundaries taken perpendicular to transect lines.

Standard criteria were used to define a burrow. An entrance was called a burrow if its tunnel extended more than 50 cm and did not connect with another entrance within 100 cm. This was determined by reaching to elbow's length (about 50 cm) into each entrance. If it did connect with another entrance within 100 cm, the two (or more) entrances were called a single burrow. In rare cases, tunnels less than 50 cm were called burrows if they contained obvious nest cups, eggs or chicks. A burrow was considered in a quadrat if at least half of its entrance fell within quadrat boundaries. If a burrow had multiple entrances, the most worn or obvious entrance was used to decide whether or not to include it in a quadrat.

Previous surveyors and researchers used habitat and location categories to describe the distribution of puffin burrows on Great Island (Nettleship 1972, Cairns and Verspoor 1980, Rodway 1994). We compared burrow density and occupancy amongst similar categories: maritime slope, maritime level, and inland slope habitats, and north, east, south, and west locations. We defined level habitat the same as Nettleship (< 15°), but changed his criterion for slope habitat from > 30° to $\geq 15^{\circ}$ in order to sample the entire colony. Slopes \geq 15° that were separated from the shore (when facing down the slope) by an intervening stretch of level or unused habitat were classified as inland slopes. Our definitions differed from those used by Cairns and Verspoor (1980) who defined level habitat as < 20°, and inland slopes as "...puffin habitat separated from the sea by a horizontal distance of at least 50 m ...[unless it] is part of a continuous slope to the sea".

2.2.2 Occupancy rate of burrows

The percentage of burrows used by breeding birds (occupancy rate) was determined by a single check of a sample of burrows during the mid-incubation period. This provided a conservative estimate of burrow occupancy because some eggs may be lost before, or laid after, burrows are checked. Occupancy was determined in 28 plots of 5 burrows each in 1993. We also present occupancy data determined in nine plots containing 20 burrows each in 1992 for comparative purposes. Sample plots were stratified by habitat and location to minimise possible biases due to position in the colony (see Nettleship 1972, Cairns and Verspoor 1980, Rodway 1994). Plots were placed at 30 m intervals along transects, or at the closest 5 m mark that fell within a particular habitat.

The sample of burrows in each plot was obtained by selecting all burrows occurring within contiguous 1 m² sections, until the desired number of burrows were identified. Sections were examined in a predetermined sequence in an expanding radius from a measured point along a transect. This selection technique avoided potential biases caused by choosing burrows that looked occupied or were easier to access. A burrow was considered occupied if an egg was found. Burrows were considered empty if all tunnel × () branches were explored and no egg was found. Signs such as a well worn entrance or droppings were not used to distinguish between occupied and empty burrows, because we found that such signs were not good indicators of occupancy. Entrances to many burrows that contained eggs and fledged chicks were obscured by grass and showed no obvious signs of habitation throughout the season, while others that never contained eggs looked persistently occupied (Rodway 1994). Exploring burrows longer than an arm's reach required the careful digging of one or more conical access holes until the end was reached. Excavated holes were immediately patched with sticks and soil. To minimise disturbance, adults and eggs were not pulled from burrows.

Cairns and Verspoor (1980) determined burrow occupancy during the late-chick period in August 1979. We also determined occupancy in the late-chick period to compare with

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that survey. However, the proportion of burrows that contain chicks in the late-chick period is not a good indicator of the number of birds breeding in a particular season because it is affected by hatching success and chick survival. Thus, we do not use that proportion to estimate breeding population.

2.2.3. Colony area

Colony area was defined to include all portions of the island where burrows with recent signs of activity (droppings, feathers, fragments of eggshell or egg membrane, worn entrances or tunnels, excavation, or fresh nesting material) were located. If there were no burrows within a quadrat, the surrounding area was searched for colony evidence to determine if the plot fell within the colony and should be used in density calculations. Precise measurements of colony boundaries were possible because puffin burrows were conspicuous and easily identified. Boundaries along transects were defined to be at the first or last burrow occurring within 5 m either side of a transect line. Colony boundaries between transects were determined by careful exploration and by measurements taken perpendicular to transect lines. All transect and other distance measurements were taken to the nearest 0.1 m using 30 and 50 m tapes. Measurements were taken along the ground and thus included surface contours.

Distance, slope, and aspect measurements taken along the transects, as well as during exploration, were used to draw colony areas on a detailed topographic map at a scale of 1:943 with 10' contour intervals. The horizontal surface area of the colony was measured on the resulting map with a Koizumi compensating polar planimeter, Type KP-23. Colony areas were divided into sections with similar slopes. Adjusting for slope, the area of individual sections was given by:

 $C_s = A_h T^2 (\cos \Theta)^{-1},$

where C_s is the colony surface area, A_h is the area on the map, T is the scale of the map, and Θ is the mean slope along the transects or, if measured areas did not fall along transects, the average slope calculated from the spacing of the 10' contour lines. Colony area calculations took into account the average uphill slope, but not the undulations between quadrats or between transects. Therefore our calculations give a conservative estimate of the total surface area available to birds for nesting.

There is no measure of error for colony area calculations and its level of precision is unknown. The accuracy of area estimates depends on precise delineation of colony boundaries by thorough exploration, careful observation, and detailed and explicit notetaking, as well as on distance and slope measurements taken along transects. Accuracy of mapping and measuring colony areas depends on the scale and detail of available topographic maps or air photos. The large scale map we had for Great Island facilitated accurate and precise representation.

2.2.4. Calculation of population estimate

The total number of burrows in the colony (B) is the product of the overall average density of burrows, as determined in the quadrats, and the total area of the colony. B multiplied by the occupancy rate, (R) gives an estimate of total nesting pairs (P). The standard error (SE) of P is calculated as follows:

 $SE(P) = (B^2 Variance(R) + R^2 Variance(B) - Variance(B) Variance(R))^{1/2} (Rodway et al. 1990).$

All means are quoted plus or minus one standard error.

3. Results

3.1. Burrow density

Burrow density in all sampled quadrats averaged 0.92 ± 0.04 burrows.m⁻² (N = 237; Appendix 2). Sampled area was 0.6% of the colony area. A two-way ANOVA indicated

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significant variation in density across habitats and location, but the interpretation of differences was complicated by a significant interaction effect (Table 1; see Appendix 2 for location and habitat classifications for all plots). Tukey post-hoc tests showed that densities at east locations were lower than at north (P = 0.009) and south (P = 0.003) locations (Table 2). Post-hoc comparisons were not significant between inland slope habitat and maritime level (P = 0.072) and maritime slope (P = 0.063) habitats. Lowest densities occurred in inland slope habitat at east and north locations.

3.2. Burrow occupancy

Proportions of burrows with eggs during the mid-incubation period averaged 76.1 \pm 3.4% (N = 9 plots) in 1992 and 87.9 \pm 3.1% (N = 28 plots) in 1993 (Appendix 3). Proportions did not vary significantly across locations or habitats (see Rodway 1994). Proportions of burrows containing chicks in the late-chick period averaged 53.3 \pm 5.0% in 1992 and 66.4 \pm 4.3% in 1993 (Appendix 3).

3.3. Colony area

Puffins nested in all grassy, perimeter areas with enough soil to support burrows and on inland slopes as far as 200 m from shore (Table 3, Fig. 4). Most burrows occurred in unforested grassy or bare peat areas. Along the northeast side of the island, especially in the vicinity of transect 3E, burrows extended as far as 17.5 m into forested habitat. New burrows being dug under trees in that area and in tall meadow grasses interior to the main burrowed slopes along the north end of the island suggest that the colony is expanding in those areas. Pockets of old, eroded tussocks along the west side, in Nettleship's "main colony" plot (see Nettleship 1972), and in the meadow on the outer, east side of the island appear to have been abandoned. Table 1. Summary table for two-way ANOVA of Atlantic Puffin burrow density by location and habitat on Great Island in 1994.

Source	Sum of squares	df	Mean square	F	Р
Location Habitat Location*habitat Error	5.28 2.32 4.56 77.04	3 2 6 225	1.76 1.16 0.76 0.34	5.14 3.39 2.22	0.002 0.036 0.042

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Category	Mean burrow density (burrows.m ⁻²)	S.E.	Ν
Location			
North East South West	1.03 0.62 1.09 0.84	0.10 0.06 0.08 0.07	40 54 58 85
Habitat			
Maritime slope Maritime level Inland slope	0.98 0.97 0.73	0.07 0.08 0.07	95 57 85
Location*habitat			
North maritime slope North maritime level North inland slope East maritime slope East maritime level East inland slope South maritime slope South maritime level South inland slope West maritime level West maritime level West inland slope	1.43 1.10 0.58 0.63 0.73 0.50 0.95 1.12 1.21 0.92 0.95 0.65	$\begin{array}{c} 0.13\\ 0.20\\ 0.14\\ 0.08\\ 0.16\\ 0.13\\ 0.21\\ 0.16\\ 0.11\\ 0.11\\ 0.15\\ 0.11 \end{array}$	20 10 10 31 12 11 5 15 38 39 20 26

Table 2. Least squares means for location, habitat, and location*habitat categories from two-way ANOVA of Atlantic Puffin burrow density on Great Island in 1994.

- 1

Transect	Edge of burrows at shore (m)	Extent of continuous colony from shore (m)	Start of separate inland section (m)	End of inland section (m)
East side				
1 2 3 4 5 6 7 8 9 10	14.0 148.0 128.0 120.0 297.0 280.8 288.0 320.0 ¹ 308.0 292.0	W-9.0 79.6 81.5 87.0 160.0 198.4 252.5 315.0' 302.5 266.0	81.3 76.0 232.0 89.5 227.6 226.6	71.4 62.0 200.0 56.0 148.8 165.0
West side				
1 2 3 4 5 6	69.6 94.0 175.0 363.0 383.0 347.0	$51.3^{2} \\78.0^{2} \\139.5^{3} \\338.5 \\336.3 \\274.0$	209.0 262.3	179.9 215.0
7 8 9	69.0 65.0 ¹ 35.0	61.7 E-21.0 13.5	197.0 E-75.8 E-122.4	160.0 E-98.6 E-134.0
10	4.0	E-36.3	E-117.0	E-151.5

Table 3. Extent of Atlantic Puffin colony along transects on Great Island in 1994. Measurements for east and west sides refer to east and west transects unless otherwise indicated (see Figs. 3 and 4). Measurements were taken along ground.

¹ Measurements were estimated because nesting murres prevented close approach

^{2.} Only a small finger of habitat extended to this distance along transect. Colony boundary just off transect 1W was at 55.6 m, and off transect 2W was at 79.6 m

^{3.} Bare rock at 3W, 155-160 m

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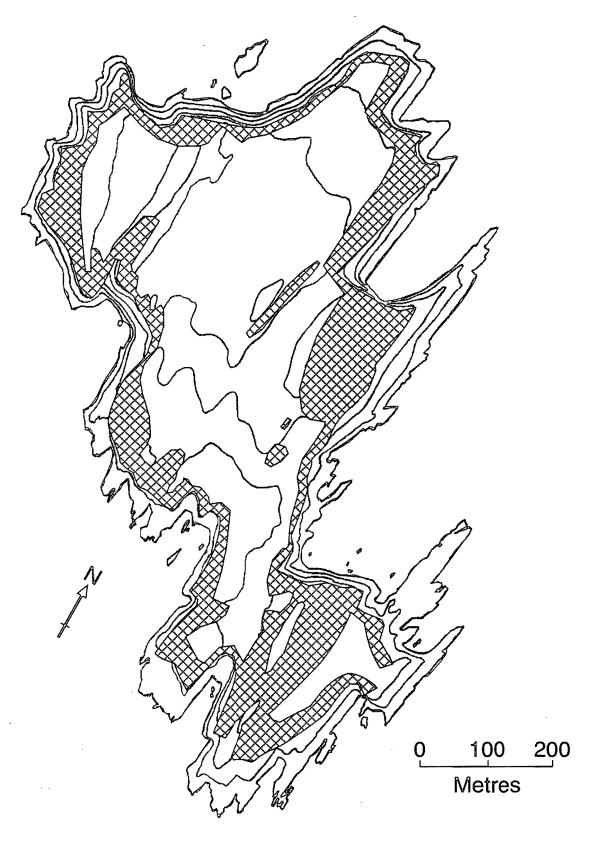


Figure 4. Atlantic Puffin colony on Great Island in 1994 (hatched). Contour lines are at 50' intervals

The total area of puffin colony measured 151,936 m² or 15.2 ha. Proportions in the three habitat categories were: 7.0 ha (46%) maritime slope, 3.9 ha (26%) maritime level, and 4.3 ha (28%) inland slope.

3.4 Breeding population

The breeding population estimate equals the product of the colony area, the average burrow density, and the maximum burrow occupancy rate from 1993. These are as follows:

- Burrow density = 0.9219 ± 0.0411 burrows.m⁻²
- Colony area = $151,936 \text{ m}^2$

(therefore total burrows = $140,070 \pm 6,245$)

- Occupancy rate = 0.8786 ± 0.0314 breeding pairs.burrow⁻¹
- Number of breeding pairs = $123,066 \pm 7,029$

Rounding off, we estimate the current breeding population of Atlantic Puffins on Great Island to be $123,000 \pm 7,000$ pairs. If we use the lower occupancy rate from 1992 the estimate is 107,000 pairs. Using the proportion of burrows containing late-stage chicks in 1992 and 1993 as a measure of occupancy rate (as did Cairns and Verspoor [1980]) yields population estimates of 75,000 and 93,000 pairs respectively.

4. Discussion

Our estimate of 123,000 pairs of Atlantic Puffins nesting on Great Island is likely conservative and underestimates the actual number due to a probable source of bias inherent in our methodology. First, the area of the colony was likely underestimated because of the complex, fractal nature of natural habitats (see Pennycuick and Kline 1986). We corrected our colony area estimate to account for differing slopes in quadrats spaced 5 m apart along transects, which were spaced 100 m apart. However, smaller hills or valleys between

quadrats or transects would not have been characterised at our scale of measurement, and could add significantly to the amount of habitat used by puffins. Our colony area estimate had no measure of error, however, sources of error other than the bias mentioned above (e.g., measurement error along ground or on maps) were likely random and thus would not act to counter the effects of small-scale slope.

Our 1993-94 estimate of the breeding population of Atlantic Puffins on Great Island was over double the previous estimate of 52,000 pairs obtained in 1979 by Cairns and Verspoor (1980). The current estimate is closer to the original one of 148,000 pairs made in 1973 (Brown et al. 1975). The 1973 population estimate was based on a cursory survey of Great Island and other seabird colonies in Newfoundland (Nettleship and Montgomerie unpubl. data). The methods for this survey have never been published and therefore we are unable to compare our results with those from 1973. However, meaningful comparisons with the 1979 census are possible because methods were well documented, and were in general similar to those used in this study (Cairns and Verspoor 1980).

The difference in the population estimates from 1979 and 1993-94 was due to a lower occupancy rate in 1979 (44.1 vs. 87.9%), and larger colony area estimate in 1993-94 (15.2 vs. 12.9 ha). Differences in occupancy rates and area estimates accounted for 86% and 14%, respectively, of the difference in population estimates between the two years. Burrow densities in 1994 and 1979 were very similar (0.92 ± 0.04 vs. 0.91 ± 0.4 burrows.m⁻², respectively).

The occupancy rate in 1979 was much lower than in 1992 and 1993 because in 1979 burrow occupancy was determined during the late chick stage. Any burrows in which an egg or chick was lost without replacement before the census would not have been considered occupied, and as a result, observed occupancy rates in 1979 were lower. In order to compare our results with those from 1979 we adjusted our census figures by using the proportion of burrows containing late-stage chicks in 1992 and 1993 as measures of occupancy rate. This yielded population estimates of 75,000 in 1992 and 93,000 pairs in

1993, both still higher than the 1979 estimate of 52,000 pairs. At face-value then it appears that the Great Island puffin population may have increased between 1979 and now. However, since occupancy rates depend on the degree of egg or chick loss before the survey, lower breeding success alone could account for the difference between the population estimate made in 1979, and our adjusted estimates. Breeding success indeed was lower on nearby Gull Island (Fig. 1) in 1979 (Rice 1985) than on Great Island in 1992 and 1993 (Rodway et al. 1996). Therefore, we conclude that the lower population estimate made in 1979. We recommend that occupancy rates should be determined early in breeding success in 1979. We recommend that occupancy rates should be standardized so that comparisons between years, habitats or other factors are not confounded by differences in breeding success.

Other evidence suggests that puffins have indeed increased in numbers on Great Island 4. in recent years. Over most of Great Island, the distribution of puffin nesting habitat was similar in 1979 and 1994, however, expansion has taken place in some areas over the intervening period. Greatest differences between colony areas mapped in the two years are (1) the existence of pockets of nesting habitat along transect 7E in 1994 that were absent in 1979, and (2) more extensive nesting on inland slopes along transect 5E and in maritime level habitat along the western and northern sides of the island in 1994 (compare our Fig. 4 with Fig. 4 in Cairns and Verspoor [1980]). New burrows being dug under forest and in tall meadow grasses interior to main burrowed areas in 1994 also suggest that the Great Island colony is expanding inland. Thus, there seems to be sufficient evidence to accept the larger colony area estimate in 1994 as indicative of real colony expansion since 1979, if we assume that exploration of the island was equally thorough and that mapping was equally accurate in the two surveys. Both assumptions are likely. Permanently marked transects and measured distances to colony boundaries along those transects in 1994 will allow more definitive conclusions about future changes in the extent of puffin nesting habitat on Great

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Island. Given that burrow density was similar in 1979 and 1994, the increase in colony area strongly suggests that the breeding population of Atlantic Puffins on Great Island has expanded since 1979.

Population estimates for the puffin colonies on Gull and Green Islands within the Witless Bay Seabird Ecological Reserve also were made in 1979 (Cairns and Verspoor 1980). If we assume that the relative numerical distribution of puffins amongst the three colonies was similar in 1993-94 then we can estimate the current total puffin population on the three islands based on our 1993-94 estimate for Great Island and the distribution. amongst the three islands in 1979. Of the total puffin population estimated for the three islands in 1979 (N = 91,300; Cairns and Verspoor 1980), 57% nested on Great Island, 10% on Green Island, and 33% on Gull Island. Therefore using the 1993-94 estimate of 123,000 pairs on Great Island gives a current estimated population of 22,000 pairs.

Table 4 shows the most up-to-date census estimates for Atlantic Puffins in North America, and includes information contained in this report. Note that some of the population estimates in Table 4 are now well over 10 years old. The total North American population of Atlantic Puffins is estimated to be 376,555 pairs of which 57% breed on the three main islands in the vicinity of Witless Bay, Newfoundland. As an indication of the importance of Great Island on a continental scale, a full 33% of North American Atlantic Puffins breed at this location. Clearly then, the fate of North American Atlantic Puffins rests significantly on the future well-being of the Witless Bay colonies and on Great Island in particular. . k

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Region	Pairs (n)	Percent of total	
Eastern Arctic	200 ¹	<1	
Labrador	87,000 ¹	23	
Gulf of St. Lawrence	17,935 ²	. 5	
Eastern Newfoundland	270,320 ³	72	
Scotian Shelf, Fundy, Gulf of Maine	1,100 ¹	<1	
Total	376,555	- · ·	-
¹ Nettleship and Evans (1985)		· · · · · · · · ·	
² Cairns et al. (1991)			ġ
^{3.} Cairns et al. (1989) and this study			1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1

Table 4. The most recent census figures for Atlantic Puffins in North America.

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Acknowledgements

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Appendix 1. Extent of vegetation types along transects on Great Island in 1994. Measurements were begun at the east end of transects and distances along east (E) and west (W) transects were measured from the centre line along ground (see Figs. 2 and 3). Measurements were recorded to the nearest 0.1 m but in many cases, especially for boundaries of woodland sections, should be considered accurate only to about 1 m. Boundaries between grass tussocks (which overlapped almost completely with puffin nesting habitat) and tall grass meadow were usually abrupt and can be considered accurate as measured.

Transect	Grass tussocks (m)	Tall-grass Rubus measow (m)	Woodland (m)	Exposed peat (m)
1	E14.0-W7.4 W55.6-69.6	W7.4-25.2 W38.6-55.6	W25.2-38.6	
2	E148.0-79.6	E79.6-68.0 ¹ E16.5-12.0 E7.0-W8.0 ¹ W24.0-43.5 W51.5-79.6 ¹	E68.0-16.5 E12.0-7.0 W8.0-24.0 W43.5-51.5	
	W79.6-94.0			
3	E135.0-99.0	W34.0-42.0 W99.0-140.0	E99.0-W34.0 W42.0-99.0	
	W140.0-155.0 ² W160.0-175.0	W 99.0-140.0		
4	E120.0-87.0 E79.0-70.6	E87.0-82.7 W210.3-338.5 ¹	E82.7-79.0 E70.6-W210.3	
	W338.5-368.0	W210.5-550.5		
5	E297.0-160.0	E160.0-156.0 E133.0-76.0	E156.0-133.0	
	E76.0-54.7 W188.3-209.0	W260.0-273.0 W332.3-336.3	E54.7-W188.3 W209.0-260.0 W273.0-332.3	
	W336.3-390.0	W 552.5-550.5		
6	E280.8-198.4	W52.7-70.5 W103.0-156.0	E198.4-W52.7 W70.5-103.0	
	W156.0-197 ² W215-253.0 W284.0-347.0		W253.0-284.0	

Transect	Grass tussocks (m)	Tall grass-Rubus meadow (m)	Woodland (m)	Exposed peat (m)
7	E288.0-252.5 E232.0-222.0 E208.0-200.0 W61.7-69.0	E252.5-232.0 ¹ W46.0-61.7 ¹	E200.0-W46.0	E222.0-208.0
8	E320-315 ³ W0.0-65 ³	E315-138.0 ¹ E120.0-102.0 E95.0-89.5 E60.0-55.5 E40.0-30.0 E24.5-21.0	E138.0-120.0 E102.0-95.0 E55.5-40.0 E30.0-24.5	E89.5-60.0 E21.0-0.0
9	E325-302.5 E227.6-184.0 E134.0-122.4 E98.6-75.8 ¹ W13.5-35	E302.5-227.6 E148.8-134.0 E122.4-98.6 E75.8-30.0 E12.3-W13.5 ¹	E30.0-12.3	E184.0-148.8
10	E292.0-266.0 E226.6-200.0 E151.5-117.0 E15.0-W4.0	E266.0-226.6 E163.7-151.5 E117.0-36.3 ¹		E200.0-163.7 E36.3-15.0

^{1.} Pockets of live spruce trees in area at 2E7-W8, 2E74.5-68, 2W51.5-79.6, 4W215-231.5, 7E252.5-234, 7W46-54, 8E235-225, 8E192-138, 9E100-12.3, and 10E64.5-41 m.

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² Bare rock at 3W155-160 and 6W197-215 m.

^{3.} Measurements were estimated because nesting murres prevented close approach.

Appendix 2. Number of Atlantic Puffin burrows, slope, aspect, and location and habitat in 2 x 2 m quadrats spaced at 5 m intervals along transects on Great Island in 1994. A dash indicates that the plot was close to nesting murres and was not surveyed to avoid disturbance. The plot at 4E-75 was not surveyed (indicated by *) because only half of the plot fell within colony boundaries. Note that the centreline (0 m) for transects 9 and 10 aligns with 260 m along transect 8E (see Fig. 3).

Transect	Distance ¹ (m)	Burrows (n)	Slope (°)	Aspect ² (°)	Location	Habitat ³
1E 1W 1W 1W 1W 1W 2E 2E 2E 2E 2E 2E 2E 2E 2E 2E 2E 2E 2E	$\begin{array}{c} (m) \\ 10 \\ 5 \\ 0 \\ 5 \\ 55 \\ 60 \\ 65 \\ 145 \\ 140 \\ 135 \\ 130 \\ 125 \\ 120 \\ 115 \\ 110 \\ 105 \\ 100 \\ 95 \\ 90 \\ 85 \\ 80 \\ 85 \\ 90 \\ 125 \\ 120 \\ 115 \\ 110 \\ 105 \\ 120 \\ 115 \\ 110 \\ 105 \\ 120 \\ 115 \\ 110 \\ 105 \\ 120 \\ 115 \\ 110 \\ 105 \\ 100 \\ 95 \\ 90 \\ 85 \\ 140 \\ 145 \\ 150 \\ 160 \\ 165 \\ 170 \end{array}$	$(n) \\ 1 \\ 5 \\ 7 \\ 2 \\ 5 \\ 10 \\ 2 \\ 6 \\ 4 \\ 8 \\ 7 \\ 9 \\ 4 \\ 7 \\ 3 \\ 4 \\ 7 \\ 6 \\ 3 \\ 3 \\ 6 \\ 10 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 6 \\ 7 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 6 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 6 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 6 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 6 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 6 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 6 \\ 7 \\ 7 \\ 6 \\ 7 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 6 \\ 7 \\ 7 \\ 6 \\ 7 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 6 \\ 7 \\ 7 \\ 6 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 3 \\ 5 \\ 5 \\ 5 \\ 1 \\ 1 \\ 6 \\ 10 \\ 7 \\ 6 \\ 7 \\ 7 \\ 6 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7 \\ 7$		$\begin{pmatrix} \circ \\ 90 \\ 90 \\ 270 \\ 270 \\ 270 \\ 270 \\ 270 \\ 270 \\ 90 \\ 90 \\ 90 \\ 90 \\ 90 \\ 45 \\ 40 \\ 45 \\ 50 \\ 70 \\ 90 \\ 90 \\ 90 \\ 90 \\ 90 \\ 90 \\ 9$	north north west west west west west north	MS ML ML MS SS MS
4E 4E 4E 4E	120 115 110 105	1 3 5 7 6	45 45 45 45	90 90 90 90	north north north north	MS MS MS MS
4E 4E	100 95	10 10	22 8	90 90	north north	MS ML

Transect	Distance ¹ (m)	Burrows (n)	Slope (°)	Aspect ² (°)	Location	Habitat ³
4E	90	4	3	90	north	ML
4E	80	2	47	90	north	IS
4E	75	*	*	*	north	IS
4W	340	2	13	270	west	ML
4W	345	1	16	270	west	IS
4W	350		0	270	west	ML
4W	355	2 7	9	270	west	ML
4W	360	5	47	270	west	MS
5E	295	5 2 3	41	270 90	east	MS
5E	290 ·	2	41	90	east	MS
5E	285	1	41	90 90	east	MS
5E	280	3	41	90	east	MS
5E	275	ŏ	45	90	east	MS
5E	270	1	45	90	east	MS
5E	265	5	45	90	east	MS
5E	260	4	45	90	east	MS
5E	255	6	45	90	east	MS
5E	250	1	50	90 90	east	MS
5E	245		45	90	east	MS
5E	240	3 5	21	142	east	MS
5E	235	ŏ	17	175	east	MS
5E	230	3	10	170	east	ML
5E	225	1	10	330	east	ML
5E	220	Ô	16	90	east	IS
5E	215	ŏ	53	90	east	IS
5E	210	, 1	9	90	east	ML
5E	205	1	10	25	east	ML
5E	200	4	11	0	east	ML
5E	195	0	11	90	east	ML
5E	190	2	13	90	east	ML :
5E	185	2 5 3 5	29	270	north	IS
5E	180	3	35	270	north	IS
5E	175	5	35	270	north	IS ·
5E	170	1	35	270	north	IS
5Ē	165	3	35	270	north	ÎS
5E	75	3 2	40	90	north	IS ⁻
5E	70	õ	40	90	north	IS
5E	65	1	30	90	north	IS
5W	180	1	15	270	west	Ί
5W	185	Ô	19	270	west	IS
5W	190		23	270	west	IS
5W.	195	2	35	270	west	IS
5W	200	4 2 5 6	43	270	west	IS
5W .	205	6	45	270	west	IS
5W	340		11	270	west	ML
5W	345	3	11	270	west	ML
5W	350	Ř	11	270	west	ML
5W	355	1 3 2 2	.9	240	west	ML
5W :	360	2	10	240	west	ML
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Transect	Distance ¹ (m)	Burrows (n)	Slope (°)	Aspect ² (°)	Location	Habitat ³
5W 5W 5W 6E 6E 6E 6E 6E 6E 6E 6E 6E 6E 6E 6E 6E	(m) 365 370 375 380 280 275 270 265 260 255 250 245 240 235 230 225 220	(n) 4 4 0 0 3 6 2 3 2 3 2 1 2 1 4	(°) 14 23 40 45 9 10 10 15 28 28 20 20 21 23 25 27 29	(°) 270 270 270 270 90 90 90 90 90 90 90 90 170 170 170 170 170 160 150 140 130	west west west east east east east east east east e	ML MS MS ML ML MS MS MS MS MS MS MS MS MS
6E 6E 6E 6W 6W 6W 6W 6W 6W 6W 6W 6W 6W 6W 6W 6W	215 210 205 200 160 165 170 175 180 185 190 195 215 220 225	4 2 3 1 1 5 6 0 1 0 5 1 2 1 2 1 2 5	29 27 25 17 40 40 40 40 13 13 13 30 45 40 30	130 130 130 140 90 90 90 90 90 270 180 180 270 270 270 270 270	east east east west west west west west west west we	MS MS MS IS IS IS ML IS IS IS IS IS
6W 6W 6W 6W 6W 6W 6W 6W 6W 6W 6W 6W 6W 6	230 240 245 250 255 260 275 280 285 290 295 300 305 310 315 320 325	2 5 2 5 7 5 2 1 0 4 4 2 4 5 0 5 5 9 1	20 25 35 40 40 30 20 20 22 24 27 27 20 20 20 20 20 20 20	240 240 240 240 240 240 240 240 240 240	west west west west west west west west	IS IS IS IS IS MS MS MS MS MS MS MS MS MS MS MS

Transect	Distance ¹ (m)	Burrows (n)	Slope (°)	Aspect ² (°)	Location	Habitat ³
6W 6W 6W 7E 7E 7E 7E	330 335 340 345 280 275 270	5 4 3 3 3 0 7	20 20 30 30 40 50 45	240 240 270 270 90 0 40	west west west east east east	MS MS MS MS MS MS MS
7E 7E 7E 7E 7E 7E 7E 7E	265 260 255 230 225 220 215	3 6 4 5 1 2 3	34 8 0 35 35 30 30	45 90 90 90 90 90 90	east east east east east east east	MS ML IS IS IS IS
7E 7E 7W 8E 8E 8E 8E 8E	210 205 65 90 85 80 75	0 - 8 3 2 2 2 2	30 20 14 40 35 23 0	90 90 110 90 90 90 270	east east east east east west	IS IS ML IS IS IS ML
8E 8E 8E 8E 8E 8E 8E 8E	70 65 60 20 15 10 5	0 4 1 0 1 3 1	70 32 18 39 23 15 20	270 270 250 90 90 240 230	west west west west west west	IS IS IS IS ML MS
8W 8W 8W 8W 8W 8W	0 5 10 15 20 25	2 2 0 0 1 3	25 28 27 27 23 23	208 208 208 208 208 208 208	west west west west west	MS MS MS MS MS MS
8W 8W 8W 8W 8W 8W 8W	30 35 40 45 50 55 60	3 6 4 3 -	37 37 37 20 -	230 230 230 180	west west west west west west	MS MS MS MS MS MS MS
9E 9E 9E 9E 9E 9E 9E 9E 9E	305 225 220 215 210 205 200 195	1 7 10 7 8 6 6 7	5 27 27 30 32 38 36 33	0 70 70 70 70 50 50 50	south south south south south south south	ML IS IS IS IS IS IS IS

Transect	Distance ¹ (m)	Burrows (n)	Slope (°)	Aspect ² (°)	Location	Habitat ³
9E 9E 9E 9E 9E 9E 9E 9E 9E 9E 9E 9E 9E 9		(n) 10 6 5 7 1 4 3 2 7 0 2 5 7 4 1 3 8 4 1 5 6 6 4 5 2 0 0 3 4 6 3 4 5 5 4 3 7 7 7 9 6 5 1 2 3 4 7		$\begin{pmatrix} (^{\circ}) \\ 60 \\ 70 \\ 70 \\ 90 \\ 90 \\ 270 \\ 270 \\ 250 \\ 250 \\ 250 \\ 250 \\ 250 \\ 250 \\ 250 \\ 250 \\ 250 \\ 250 \\ 250 \\ 90 \\ 90 \\ 90 \\ 90 \\ 90 \\ 90 \\ 90 \\ $	south south	IS IS IS ML IS IS IS IS IS IS IS IS ML ML IS
10E 10E	10 5	6 5	12 23	270 270	south south	ML MS

Transect	Distance ¹ (m)	Burrows (n)	Slope (°)	Aspect ² (°)	Location	Habitat ³
10W	0	4	38	270	south	MS

¹ Distance along ground from centre line (see Fig. 3).

² Compass direction of line directly down-slope within quadrat.

³ MS = maritime slope, ML = maritime level, IS = inland slope.

Appendix 3. Occupancy of Atlantic Puffins burrows during the mid-incubation and latechick periods on Great Island in 1992 and 1993. Burrows checked for occupancy during the incubation period in 1992 were subsequently used to investigate hatching dates and chick growth (see Rodway 1994). Due to the effects of researcher disturbance during that study (Rodway et al. 1996) we used previously undisturbed burrows in control plots at the same locations to determine occupancy during the chick period. The same burrows were used to check occupancy during incubation and the chick period in 1993

Plot	Number of burrows in sample	Number with eggs (incubation period)	Number with chicks (chick period)
1992 2E-85 2E-120 5E-70 5E-230 5E-280 7E-220 9W-20 9E-95 10E-5	20 20 20 20 20 20 20 20 20 20 20	16 12 12 15 15 15 18 17 16 16	9 8 6 8 13 12 13 15 12
1993 1E-5 2E-95 3E-100 3E-120 4E-80 4E-90 5E-180 5E-200 5E-250 6E-210 6E-240 6E-270 7E-260 1W-50 1W-55 2W-80 3W-140 3W-160 4W-340 4W-360 5W-200 5W-350 5W-370 6W-160 6W-240 6W-300 6W-325 7W-65	5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5	5 3 5 5 4 5 3 5 5 5 5 5 5 5 5 5 5 5 5 5	3 2 4 5 4 5 2 5 3 4 5 2 5 3 4 3 2 3 5 4 4 2 2 2 2 5

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APPENDIX 4. Incidental information on other seabirds and mammals on Great Island in 1992-1994.

Data on other species nesting or present on Great Island were collected during studies conducted in 1992-94 by Regehr (1994) and Rodway (1994). We present anecdotal and quantitative information for some other seabird species nesting on the island and for known predators of those species. For some species we had sufficient information to make population estimates. The quality of those estimates vary and the reader should be cautious when interpreting results. We discuss the limitations of estimates for each species.

Northern Fulmar (Fulmaris glacialis)

We kept records of incidental observations but did not thoroughly explore perimeter cliffs for fulmar nests. We observed 24 nests with adults on or at them along the east side of Southern Cove, two on the east side of Big Cove, two on the west side just north of the end of transect 4W, and one on the east side of North Point. Breeding was not confirmed at all nests.

Leach's Storm-Petrel (Oceanodroma leucorhoa)

Leach's Storm-Petrels were nesting in all vegetated areas not inhabited by puffins, except in some areas of very thick, tall meadow grasses along transect 5E and 4W. Petrel burrows generally extended only a few metres into puffin habitat, but petrels were found nesting sporadically throughout puffin habitat, often nesting in small tunnels off the sides or ends of inactive and even active puffin burrows. The distribution of petrel burrows in 1992 was qualitatively similar to that reported by Cairns and Verspoor (1980) in 1979.

We did not determine burrow density or measure colony area in this study. Burrow occupancy was determined in five plots of 20 burrows each on 4-5 August 1992. Plots were located along transects at 4E-60, 5W-80, 6E-70, 7E-120, and 8E-120 m. Of the 20 burrows in each plot, 19, 16, 20, 15, and 17 contained eggs or chicks, respectively, giving an estimate for burrow occupancy of $87.0 \pm 4.6\%$.

Occupancy was higher in 1992 than in 1979 (63.9%), but differences may have been due to later timing of burrow checks in 1979 (see Cairns and Verspoor 1980) than in 1992, as was the case for puffins. We suspect that the size of the breeding population of petrels on Great Island in 1992 was similar to that in 1979, and that the numbers are slightly higher than estimated by Cairns and Verspoor (1980) due to an under-estimate of occupancy rate in that survey. Using the 1992 occupancy rate, and assuming similar colony area (28.6 ha) and burrow density (1.38 ± 0.09 burrows.m⁻²) as in 1979 (Cairns and Verspoor 1980), would indicate a breeding population of about 340,000 pairs.

Black-legged Kittiwake (Rissa tridactyla)

Black-legged Kittiwakes were nesting on most cliffs surrounding Great Island (Cairns and Verspoor 1980). As part of a study on breeding success in 1992-93 (Regehr 1994), kittiwake nests were counted on sections of cliffs that were easily visible from land on 7-10 August 1993. Counts were conducted from vantage points (See Regehr 1994) and all visible nests were included. A total of 13,541 nests were counted. We estimated the proportion of total nesting habitat that was surveyed in 1993 by comparing the linear extent of our survey areas with the linear extent of the nesting area mapped by Cairns and Verspoor (1980) in 1979. Using the proportion of habitat surveyed for different sections of the island, and the numbers of nests counted in areas that were surveyed, we estimated that 10,246 nests had not been counted in 1993. This resulted in a total estimate of 23,787 breeding pairs, an estimate that is very similar to the 23,229 pairs reported in Cairns et al. (1989). Although the method of estimating numbers of nests in areas which were not surveyed is approximate, our figures suggest that kittiwake numbers have not changed substantially since 1968 (Brown and Nettleship 1975).

Great Black-backed Gull (Larus marinus)

Great Black-backed Gulls nested sporadically amongst Herring Gulls in rocky, grass tussocks, and meadow habitat. We made observations of behaviour and kept records of all nests found during our explorations of the island. We discovered 27 nests in 1992-94. This cannot be considered a complete count of Great Black-backed Gulls nesting on Great Island because we did not explore some rocky shoreline and some grassy areas. However, we think that we counted a majority of the nests on the island and estimate a maximum nesting population of about 40 pairs.

We found prey remains of Atlantic Puffin adults and chicks, Black-legged Kittiwake adults and eggs, and Common Murre adults at Great Black-backed Gull nests. We observed several predation events involving Great Black-backed Gulls and other seabirds on Great Island. Atlantic Puffins were sometimes caught in the air and then killed on the water or land, but most were caught on the ground. We found piles of up to 26 puffin carcasses near specialist gull territories. We counted 115 adult puffin carcasses in 1992-94, mostly around 8 gull territories, and estimated that Great Island Great Black-backed Gulls were killing up to 200 adult puffins per year. Many depredated puffins were immature birds with 0-1 bill grooves. Gulls were frequently observed robbing eggs from kittiwake nests (Regehr 1994).

Herring Gull (Larus argentatus)

Herring Gulls nested on most bare rocky areas on the perimeter and inland, in grass tussock puffin habitat, and in grass-*Rubus* meadows, with the exception of some steeper puffin slopes and where meadow grasses were especially tall and dense. We did not attempt to count Herring Gull nests on the island. Herring Gulls preyed on Atlantic Puffin chicks that were close to burrow entrances or were leaving their burrows when fledging, and scavenged puffin eggs that had been removed from burrows by adult puffins (Rodway 1994). Herring Gulls also were observed taking some Black-legged Kittiwake eggs (Regehr 1994). ġ.Ţ

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Common Raven (Corvus corax)

A maximum of four Ravens were seen. We observed Ravens preying on Black-legged Kittiwake eggs (Regehr 1994).

River Otter (Lutra canadensis)

We discovered fresh tracks in mud along the centreline between transects 3 and 4 on 6 June 1992, and found a small denning site, one fresh fish scat, scattered remains and scats containing Leach's Storm-Petrel parts, and two petrel burrows freshly dug open at transect 5W-120 on 19 June 1992. Based on our extensive coverage of the island and limited observations of signs of otter activity we do not think that the presence of an otter on Great Island is cause for concern in relation to seabird conservation.