

HABITAT SELECTION AND REPRODUCTIVE PERFORMANCE OF FOOD-STRESSED HERRING GULLS¹

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Abstract. Recently increasing populations of Herring Gulls (*Larus argentatus*) in Newfoundland were food stressed by the late arrival of capelin (*Mallotus villosus*), the main prey fed to chicks, to inshore waters in 1992-1993. Our purpose was to determine how this food shortage would affect inter-habitat differences in breeding performance on Great Island, Newfoundland. A previous study comparing breeding success among rocky, puffin, and meadow habitats identified rocky as the preferred habitat and provided equivocal support for an ideal-free distribution. We predicted that food stress would accentuate differences between birds assorted by competitive ability and result in higher breeding success for pairs nesting in preferred habitat, as predicted by ideal-despotic and phenotype-limited ideal-free habitat selection models. Responses to food shortage included later hatching, smaller clutches, and reduced hatching and fledging success. Arrival of capelin four weeks after hatching began resulted in an advantage for late-hatched chicks and a reversal of the typical positive relationship between breeding success and large, early laid clutches. Higher and buffered nest density, and a greater proportion of pairs laying eggs indicated that rocky was still the preferred habitat. However, breeding success was as high or, more frequently, higher in other habitats in this and previous studies, contrary to predictions of habitat selection models. That rocky was the original nesting habitat on Great Island suggests an ultimate, probably genetic, component to habitat selection by Herring Gulls, which, in the absence of consistent trends in habitat suitability, may have maintained the preference for rocky habitat.

Key words: breeding failure, capelin, food shortage, habitat selection, Herring Gull, ideal-free distribution, *Larus argentatus*.

INTRODUCTION

Populations of Herring Gulls (*Larus argentatus*) in the western Atlantic increased dramatically during the first half of this century (Drury 1973). Population increases in Newfoundland during the 1970s and 1980s matched increases in the production of fish offal, and resulted in colonization of new habitat and displacement of other species (Howes and Montevecchi 1993). Off-shore dumping of fisheries waste and the imposition of a fisheries moratorium in eastern Newfoundland in 1992 is expected to reverse this trend (Pons 1992, Howes and Montevecchi 1993). In addition, capelin (*Mallotus villosus*), the main prey fed to Herring Gull chicks on Great Island, Newfoundland (Pierotti and Annett 1987), were smaller and arrived in inshore waters later than normal following anomalous oceanographic conditions in the northwest Atlantic in the 1990s (Nakashima 1996). We thus had an opportunity to exploit a natural experi-

ment and investigate breeding performance in relation to habitat selection during a period of reduced food availability.

Expanding Herring Gull populations have dispersed into a wide variety of nesting habitats (Kadlec and Drury 1968). Habitat selection theory predicts that intraspecific competition will broaden habitat use (Svardson 1949) and that individuals will disperse among habitats so as to maximize their fitness (Fretwell and Lucas 1970, Rosenzweig 1991). Theories typically assume that population density correlates with resource abundance and highest densities will occur in preferred habitats (Rosenzweig 1991), although "source-sink" dynamics can result in higher densities in sink habitats (van Horne 1983). Two models of Fretwell and Lucas (1970) predict that birds will not disperse from preferred habitats until either density-dependent effects reduce fitness to that expected in alternate habitats (ideal-free distribution) or territorial behavior of established breeders forces others to settle in less-preferred habitats (ideal-despotic distribution). Density-dependent effects of intraspecific aggression and predation have been implicated in the reduction of Herring Gull breeding success

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associated with increased nesting density following population expansion (Spaans et al. 1987). Fitness across habitats may equilibrate if individuals are "ideal-free" (Fretwell and Lucas 1970), but, more realistically for territorial species like Herring Gulls, intraspecific competition among unequal competitors (Pierotti and Annett 1994) will result in assortative distribution with the most competitive individuals occupying the best sites (Partridge 1978, Parker and Sutherland 1986). Fitness will then be higher in preferred habitats, as predicted by both ideal-despotic models of Fretwell and Lucas (1970) and phenotype-limited ideal free models of Parker and Sutherland (1986).

Higher nest density, competitively superior individuals, and colonization history indicated that "rocky" habitat was the preferred breeding habitat of Herring Gulls on Great Island, Newfoundland (Pierotti 1982). Similar breeding success in rocky and "puffin" habitat agreed with the prediction of an ideal-free model that birds will disperse into puffin habitat following reduction in fitness with increasing density in rocky habitat. However, breeding success may not have been an adequate measure of fitness because chicks in rocky habitat grew faster and fledged earlier and thus may have had higher post-fledging survival (Parsons et al. 1976). Also, the distribution of pairs nesting in a third, "meadow" habitat at low density that experienced lower breeding success could not be explained with an ideal-free model. Although pairs nesting in rocky habitat suffered highest levels of intrusion by prospecting conspecifics and exhibited high levels of aggression (Pierotti 1987), very few new pairs were able to establish themselves in that habitat compared to the other two habitats. Thus, territorial behavior prevented "free" distribution, violating one of the assumptions of the ideal-free model. Territorial behavior, phenotypically superior individuals in preferred rocky habitat, and possible higher fitness in rocky habitat if post-fledging survival is considered, suggest that the distribution of nesting Herring Gulls on Great Island would provide more support for an ideal-despotic or a phenotype-limited ideal-free than an ideal-free model.

Several factors make it important to investigate habitat selection during stressful periods. Stressful conditions can increase costs of reproduction that may not be realized under favorable conditions (Pons and Migot 1995). Secondly,

specific physical and social nest-site characteristics, such as shelter for chicks or central nest location, may be important only during adverse conditions (Montevocchi 1978, Regehr et al. 1998). Thus, the selective advantage of habitat choices may not be apparent in benign environments. Finally, individuals that reproduce successfully during periods of generally poor breeding success can contribute greatly to future generations, even though their average success may be low (Newton 1989).

We investigated breeding performance of Herring Gulls on Great Island in 1992 and 1993 in the same three habitats used by Pierotti (1982). Our objectives were to: (1) determine the effects of changes in food availability on breeding performance, (2) investigate how increased stress associated with food shortage affects inter-habitat differences, and (3) test the predictions of ideal-despotic and phenotype-limited ideal-free models that fitness will be higher in preferred habitats. We predicted that the stress of food shortage would accentuate differences among birds differing in competitive ability (Sydeman et al. 1991, Murphy et al. 1992), resulting in higher breeding success in preferred rocky habitat. We also expected delayed breeding, decreased numbers of pairs attempting breeding, and reductions in egg and clutch sizes as responses to food shortage. Evidence of food shortage was obtained by assessing diets of adults and chicks to determine when capelin were available to gulls, and what alternate foods were used prior to capelin arrival.

METHODS

Great Island (47°11'N, 52°46'W) lies in the Witless Bay Ecological Reserve in eastern Newfoundland and has been described in detail by Rodway et al. (1996b). Recent gull censuses have not been conducted, but numbers of Herring Gulls apparently increased from 2,100 pairs in 1976 (Pierotti 1982) to 2,770 pairs in 1979 (Cairns et al. 1989).

We compared Herring Gull breeding performance in three nesting habitats identified by Pierotti (1982): "rocky" (exposed rocky shoreline terraces), "puffin" (perimeter areas covered with grassy hummocks where puffins nested in large numbers), and "meadow" (areas interior to puffin habitat covered with tall grass, *Rubus*, and scattered spruce [*Picea mariana*] shrubs). Two study plots were established in each habitat

at the south end of the island. Dimensions of plots were measured and areas calculated to estimate average nest density. In 1992, all nest sites within plots were marked with metal stakes so they could be followed through both years of the study. We assumed that the same pair was associated with a specific nest site in both years. All new nests in 1993 were located and marked with metal stakes.

Study plots were visited at least every 10 days and often every 5 days between 3 June and 13 August 1992, and between 11 June and 21 July 1993. Visitation schedules were chosen as a compromise between potential biases due to investigator-induced mortality caused by frequent visits (Burger 1981) and due to missing eggs and chicks that were depredated between infrequent visits. The first visit to the plots was later in 1993 because poor weather delayed our arrival on the island. Eggs and small chicks were easily recorded on visits to the study plots, but as chicks grew older they became increasingly difficult to locate because they scattered and hid when disturbed. We found in 1992 that searching from a distance by telescope for large chicks was more effective than exploring plots on foot. Because we were not disturbing the birds, we observed nests until we were confident that all chicks had been located. Undisturbed chicks spent time in the openings around their nests, especially when feedings occurred, and could be dependably located even in meadow habitat where tall grasses provided concealment for disturbed chicks. Thus, in 1993, once chicks were large enough to run and hide, we only used telescope observations to determine chick survival, and we believe that telescope observations provided accurate estimates of chick survival in both years. Due to time constraints and because survival to fledging of large chicks was very high in 1992 (96.6% for chicks alive on 21 July), chicks were not monitored through the late nestling period in 1993. Thus, estimates of fledging success in 1993 are maximal.

The condition and contents of nests were recorded during each visit to the study plots. Nests were considered active if they were well formed and appeared to be ready for laying. Scrapes and started nests were not considered active if they did not progress beyond that point. At each nest, eggs were identified and marked using a waterproof pen and laying order was recorded if known. Clutch size was considered the maxi-

imum number of eggs found in a nest at one time.

Unless known, hatch dates were estimated as the midpoint between visits when chicks were first found. Thus, hatch dates were known ± 5 days for all chicks and $\pm 2-3$ days for many chicks. Exact hatch dates were known for 13 and 28 chicks in 1992 and 1993, respectively. Small chicks were marked for identification with one or two spots of differing color under the chin from a waterproof pen, and later, when possible, were banded with U.S. Fish and Wildlife Service metal bands.

Adult and chick diets were assessed. Prey remains at nests during the incubation period were recorded and categorized as garbage, mussels, or petrel (see Pierotti and Annett 1987), prey were identified in boluses regurgitated by chicks when they were handled, and 18 chicks that were found dead at nests were dissected and the contents of their stomachs recorded.

DATA ANALYSIS

Logit models (Fienberg 1977) were used to analyze dichotomous measures of breeding success (e.g., egg hatched or not hatched) in relation to year and habitat categories. Likelihood ratio chi-squares (G^2), comparing observed and expected frequencies, were used to test hypotheses. Tests for individual terms were given by the change in G^2 between two models that differed only by the inclusion of that term (Elliot 1988). Terms were added to the null-logit model in a predetermined, hierarchical sequence (year then habitat) because we wished to test the effects of habitat after year had been considered.

Mean clutch size, number of chicks fledged, and hatching date were compared between years and among habitats using 2-way ANOVA. Tolerance for type I error was set at 5% for all analyses. Residuals were examined for normality and independence for both logit and ANOVA models. Analyses were conducted using SYSTAT (Wilkinson 1990). Means are given \pm SD.

RESULTS

Fewer nests were built in study plots in 1993 than 1992 (Table 1), especially in puffin habitat (differences among habitats: $\chi^2_2 = 5.8$, $P = 0.05$). Nests were more likely to be rebuilt in 1993 at the same locations used in 1992 in rocky (74%) and meadow (74%) habitats than in puffin (42%) habitat ($\chi^2_2 = 29.6$, $P < 0.001$). Average

TABLE 1. Breeding performance of Herring Gulls in different habitats on Great Island, Newfoundland in 1992 and 1993. Hatching, fledging, and breeding success are the proportions of chicks hatched per egg laid, chicks fledged per chick hatched, and chicks fledged per egg laid, respectively. For hatching dates, 1 = 1 June.

Year and habitat	No. active nests	No. nests with eggs (%)	Mean clutch size (\pm SD)	Hatching success (%)	Mean hatch dates [\pm SD (<i>n</i>)]	Fledging success (%)	Breeding success (%)	Mean No. chicks fledged per nest with eggs (\pm SD)
1992								
Rocky	85	70 (82.3)	2.06 \pm 0.78	30.8	22.8 \pm 8.3 (45)	20.0	6.2	0.13 \pm 0.41
Puffin	109	68 (62.4)	1.82 \pm 0.73	24.0	28.1 \pm 9.4 (30)	33.3	8.0	0.15 \pm 0.53
Meadow	97	64 (66.0)	2.14 \pm 0.75	46.7	21.4 \pm 7.4 (64)	14.1	6.6	0.14 \pm 0.35
1993								
Rocky	78	65 (83.3)	1.89 \pm 0.69	41.5	26.7 \pm 7.2 (51)	29.4	12.2	0.23 \pm 0.52
Puffin	59	44 (74.6)	1.91 \pm 0.56	31.0	28.9 \pm 5.0 (26)	7.7	2.4	0.05 \pm 0.21
Meadow	77	49 (63.6)	2.08 \pm 0.67	66.7	24.2 \pm 6.0 (68)	48.5	32.3	0.67 \pm 0.90

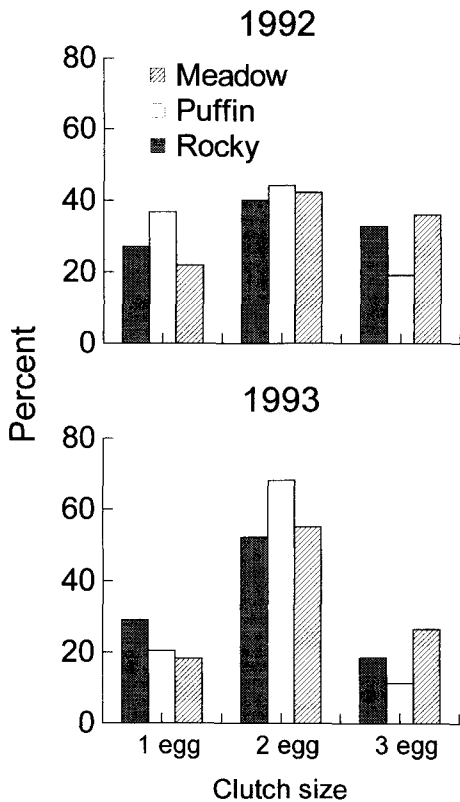


FIGURE 1. Differences in clutch sizes of Herring Gulls in rocky, puffin, and meadow habitats and between 1992 and 1993 on Great Island, Newfoundland. Sample sizes in 1992: 70, 68, and 64; 1993: 65, 44, and 49, in rocky, puffin, and meadow habitats, respectively.

nest density was highest in rocky habitat (0.047 and 0.043 nests m^{-2} in 1992 and 1993, respectively) and was similar in puffin (0.021 and 0.011 nests m^{-2} in 1992 and 1993, respectively) and meadow (0.019 and 0.015 nests m^{-2} in 1992 and 1993, respectively) habitats.

The proportion of completed nests in which eggs were laid did not differ significantly between years and was highest in rocky habitat in both years (Tables 1, 2). Proportions of 1-, 2-, and 3-egg clutches differed between years ($G^2_2 = 9.1$, $P = 0.01$) and among habitats ($G^2_4 = 10.1$, $P = 0.04$; Fig. 1). Two-egg clutches were more frequent in 1993, and puffin habitat had more 1- and 2- and less 3-egg clutches than meadow habitat (Fig. 1), resulting in a larger mean clutch size in meadow than puffin habitat (2-way ANOVA with year: $F_{2,354} = 3.3$, $P = 0.04$; Tukey: $P = 0.03$; Table 1). Nests with larger clutches in 1992 were more likely to be rebuilt at the same locations in 1993 than nests with smaller clutches in 1992 (40, 57, 79, and 76% of nests with 0, 1, 2, and 3 eggs, respectively, were rebuilt in 1993; $\chi^2_3 = 33.6$, $P < 0.001$).

Hatching, fledging, and breeding success were significantly higher in 1993 than 1992, although lower fledging and breeding success in puffin habitat in 1993 than 1992 yielded significant year \times habitat interaction effects for those measures (Tables 1, 2). Hatching success was highest in meadow and lowest in puffin habitat in both years (Table 1). Fledging success did not vary significantly among habitats, but highest success in puffin habitat in 1992 and in meadow habitat in 1993 (Table 1) contributed to the significant year \times habitat interaction (Table 2).

TABLE 2. Summary of logit-model analyses of differences in proportions of Herring Gull nests with eggs, and in hatching, fledging, and breeding success among habitats and between 1992 and 1993 on Great Island, Newfoundland. Terms were added hierarchically in the order listed. G^2 values listed. ** = $P < 0.01$, *** = $P < 0.001$.

Source	df	Nests with eggs	Hatching success	Fledging success	Breeding success
Null-logit	5	19.5**	54.6***	28.6***	51.0***
Year	1	1.2	12.1***	7.4**	15.6***
Habitat	2	16.2***	40.9***	2.5	17.6***
Year × habitat	2	2.1	1.6	18.7***	17.8***

Mean number of chicks fledged per nest increased from 0.14 ± 0.44 in 1992 to 0.32 ± 0.66 in 1993 (2-way ANOVA: $F_{1,354} = 10.1$, $P = 0.002$). Breeding success was similar across habitats in 1992 and was highest in meadow habitat in 1993 (Table 1), resulting in a significant year × habitat interaction (Table 2). Overall breeding

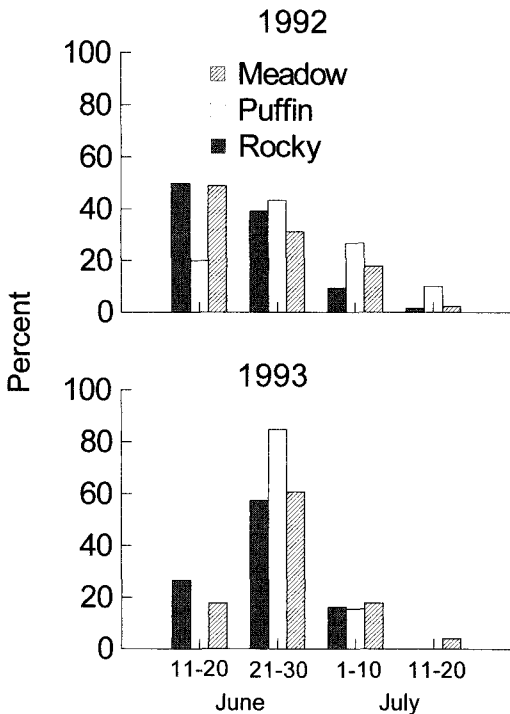


FIGURE 2. Differences in hatching dates of Herring Gull chicks among rocky, puffin, and meadow habitats ($G^2_6 = 15.1$, $P = 0.02$) and between 1992 and 1993 ($G^2_3 = 25.4$, $P < 0.001$) on Great Island, Newfoundland. Sample sizes in 1992: 45, 30, and 64; 1993: 51, 26, and 68, in rocky, puffin, and meadow habitats, respectively.

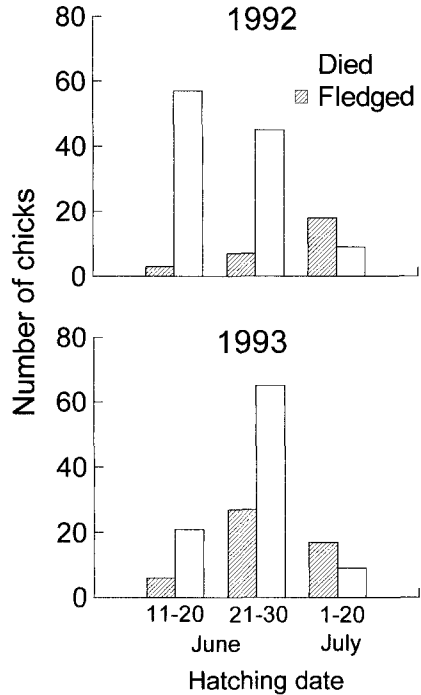


FIGURE 3. Fate relative to hatching date of Herring Gull chicks on Great Island in 1992 ($\chi^2_2 = 46.3$, $P < 0.001$) and 1993 ($\chi^2_2 = 13.9$, $P = 0.001$).

success in all habitats combined was 6.9% in 1992 and 16.2% in 1993.

Distribution of hatching dates differed between years and among habitats (Fig. 2). Mean hatching date was 2 days later in 1993 than 1992 (Table 1). A 2-way ANOVA indicated significant effects due to habitat ($F_{2,278} = 7.0$, $P = 0.001$) and the interaction of year × habitat ($F_{2,278} = 3.4$, $P = 0.04$), but not year ($F_{1,278} = 2.7$, $P = 0.10$). Hatching was earlier in meadow than in puffin habitat (Tukey: $P = 0.001$). Similar mean hatching dates in puffin habitat in 1993 and 1992 and later hatching in meadow (3 days) and rocky (4 days) habitats in 1993 than in 1992 (Table 1) contributed to the significant interaction effect. Significantly more late-hatching chicks survived to fledging than early-hatching chicks in both 1992 and 1993 (Fig. 3).

In relation to clutch size, hatching dates of first-hatched chicks were earlier in larger than in smaller clutches in 1992 ($F_{2,80} = 14.3$, $P < 0.001$) and 1993 ($F_{2,91} = 12.3$, $P < 0.001$; all Tukey pairwise comparisons: $P < 0.05$; Table 3). Hatching success per egg was highest for 3-egg and lowest for 1-egg clutches in 1992 ($F_{2,199}$

TABLE 3. Hatching date and breeding success in relation to clutch size of Herring Gulls on Great Island, Newfoundland in 1992 and 1993. Sample size given in parentheses.

Year and clutch size	Hatch date of first-hatched chick (1 = 1 June)	Mean success		
		Hatching (per egg)	Fledging (per chick)	Breeding (per egg)
1992				
1 egg	37.3 ± 9.1 (4)	0.07 ± 0.26 (58)	0.50 ± 0.56 (4)	0.03 ± 0.18 (58)
2 eggs	26.9 ± 9.4 (35)	0.31 ± 0.40 (85)	0.29 ± 0.43 (35)	0.09 ± 0.23 (85)
3 eggs	20.0 ± 5.9 (44)	0.47 ± 0.33 (59)	0.13 ± 0.29 (44)	0.06 ± 0.18 (59)
1993				
1 egg	30.9 ± 6.2 (18)	0.49 ± 0.51 (37)	0.50 ± 0.51 (18)	0.24 ± 0.44 (37)
2 eggs	25.6 ± 6.2 (49)	0.40 ± 0.41 (91)	0.31 ± 0.45 (49)	0.15 ± 0.34 (91)
3 eggs	22.1 ± 5.1 (27)	0.61 ± 0.30 (30)	0.25 ± 0.38 (27)	0.16 ± 0.27 (30)

= 19.9, $P < 0.001$; all Tukey pairwise comparisons: $P < 0.05$) and higher for 3-egg than 2-egg clutches in 1993 ($F_{2,155} = 3.1$, $P = 0.05$; Tukey: $P = 0.04$). Hatching success of 1-egg clutches was much higher in 1993 than 1992 (Table 3). Fledging success per chick hatched was highest from 1-egg and lowest from 3-egg clutches (1-way ANOVA: $F_{2,174} = 5.7$, $P = 0.004$), but the effect was entirely due to later hatching dates of smaller clutches (ANCOVA with hatching date: $F_{2,173} = 0.2$, $P = 0.8$ and $F_{1,173} = 30.9$, $P < 0.001$ for effects of clutch size and hatching date, respectively). Breeding success per egg did not vary significantly by clutch size ($F_{2,357} = 0.3$, $P = 0.8$; Table 3).

Most eggs that did not hatch disappeared from nests (94% in 1992 and 86% in 1993). Many were taken by conspecifics and Great Black-backed Gulls (*Larus marinus*). Small numbers were addled, died while pipping, or were broken. Most chick mortality occurred within 10 days of hatching in both years (71% in 1992 and 94% in 1993). Of chicks that did not fledge, proportions that were found dead at the nest did not differ between years ($G^2_1 = 1.6$, $P = 0.2$) but varied among habitats ($G^2_2 = 7.8$, $P = 0.02$). Proportions found dead at the nest were highest in meadow (27%, $n = 90$) and lowest in puffin habitat (9%, $n = 44$; 17%, $n = 72$ in rocky habitat). The stomachs of 18 dead chicks (found between 30 June and 12 July 1992 and 25 June and 10 July 1993) that were dissected contained only small amounts of grass and fiber (13 chicks), insect exoskeletons (4 chicks), or stones (3 chicks). The only exception was a stomach full of Leach's Storm-Petrel (*Oceanodroma leucorhoa*) feathers.

Mussels (*Mytilus edulis*), garbage, and petrels

were the main prey remains found at nests. Garbage was most common in all habitats (83, 44, and 45% of recorded remains in rocky, puffin, and meadow habitats, respectively; $n = 122$). Petrel remains were found primarily in meadow (36%), were less common in puffin (26%), and were not recorded in rocky habitat. Mussels formed 17, 30, and 19% of remains found in rocky, puffin, and meadow habitats, respectively. Capelin and their roe comprised the majority (20 of 31) of regurgitations collected from chicks. Other boluses regurgitated contained fish offal (3), mussels (2), 15–20 caterpillars (2), sow bugs and chicken (1), several hundred ants (1), partridge berries (*Vaccinium* spp.—1), and grass (1). Capelin were first recorded in chick regurgitations on 5 July and were the only item found in regurgitations after that date in both years.

DISCUSSION

Reproductive performance may be influenced by a suite of interacting factors that differentially affect birds in different habitats during periods of food shortage. Increased costs may induce some pairs, especially younger birds, to forgo breeding (Pyle et al. 1997). Those that do breed may be older, higher-quality individuals that, because of better skills and accumulated experience, are better able to cope with food stress (Greig et al. 1983). Food stress may produce density-dependent (e.g., increased cannibalism—Brouwer and Spaans 1994) and density-independent (e.g., lower nest attendance—Bukacinska et al. 1996) changes in behavior that affect breeding success. Relative importance of structural characteristics of habitats and the social environment may differ during stressful and benign conditions. Thus, differences in breeding

performance among individuals that vary in competitive ability, and among habitats that vary in their associated costs and benefits for their inhabitants, may be difficult to predict during stressful periods.

Herring Gulls on Great Island in 1992 and 1993 were food stressed by the late arrival of capelin and the lack of alternate prey prior to capelin arrival. Egg and clutch sizes were smaller (although our estimates of clutch size may be biased downward because of the high rate of egg disappearance) and mean hatching dates were later than in 1976–1978 (Pierotti 1982). Breeding success was 7–16% during 1992–1993 compared to 56–64% in 1976–1978. Both hatching and fledging success were reduced. Smaller clutch sizes acted to further reduce the number of chicks fledged compared to 1976–1978. Success was lower in all habitats, except hatching success in meadow habitat in 1993 (67%) which was similar to that found by Pierotti in that habitat in 1977 (68%). Productivity in 1992–1993 was insufficient to maintain population levels over the long-term (Kadlec and Drury 1968), and reversal of recent population trends can be expected if oceanographic and anthropogenic changes persist (Howes and Montevicchi 1993).

Arrival of capelin in inshore waters was delayed over a month in 1992–1993 (Nakashima 1996) compared to 1977–1978 (Pierotti and Annett 1987). Herring Gull chicks were fed capelin as soon as they hatched in 1977–1978, whereas capelin were first seen in chick diets in 1992–1993 almost 4 weeks after hatching began and after most chicks had hatched. All dead chicks dissected in 1992–1993 appeared to have died of starvation. The variety of unusual items in the diet of chicks and the large number of chicks that died prior to capelin arrival indicate that alternate food sources were not readily available. Difficult foraging conditions also probably contributed indirectly to high egg and chick mortality by reducing adult attendance at nests (Oro et al. 1997) and increasing predation from conspecifics and Great Black-backed Gulls (Hatch and Hatch 1990).

Our results differ from those of both Murphy et al. (1992) and Järvinen and Väisänen (1984) who found positive and negative relationships, respectively, between clutch size and hatching and fledging success during stressful periods. In this study, larger clutches and earlier laying, behavior generally associated with older, more ex-

perienced and higher quality individuals (Nelson 1988), were positively related to hatching success, as found by Murphy et al. (1992). However, fledging success was inversely related to clutch size because of the later hatching dates of smaller clutches. Late arrival of capelin resulted in an advantage for late-hatching chicks, contrary to trends found in 1976–1978 on Great Island (Pierotti 1982) and in many other studies (Brouwer et al. 1995). Lower post-fledging survival may have diminished the advantage for late-hatching chicks (Parsons et al. 1976), but the late arrival and protracted spawning period of capelin in 1992–1993 (Nakashima 1996) could have provided an adequate food source that allayed somewhat the typical disadvantage of fledging late in the season. Differences in the relationships between clutch size and hatching and fledging success found in our study and those of Murphy et al. (1992) and Järvinen and Väisänen (1984) indicate that responses to food shortage are variable and probably depend on the degree and timing of food shortage in relation to breeding chronology (Vermeer 1980, Murphy et al. 1984).

Trends across habitats differed from those found by Pierotti (1982). Success tended to be lowest in meadow and highest in puffin and rocky habitats in 1976–1978 and highest in meadow and lowest in puffin habitat in 1992–1993. Results did not match predictions of ideal-free or ideal-despotic models that success in preferred habitat would be equal to or greater than success in other habitats. That rocky was still the preferred habitat, as concluded by Pierotti (1982), was evidenced by higher nest density, a greater proportion of completed nests that had eggs laid in them suggesting a greater proportion of females with sufficient body reserves to initiate breeding, and minimal reduction in the number of nests between 1992 and 1993 compared to puffin and meadow habitats (Table 1). Buffering of nest density (Kluyver and Tinbergen 1953, Brown 1969) in rocky habitat also was apparent during favorable periods when populations were increasing in the late 1970s (Pierotti 1982). In contrast, variation in nest density was highest in puffin habitat (27% increase in 1976–1978 and 46% decrease in 1992–1993). Such large interannual variation in nesting attempts suggests that puffin may be the least preferred habitat, inhabited by a greater proportion

of younger birds that are less site tenacious and more likely to forgo breeding in a poor year.

Predictions of theoretical models of habitat selection are difficult to test when habitat suitabilities vary over time as found in this study. Interannual differences within and between this study and Pierotti's (1982) indicate that breeding performance is highly variable across habitats and that trends are difficult to predict. Analyses of data from 1992–1993 revealed significant interactions between year and habitat for timing of breeding, fledging success, and breeding success. Pierotti (1982) found similar interannual differences in trends across habitats for timing of breeding, clutch size, hatching success, chick growth rates, fledging success, and breeding success. In both studies, components of breeding performance did not vary concordantly among habitats, suggesting differential impacts of environmental and behavioral changes on performance measures in each habitat (cf. Hatch and Hatch 1990, Bunin and Boates 1994).

Several factors may have contributed to generally higher hatching and fledging success in 1993 than in 1992. Age composition of breeding pairs may have shifted towards more older, experienced birds because pairs laying smaller clutches in 1992 were less likely to renest in 1993. Timing of hatching was later, at least in meadow and rocky habitats, thus reducing the portion of the nestling period when capelin were unavailable. Finally, oceanographic conditions ameliorated, evidenced by earlier arrival of capelin inshore (Nakashima 1996) and concordant higher breeding success for Atlantic Puffins (*Fratercula arctica*; Rodway et al. 1996b) and Black-legged Kittiwakes (*Rissa tridactyla*; Regehr and Montevecchi 1997) on Great Island. Lower fledging success in 1993 than in 1992 in puffin habitat presents an anomalous trend. Later hatching in puffin than in meadow and rocky habitat would have provided an advantage relative to capelin arrival and may account for highest fledging success in puffin habitat in 1992. Hatching was not delayed in 1993 compared to 1992 in puffin habitat as it was in meadow and rocky habitat, but still was later in puffin than in the other two habitats. Thus, if timing of hatching relative to capelin arrival was the differentiating factor, it is puzzling why fledging success was so low in puffin habitat in 1993. We suspect that predation was another important factor contributing to habitat trends.

Conspecific and Great Black-backed Gull predation were probably the main causes of Herring Gull egg and chick disappearance (Haycock and Threlfall 1975, Pierotti 1982, 1987). Pierotti (1982) blamed lower hatching and fledging success in meadow habitat in 1976–1978 (although hatching success was lowest in meadow habitat in only 1 of 3 years—Table 12 in Pierotti 1982) on egg and chick predation by Great Black-backed Gulls that nested preferentially in meadow habitat (Pierotti and Annett 1991). Great Black-backed Gull nests were uniformly distributed among habitats in our study plots used in 1992–1993 (2, 3, and 2 nests in rocky, puffin, and meadow habitats, respectively) and differential effects of Great Black-backed Gull predation may not have been important. We suspect that the main factors that contributed to higher success in meadow habitat in 1992–1993 were low density and greater nest cover. Most nests (67%) in meadow habitat (compared to 7% in puffin habitat) were placed under cover of low-lying spruce shrubs or small trees. Remaining nests in the open in meadow habitat were generally surrounded by 30–60 cm tall grasses. Thus, the majority of nests in meadow habitat were obscured from view, and all nests provided good hiding places nearby for mobile chicks (we often found it impossible to find chicks that ran into tall grasses at our approach, which was one of the reasons we resorted to telescope observations to determine chick survival). Because nest density was low, chicks could scatter into the grasses without suffering attacks from neighboring adults. Chicks in puffin or rocky habitat were visible from a distance and we generally had little trouble finding them, even if they hid in the mouth of a puffin burrow. We have no direct evidence to evaluate the importance of cover in reducing predation in meadow relative to other habitats, but the consistently higher hatching success and the greater proportion of chicks found dead at the nest that had not been taken by predators or scavengers in meadow habitat provides indirect evidence to support this idea.

In addition to changes in the distribution of Great Black-backed Gull nests, two other changes may have altered habitat suitabilities since Pierotti's study. Pierotti (1987) observed that Herring Gulls foraging on Leach's Storm-Petrels in meadow habitat cannibalized eggs and chicks and induced increased levels of intraspecific ag-

gression among gulls nesting in that habitat. Few storm-petrels nested in Herring Gull study plots in meadow habitat in 1992–1993, and gulls specializing on petrel were unlikely to be foraging among nests of conspecifics. In puffin habitat, Pierotti (1987) observed low levels of aggression between residents and intruders and reported only resident gulls kleptoparasitizing puffins (Pierotti 1983). In 1992–1993, kleptoparasitic intruders outnumbered resident gulls, at least doubling the “effective density” (Jehl 1994), and aggressive encounters between them were common (Rodway, unpubl. data). Thus, changes in foraging behavior of Herring Gulls preying on petrels and kleptoparasitizing puffins in combination with changes in the distribution of predatory Great Black-backed Gulls may have contributed to reversal of the relative suitabilities of puffin and meadow habitats since Pierotti’s study.

Changing suitabilities in variable environments may result in poor tracking of resources (Wiens 1985). Information gained by prospecting birds on conspecific, habitat-related breeding success could result in preferential settlement in habitats where breeding success has recently been high (Boulinier and Danchin 1997). Inter-annual differences in relative success among habitats due to variable environmental conditions could serve to maintain flexibility in habitat choice among recruiting individuals (Hilden 1965, Partridge 1978) and encourage unsuccessful breeders to re-assess their habitat choices (Switzer 1993, Boulinier and Danchin 1997). However, if habitat suitabilities vary at the same or smaller temporal scales as the time lag between prospecting and recruitment, then optimal habitat would not be well tracked by recruiting birds, and habitat selection may be to a large extent independent of current habitat suitability (Cody 1985, Orians and Wittenberger 1991). One interesting result of this and Pierotti’s study is that rocky habitat apparently is still the preferred habitat of Herring Gulls on Great Island even though breeding success has been as high or, more frequently, higher in other habitats over the 5 years they have been compared. In addition, rocky habitat comprises only about 10% of the nesting habitat on Great Island and most recruitment during periods of population growth probably comes from less-preferred habitats (Pierotti 1982). That rocky was the original nesting habitat on Great Island (Pierotti 1982) sug-

gests an ultimate, probably genetic component to habitat selection (Hilden 1965, Jaenike and Holt 1991) by Herring Gulls, which, in the absence of consistent trends in habitat suitability, has maintained the preference for rocky habitat observed in the two studies. Longer term studies comparing lifetime reproductive success will be required to determine whether this behavior is still adaptive.

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