

BEHAVIORAL CONSEQUENCES OF HABITAT SELECTION IN THE HERRING GULL

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ABSTRACT.—Data were collected on time budgets, rates of chick provisioning, and patterns of aggressive behavior in Herring Gulls *Larus argentatus* that nested in three distinct habitats on Great Island, Newfoundland. Exposed marine terraces (rocky habitat) had the highest nest density, and territories were subject to high levels of intrusion by prospecting conspecifics. This resulted in high levels of aggressive interaction, yet these birds had high breeding success. In contrast, gulls nesting in meadows suffered a high rate of predation on eggs and young. This predation pressure forced male birds to remain on their territories to defend their nests, which resulted in high rates of neighbor-neighbor aggressive interaction, and a reduced rate of chick provisioning by males. The third habitat, grass-hummock covered maritime slopes (puffin habitat) had low nest density and little or no predation pressure. This resulted in low levels of aggressive interaction and reduced vigilance with no apparent decline in offspring production. The results of this study demonstrate how habitat choice can have behavioral consequences that contribute to variation in offspring production within a species.

Most investigations of habitat selection in birds stress comparisons between species (e.g., Klopfer 1963, Hilden 1965; Partridge 1974, 1976, 1978), or the adaptation of species to specific types of habitat (e.g., Cullen 1957). These studies emphasize specific adaptations to particular habitats and how these adaptations allow different species to coexist (e.g., Cody 1985). Another important, but often ignored, aspect of avian ecology is variation within one species in the selection of a habitat for nesting, and the costs and benefits of settling in one habitat as opposed to another, since selection pressures—e.g., intensity of predation, availability of food—may vary among habitats. Investigations of these costs and benefits provide insights into how natural selection works by demonstrating how fitness (measured as the number of surviving offspring) varies within a population.

Studies of seabird breeding biology have provided some of the best examples of this phenomenon. Nettleship (1972) demonstrated variation in reproductive output over two seasons between habitats in the Atlantic Puffin (*Fratercula arctica*). Burger (1984) has shown that nest density and reproductive output varied among habitats in Herring Gulls (*Larus argentatus*) in New Jersey, although in this study data were lumped from different habitats over a three-year period. Finally, Pierotti (1982) showed that laying and hatching dates, clutch size, egg weight, hatching success, chick growth rates, and fledging success varied consistently among habitats and between years in the Herring Gull in Newfoundland.

To effectively demonstrate the costs and benefits of settling in a particular habitat, it is necessary to collect data on the behavior, ecology, and reproductive output of different individuals of the same species and sub-populations that live

in neighboring but different habitats. Observations of the amount of time spent in various activities—e.g., anti-predator activities or foraging—by different individuals in different habitats allows the assessment of the magnitude of various selection pressures and the possible impact of interactions between these factors. Data have been published on breeding biology of Herring Gulls in three habitats on Great Island, Newfoundland (Pierotti 1982). In this paper, data collected on activity budgets, rates of chick provisioning, the nature and rates of aggressive interaction, and the impact of predation and intraspecific competition on these factors in Herring Gulls in the same three habitats will be described.

METHODS

This study was carried out between 10 June and 10 August 1976, and 5 May through 10 August in 1977 and 1978 on Great Island, Newfoundland (47°11'N, 52°46'W). For general descriptions of the island see Nettleship (1972) and Pierotti (1982). Data were collected in three distinct habitats, which were designated as "rocky" (exposed marine terraces at the southern and western periphery of the island), "puffin" (maritime slopes covered with grassy hummocks where Atlantic Puffins nested in large numbers), and "meadow" (flat, grassy areas on flat plateaus atop the southern portion of the island). Data were collected daily on breeding biology (laying and hatching dates, egg and clutch size) from 5 May until 1 June, and then on alternate days from 1 June until 31 July (hatching dates, chick growth and mortality; see Pierotti 1982).

In 1977 and 1978, continuous, all day (0600–2100) observations of behavior were conducted from blinds located in each of the three habitats on a rotating basis from the first week of June until August. These all-day watches were alternated with days during which data on breeding biology were collected, so that three or four days a week were spent observing behavior until the end of July. Observations were conducted using a zoom (20–60×) spotting scope or 10 × 50 binoculars.

To minimize disturbance, an effort was made to recognize individuals without handling adult birds. Some birds were identified using a system in which distinct

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TABLE 1
SIZES OF MEALS FED TO HERRING GULL CHICKS ON
GREAT ISLAND, NEWFOUNDLAND

Year	Habitat	Capelin per meal Mean \pm SD (N)	Squid per meal Mean \pm SD (N)
1977	Rocky	3.6 \pm 0.8 (112)	2.2 \pm 0.3 (61)
	Puffin	3.5 \pm 1.0 (63)	2.0 \pm 0.4 (35)
	Meadow	3.5 \pm 0.7 (87)	2.1 \pm 0.4 (29)
1978	Rocky	4.2 \pm 1.1 (73)	2.3 \pm 0.6 (24)
	Puffin	3.8 \pm 1.3 (62)	2.1 \pm 0.8 (16)
	Meadow	3.9 \pm 1.0 (84)	2.2 \pm 0.8 (29)

natural markings (e.g., holes or tears in webbing of feet, scratches on bill) were noted (Pierotti 1981). Males and females were identified by noting the role taken in copulation, by natural markings, and by the larger size of the male (Fox et al. 1981, Pierotti 1981). Many individuals were also dyed for identification using Rhodamine (puffin habitat), Malachite green (meadow habitat), and picric acid (rocky habitat). The technique employed was to remove the entire clutch from a nest. A piece of plastic wrap and a dummy clutch (of hard-boiled gull eggs) were then placed in the nest cup, and dye was poured over these eggs. When birds returned to the nest they marked themselves by sitting on and shifting the eggs. After a period of one to two hours, the dummy eggs and plastic wrap were removed and the original clutch was returned. This procedure appeared to have no effect on subsequent hatching or fledging success.

In each of the three habitats, twelve territories on which both the male and female were individually recognizable were selected for monitoring during the 1977 breeding season. The same 12 pairs were monitored in rocky habitat during both 1977 and 1978. In puffin habitat 10 of the original 12 pairs, and in meadow habitat 11 of the original 12 pairs were monitored in both years. These individuals were recognizable from one year to the next by individual markings. The same number of days were spent observing birds in each habitat.

Data on time budgets were collected using a combination of scan-sampling and ad libitum sampling (Altmann 1974) on the 12 focal territories. Every 15 minutes all twelve nests were scanned and the presence or absence of individuals and the activity in which they were engaged, if present—e.g., incubating, sleeping—was noted. Data on discrete behavioral acts (e.g., chick feeding, aggressive acts) were recorded during the intervals between scans. During observation periods, the type and number of food items presented to chicks in a given feeding were noted whenever possible. This was not difficult, because Herring Gulls typically regurgitated entire freshly caught fish or squid. All such data were collected by observation through the spotting scope.

Acts of aggressive behavior were noted as to type, identity of aggressor, and identity of recipient of the aggression (e.g., neighbor male, intruder female; all neighbors were individually recognizable). Eight distinct aggressive displays were noted and subdivided into three levels of aggressive intensity that reflect the

possible energetic cost and risk of the display. Aggressive uprights, long-calls, and choking (see Tinbergen 1960) were simple displays and considered to be of low intensity (Level 1). More active and energetically costly displays, e.g., grass-pulling and supplants (running at an individual and causing it to take flight), were considered to be of moderate intensity (Level 2). Interactions involving active pursuit or physical contact, e.g., fights, hitting, supplants followed by aerial pursuit, were considered to be of high intensity (Level 3). Long calls and choking may occur in both aggressive and sexual contexts (Hand 1979); therefore, the contexts of displays were noted, and those acts performed between members of a pair were not included in the analysis of aggressive behavior.

I also noted the number of adult gulls other than neighbors that intruded into territories during 15 hours of observation in each habitat in 1978 during which no other data were collected. These birds were clearly not residents of the area since they were not recognizable, and were probably non-breeding birds scouting for available space for nesting. Using a stopwatch, I timed the interval from the time one of these "intruders" landed until it was evicted by a resident individual.

All data sets were tested for normality and homoscedasticity. Where these conditions were met, parametric statistics (t-test, ANOVA) were employed. In cases where distributions were either non-normal or excessively heteroscedastic, other statistical tests were employed, e.g., Chi-square, Wilcoxon's signed-ranks test, or Kruskal-Wallis test. In cases where ANOVAs were found to show significant differences among samples, Student-Newman-Keuls (SNK) tests were used to examine range differences among samples (Sokal and Rohlf 1981).

RESULTS

TIME BUDGETS

The 1977 reproductive period was very stormy early in the breeding season and food appeared to be difficult to obtain because (1) more Herring Gulls were observed to feed on garbage, a food on which they did more poorly (31% of population specialized on garbage) early in the breeding season than in 1978 (21% garbage specialists; Pierotti and Annett 1986), and (2) meal sizes of capelin (*Mallotus villosus*: a principal food fish of seabirds on Great Island) were smaller than in 1978 (Table 1). In 1977, capelin did not appear in large numbers in the waters around the island (Pierotti and Annett 1986). As a result, egg-laying was delayed, egg and clutch sizes were smaller, and chicks grew at a slower rate than during the 1978 breeding season (Pierotti 1982).

The 1978 breeding season was very calm compared with 1977, and food appeared to be abundant. Garbage declined in the diet (Pierotti and Annett 1986). Capelin were abundant in the waters around Great Island beginning in early June as indicated by the increase in meal size, the foraging patterns of the gulls, and the presence in the area of large numbers of humpback

whales, *Megaptera novaeangliae*, which also feed on capelin. Egg size, clutch size, and chick growth rates all increased significantly compared with 1977 (Pierotti 1982).

Incubation period

I define the incubation period as the period from the laying until the hatching of the first-laid egg. During this period, one member of each pair was on the nest except when disturbed, or during brief (1–2 minute) absences to defecate or drive off an intruder.

During the 1977 breeding season female Herring Gulls nesting in puffin habitat were present on their territories significantly less time per day than female gulls in either rocky or meadow habitat (mean = 64 ± 16.3 minutes, $P < 0.05$ by ANOVA). Male and female gulls spent equivalent amounts of time present on their territories in puffin and meadow habitat, whereas male gulls in rocky habitat were present significantly less than their mates (Fig. 1a). Overall, puffin habitat had the lowest percentage of time when both the male and female were present together on the territory, whereas meadow habitat had the highest percentage of time when both members of the pair were present.

The role of male and female gulls in incubation in the three habitats reveals a similar pattern. There were significant differences in the amount of time spent in incubation between the sexes in all three habitats, with females spending more time incubating. This difference was smallest in puffin habitat where males spent significantly more time in incubation than males in other habitats (Fig. 1a). In contrast, male gulls in rocky habitat spent the least time in incubation. Male gulls in rocky habitat spent only 51% of their total time on the territory incubating compared with 70% for males in puffin habitat.

Time budgets were quite different in rocky and meadow habitats during the 1978 breeding season. As in 1977, female gulls nesting in puffin habitat were present less (mean = 47 ± 14.7 minutes, $P < 0.05$ by ANOVA), and males and females spent less time together on the territory than in the other habitats. There was, however, no significant difference between males and females in amount of time spent incubating in puffin habitat in 1978. In meadow habitat females spent more time than males on the territory, which was not the case in 1977, and in incubation (cf. Fig. 1a and 1b). Also in contrast to 1977, there was no difference in the amount of time male and female gulls in rocky habitat were present, although males spent slightly less time incubating. Male gulls in meadow habitat, however, were present significantly more in 1977 than in 1978.

This variation in attendance of male gulls in meadow habitat appeared to be related to intensity of nest predation. During all three years of this study, the number of eggs and chicks that disappeared was greatest in meadow habitat (Table 2). Most of these disappearances were probably attributable to predation both by conspecifics and by Great Black-backed Gulls, *Larus marinus*, which nested almost exclusively in meadow habitat. In 1977, when food supplies were low, percentages of egg and chick disappearance were higher than in any other year (Table 2). This increase in nest predation was most marked in meadow habitat where nearly 20% of the eggs and 35% of the chicks produced by the 90 pairs monitored in this habitat disappeared. During such periods, male vigilance increased, as indicated by the increased amount of time spent on the territory by male gulls in meadow habitat, and by the increased rate of aggressive interaction shown by males in this habitat during 1977 (see below).

Chick period

For each nest, the chick period was defined as the period from when the first chick hatched until the last surviving chick fledged from the nest. Chicks were considered fledged when they were capable of sustained, independent flight away from the natal territory. Typically at least one parent was in attendance on the territory at all times during this period.

In contrast to the incubation period, there were no significant differences in the amounts of time spent on the territory by males and females in any of the three habitats during either year (Fig. 1a, b). There were also no significant differences in attendance patterns among the habitats, since either the male or female was present on the territory at all times.

During the 1977 season broods of chicks in puffin habitat were fed significantly less frequently than broods in the other two habitats (Table 3). During both years there were significant differences in feeding rate between male and female gulls in rocky habitat, and the rates of chick feeding by males and females were identical in meadow habitat (Table 3). Despite the difference in feeding rates, there were no significant differences in meal sizes among the habitats for either capelin or squid (*Illex illecebrosus*; Table 1). These two food types constituted over 95% of all chick feedings observed.

There was no obvious relationship between feeding rates and chick survival (Table 3). During 1977 in territories monitored during behavioral observations, fledging success was highest in rocky habitat, followed by puffin habitat. Meadow habitat had the lowest fledging success ($P < 0.01$ by

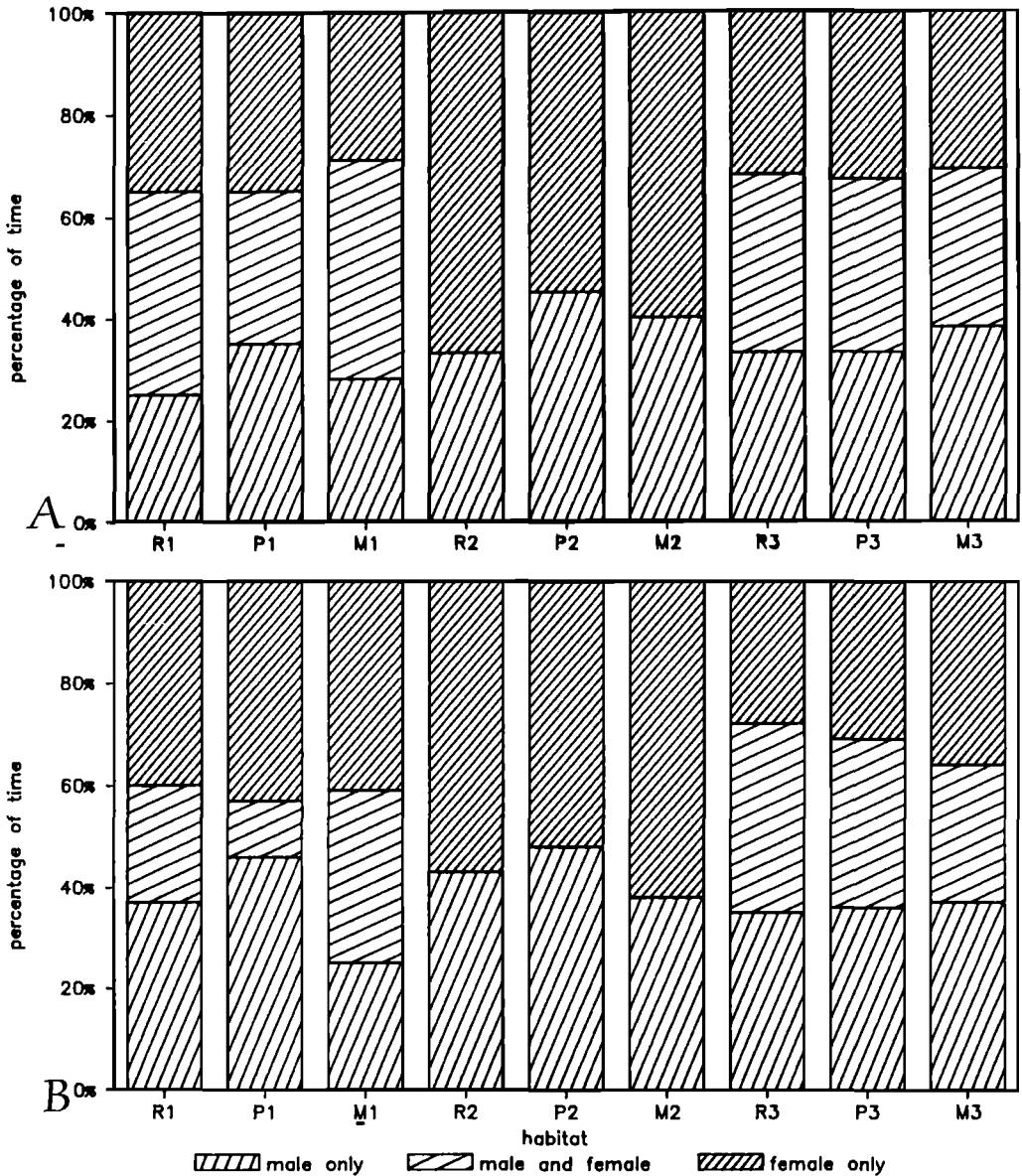


FIGURE 1. Activity budgets of male and female gulls during 1977 and 1978 breeding seasons. Data expressed as percentage of total time spent in observation = 15 hours/day over 6 days in both years. R1, P1, and M1 = birds present in rocky (R), puffin (P) and meadow (M) habitats, respectively, during May and early June (incubation period); R2, P2, and M2 = birds on nests incubating; R3, P3, M3 = birds present on territories during late June and July (chick-rearing).

A. 1977 season: Amount of time spent on territory during incubation differs among habitats for females and for males and females together at 0.5 level by ANOVA (for 1's, P less than R and M at .01 level by SNK). Males incubate significantly less than females in all three habitats (paired sample t test; for R, $P < .001$, for P, $P < .05$, and for M, $P < .01$).

B. 1978 season: Results similar except that males incubated significantly less than females only in R and M (paired sample t test; for R, $P < .05$, and for M, $P < .01$).

TABLE 2
PERCENTAGES OF HERRING GULL EGGS AND CHICKS THAT EITHER DISAPPEARED OR WERE EATEN DURING
THREE YEARS ON GREAT ISLAND, NEWFOUNDLAND

Year	Habitat			% Killed by GBBG (meadow habitat only)
	Rocky	Puffin	Meadow	
A. Eggs¹				
1976 ³	0.6 (161) ²	3.2 (155)	5.9 (188)	not applicable
1977 ⁴	9.4 (286)	11.6 (301)	18.9 (228)	n.a.
1978 ⁴	8.6 (304)	7.7 (363)	13.0 (223)	n.a.
B. Chicks				
1976 ⁴	5.5 (121)	21.3 (122)	31.5 (143)	9.8
1977 ⁴	7.6 (131)	16.7 (138)	34.2 (111)	9.9
1978 ⁴	2.1 (141)	9.4 (202)	17.1 (111)	14.4

¹ Data in 1976 incomplete because of arrival on island after peak of clutch completion.

² (N) = total number monitored in each habitat

³ $P < .05$ by Chi Square test (among habitats).

⁴ $P < .001$ by Chi Square test (among habitats).

chi square, 4 df) despite the fact that chicks in this habitat were provisioned at the same rate as in rocky habitat. This pattern was similar to the pattern observed for all nests monitored on Great Island in 1977, except that rocky and puffin habitat had similar rates of fledging success (Pierotti 1982). In 1978, there were no significant differences in fledging success, although the pattern observed in provisioning rate among the three habitats for the 12 pairs monitored during behavioral observations was the same as in 1977 (Table 3). For all nests monitored during 1978 there were no significant differences in fledging

rates between rocky and puffin habitats but pairs in meadow habitat had significantly lower fledging success (Pierotti 1982). In both years, however, chicks in rocky habitat grew at significantly faster rates than did chicks in the other two habitats (Pierotti 1982, tables 5-7).

AGGRESSIVE BEHAVIOR

Patterns of aggressive behavior in both male and female gulls varied among habitats. This variation could be related to differences in time budgets, fledging success, and the three-dimensional structure of the habitats. Rocky habitat

TABLE 3
RATE OF BROOD PROVISIONING IN RELATION TO BREEDING SUCCESS IN ALL THREE HABITATS ON GREAT ISLAND
DURING THE BREEDING SEASONS OF 1977 AND 1978

Habitat	Sex	Chick feedings/hr ^{a,b} (mean \pm sd)	Chicks fledged/pair (mean \pm sd)
A. 1977			
Rocky (N = 12)	Male	0.19 \pm 0.04 ^{c,d}	2.00 \pm 0.68 ^e
	Female	0.12 \pm 0.02	
Puffin (N = 12)	Male	0.13 \pm 0.03	1.67 \pm 0.65
	Female	0.10 \pm 0.03	
Meadow (N = 12)	Male	0.15 \pm 0.04	1.08 \pm 0.79
	Female	0.15 \pm 0.04	
B. 1978			
Rocky (N = 12)	Male	0.18 \pm 0.05 ^d	1.68 \pm 1.01
	Female	0.11 \pm 0.03	
Puffin (N = 12)	Male	0.14 \pm 0.04	1.75 \pm 0.83
	Female	0.10 \pm 0.04	
Meadow (N = 12)	Male	0.14 \pm 0.04	1.77 \pm 0.89
	Female	0.14 \pm 0.05	

^a Chick feedings/hr represent the number of times an adult male or female gull returned to the territory after an absence greater than 20 minutes and fed chicks. It does not include repeat feeds from the same feeding bout.

^b For both years, the total rate of chick provisioning (male + female) was significantly different among habitats at the .05 level by ANOVA ($P < .05$, M at .05 level by SNK).

^c For rate of male provisioning, differences among habitats significant at .05 level by ANOVA (R greater than P, M at .05 level by SNK).

^d In rocky habitat in both years, difference in provisioning rate by male and female gulls significant at .05 level by paired sample t test.

^e In 1977, difference among habitats in fledging rate significant at .05 level by Chi Square test, with 4 df.

TABLE 4
FREQUENCY OF AGGRESSIVE INTERACTIONS (NUMBER PER HOUR) OF MALE AND FEMALE HERRING GULLS ON GREAT ISLAND DURING THE REPRODUCTIVE SEASONS OF 1977 AND 1978

Habitat (N = no. pairs)	Sex	Interactions between neighbors*			Total between neighbors	Interactions between residents and intruders			Total between resident and intruder
		Level 1	Level 2	Level 3		Level 1	Level 2	Level 3	
A. 1977									
Rocky (12)	Male ^b	1.45	1.85	0.56	3.86	0.74	2.91	1.23	4.88
	Female ^c	0.72	0.24	0.07	1.03	0.57	1.43	0.29	2.29
Puffin (12)	Male	1.00	3.38	0.78	5.16	0.28	1.05	0.41	1.74
	Female	0.32	0.13	0.04	0.49	0.13	0.53	0.76	1.42
Meadow (12)	Male	1.88	5.74	1.08	8.70	0.51	1.39	0.25	2.15
	Female	0.85	0.43	0.12	1.40	0.30	0.46	0.08	0.84
B. 1978									
Rocky (12)	Male ^b	1.70	1.84	0.41	3.95	1.35	2.49	1.00	4.84
	Female ^c	1.10	0.30	0.10	1.50	0.64	0.94	0.24	1.82
Puffin (12)	Male	0.97	2.45	0.20	3.62	0.26	0.44	0.27	0.97
	Female	0.46	0.17	0.01	0.64	0.13	0.31	0.04	0.48
Meadow (12)	Male	2.17	3.41	0.63	6.21	0.64	0.66	0.23	1.53
	Female	1.00	0.99	0.31	2.30	0.21	0.31	0.24	0.76

* In meadow habitat neighbors include Great Black-backed Gulls.

^b Rates of aggression among habitats significantly different for males at .001 level by Chi Square test, 5 df.

^c Rates of aggression among habitats significantly different for females at .01 level by Chi Square test, 5 df.

was most heterogeneous, with the highest density of nesting birds (Pierotti 1982). Puffin habitat was the least spatially heterogeneous with the lowest nesting density and meadow habitat was intermediate in both variables.

During both years of the study, male and female gulls in rocky habitat directed more aggression towards nonresident conspecifics (intruders) than towards neighbors (Table 4; $P < 0.001$, Fisher's exact test). The rate of intrusion in rocky habitat was more than twice the rate of intrusion in either of the other habitats (Table 5). During both 1977 and 1978, female gulls in rocky habitat directed more aggression at intruders than did

male gulls in either puffin or meadow habitat (Table 4). These intruders were not "loafers," seeking temporary resting sites. Nearly all were adult birds and appeared to be seeking nesting sites. When not displaced by resident birds, they were often joined by a partner of the opposite sex, with whom they would participate in chok-ing displays and initiate nest construction. Other intruders not displaced by resident birds would approach residents while producing vocalizations typical of pair-formation or bonding, e.g., begging calls or mew calls (Tinbergen 1960, Hand 1979). As a result, intruders elicited responses of moderate and high intensity at a significantly

TABLE 5
INTRUDER DISPLACEMENT BEHAVIOR OBSERVED DURING 1978 BREEDING SEASON (EACH HABITAT OBSERVED FOR 15 HOURS)

Resident-intruder	Time until intruder displaced (mean \pm SD in seconds)		
	Rocky habitat (N)	Puffin habitat* (N)	Meadow habitat* (N)
Male vs. Male ^{b,c}	11.3 \pm 15.9 (54) ^d	36.7 \pm 43.7 (10)	35.6 \pm 46.2 (15)
Male vs. Female ^c	15.4 \pm 19.7 (36) ^d	34.8 \pm 29.4 (10)	99.7 \pm 82.9 (23)
Male vs. Intruder (total) ^c	12.9 \pm 16.2 (90) ^d	35.8 \pm 36.5 (20)	60.4 \pm 66.5 (38)
Female vs. Male	21.1 \pm 20.3 (15)	None observed	18.2 (1)
Female vs. Female ^c	17.3 \pm 21.1 (15)	22.9 \pm 29.2 (4)	62.9 \pm 88.5 (11)
Female vs. Intruder (total) ^c	19.7 \pm 20.4 (30) ^d	33.9 \pm 29.2 (4)	59.1 \pm 83.2 (12)

* Intruders that remained for at least 300 seconds (5 minutes) before being displaced are not included in calculations (there were 12 such birds in meadow habitat and 7 in puffin habitat, none was observed in Rocky).

^b Male vs. Male = Male resident displacing male intruder, etc.

^c Difference in duration among habitats significant among habitats at .001 level by Kruskal Wallis test.

^d Difference in number of intruders significant at .01 level by Chi Square test.

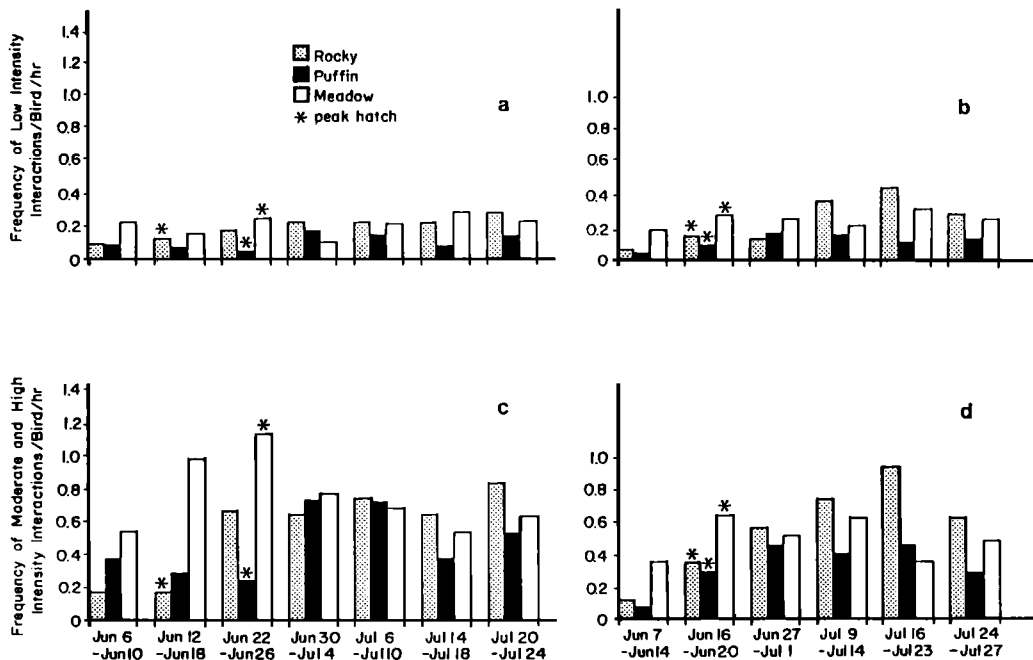


FIGURE 2. Temporal pattern of aggressive behavior by male Herring Gulls during the breeding season. 2a,c: 1977; 2b,d: 1978. In both years at all levels of intensity, patterns of aggression among habitats are significantly different at the .001 level by χ^2 contingency test with 12 df.

greater rate than did interactions between neighbors ($P < 0.001$ by chi square test, 2 df).

In contrast to rocky habitat, gulls in the other habitats typically directed aggression at a much higher rate at neighbors than at intruders (Table 4, $P < 0.001$, Fisher's exact test). During both 1977 and 1978, male and female Herring Gulls nesting in puffin habitat showed the lowest frequencies of aggressive interaction against both neighbors and intruders combined. Despite the low nest density in this habitat, however, rates of interaction between neighboring male gulls were higher in puffin habitat than in rocky habitat in 1977. Rates of interaction between neighbor males were similar in these two habitats in 1978 (Table 4). During both years of this study, gulls in meadow habitat suffered high rates of egg and chick loss (Table 2), and showed the highest rates of neighbor-neighbor aggression ($P < 0.001$ by Chi square, 4 df). The perpetrators of this aggression were resident male gulls that spent more time on their territories after losing eggs early in the season. In addition to guarding mates and young, these males also foraged in this habitat. Most of these males were specialist predators on Leach's Storm Petrel, *Oceanodroma leucorhoa*, which nested in large numbers in this habitat (Pierotti and Annett 1986). Some of these males also stole and ate eggs and young of neigh-

boring conspecifics. This predation led to increased vigilance and aggression by their victims, and this pattern occurred repeatedly until nearly all birds in this habitat were aggressive towards neighbors. In 1977 when food was less abundant, both the percentage of egg and chick disappearance and rates of aggression were higher than in 1978 when food was abundant (cf. Tables 2 and 4).

These high rates of aggression directed at neighbors appeared to result initially from harassment and predation by Great Black-backed Gulls. In every case where a pair of Herring Gulls was observed to lose one or more chicks or eggs to predation in meadow habitat ($n = 19$), there was a significant increase in rates of aggression by both the male and female parents within 12 hours ($P < 0.001$ by Wilcoxon signed-ranks test). Similar increases in rates of aggression were observed in pairs in rocky and puffin habitats following loss of chicks ($n = 11$, $P < 0.01$ by Wilcoxon). Neither infanticidal behavior nor increased rates of aggression were detected in pairs that did not lose eggs or chicks.

Temporal changes in rates of aggressive behavior were found in all three habitats in relation to the stage of the breeding cycle. During the latter stages of incubation until the peak of hatching (6–22 June) in both 1977 and 1978, male

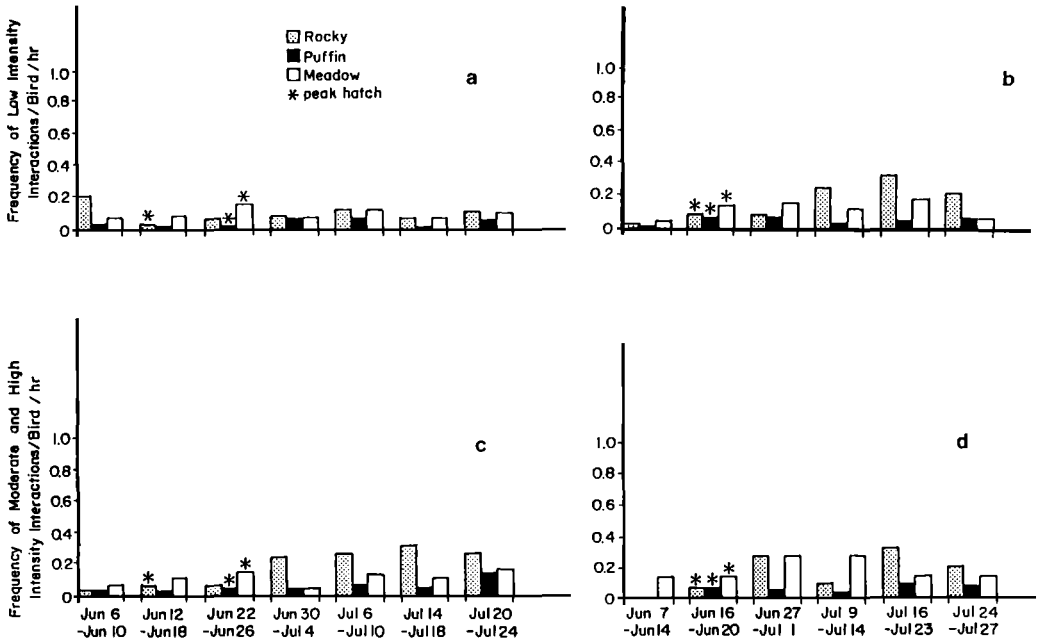


FIGURE 3. Temporal pattern of aggressive behavior by female Herring Gulls during the breeding season. 3a,c: 1977; 3b,d: 1978. In both years at all levels of intensity, patterns of aggression among habitats are significantly different at the .001 level by χ^2 contingency test with 12 df.

gulls in meadow habitat showed the highest rates of both low and high intensity aggressive behavior (Fig. 2). This was the result of increased aggressiveness by male gulls in this habitat after losing eggs or newly hatched chicks. Within a week after peak hatch, there was a marked increase in aggression by male gulls in rocky habitat, and from this point until the end of July in both years, male gulls in rocky habitat had the highest rates of aggressive interaction (Fig. 2). These birds were responding to frequent intrusions by prospecting birds, and to attacks on chicks by neighbors in this high density habitat, where chicks were more likely to cross boundaries than in other less dense habitats. A similar, but smaller scale increase in rate of aggression was observed to occur in puffin habitat.

Female gulls showed a pattern similar to that of their mates but with overall lower rates of aggression (Fig. 3). Rates of female aggression were highest in meadow habitat until peak hatching, and thereafter were highest in rocky habitat. Most aggression by female gulls in rocky habitat was directed at intruders or neighbors that approached chicks.

Intruders landing on occupied territories were observed far more frequently in rocky habitat and were displaced most rapidly in this habitat (Table 5). Female gulls in rocky habitat displaced intruders of both sexes more rapidly than did males in either of the other habitats. Adult in-

truders elicited the most rapid and intense responses, especially when they landed near chicks. In puffin habitat some intruders were able to establish territories, build nests, and lay eggs. In meadow habitat some intruders were able to remain long enough to initiate nest-building. In rocky habitat no intruder was observed to remain long enough to even attempt such behavior.

DISCUSSION

Settling in the three habitats appeared to impose varying costs on breeding Herring Gulls. Costs in terms of time and energy were probably highest in meadow habitat because of the need for increased vigilance to guard eggs and young. These costs took three forms: First, energy expenditure in aggression was great in this habitat because rates of aggression were high here during both years. Second, the need for vigilance probably reduced time available for foraging. This was especially true where foraging by males was concerned, since male gulls usually provide more food to offspring than females (Burger 1981, Pierotti 1981, Bellrose 1983). In meadow habitat male gulls provided less food than did males in rocky habitat. The final cost in this habitat was a reduction in fitness, as indicated by the fact that the fledging rate was lowest here during all three years of this study (Pierotti 1982).

In rocky habitat benefits appeared to exceed costs. The rocky marine terraces at the periphery

of the island appeared to be the preferred habitat for nesting, and were occupied by phenotypically superior individuals (Pierotti 1982). Rocky habitat was the best because it was the most spatially heterogeneous habitat and contained numerous sites for nesting that were well sheltered from prevailing winds and storms (Pierotti 1982, tables 9, 10). In addition, this area was sparsely vegetated. During rain or heavy fog (which are common in Newfoundland during the spring and summer), the rocks that make up most of the habitat did not become saturated with moisture and dried quickly. In meadow and puffin habitats the abundant vegetation took up moisture, and the plumage of birds (especially downy chicks) remained soaked for hours or days afterward. These soaked chicks almost certainly lost heat at greater rates than did dry chicks, and so had less energy available for growth. Chicks in meadow habitat grew more slowly than chicks in rocky habitat during both years even though they were fed at identical rates (Table 3 and Pierotti 1982).

There were two apparent costs to nesting in rocky habitat, and both appeared to result from the apparent preference of Herring Gulls for settling in this habitat. The first cost was the consistently high rate of intrusion by unestablished adults which provoked aggressive responses of high and moderate intensity from residents. The second cost was the high nest density in this habitat and the resultant high level of aggression. Internest distances and territory sizes were significantly smaller in rocky habitat than in puffin and meadow habitat (Pierotti 1982, table 9). Since this habitat was heterogeneous, there was relatively little interaction between neighbors during the incubation period, possibly because as suggested by Burger (1977), these birds could not see each other while sitting on nests. After hatching, however, adults and chicks moved about their territories, some chicks were attacked, and some adults that lost chicks became egg or chick predators (see also Davis and Dunn 1976, Pierotti 1980). This combination of factors resulted in an increase in rate of aggressive behavior which began within one or two weeks after hatching and continued for the remainder of the breeding season.

The direct relationship between aggression and nest density is further supported by the data from puffin habitat which had the lowest density (Pierotti 1982, table 9), and the lowest rates of aggressive interaction during all phases of the breeding season in both years. The large distances between neighbors in this habitat apparently required little vigilance and reduced attendance on the territory during the incubation period. There appeared to be no cost to nesting in puffin habitat, since despite the lack of vigilance and the lowest rate of offspring provision-

ing in the three habitats, fledging success was as high or higher than in the other habitats. This situation apparently resulted from the absence of predatory Great Black-backed Gulls in this habitat, and the low preference for nesting in this habitat, which had significantly fewer nesting birds than were expected (Pierotti 1982, table 1). A reduction in rate of aggressive interaction under conditions of low nest density has also been reported in the Western Gull, *Larus occidentalis* (Ewald et al. 1980, Pierotti 1981).

Other investigations of gull breeding biology have demonstrated that increased nest density may lead to increased costs of reproduction. Schreiber et al. (1979) found that Laughing Gulls, *Larus atricilla*, laid equally large first and second eggs during the first year of their study. Nest density increased in the second year and although first-laid eggs remained similar in size to the previous year, there was a decrease in the size of second-laid eggs. Coulson et al. (1982) found that a reduction of nest density led to an increase in both adult body weight and egg weight in Herring Gulls. Finally, Burger (1984) showed an inverse relationship between fledging success and nest density in Herring Gulls in New Jersey that was apparently related to increased rates of egg predation and aggressive interaction at high nest density. My results demonstrate that nesting at high densities may lead to increased rates of aggressive interaction, which could reduce energy reserves necessary for egg production, or lead to reduced adult weight.

Although the results of this study and of Burger (1984) both suggest a cost to nesting at high density in Herring Gulls, our data actually reveal markedly different patterns. Burger concludes that fledging success is highest on intermediate-sized territories (internest distance = 6–7 m) and lowest in areas of high nest density (internest distance = 3–4 m; Burger 1984, table 35). The results of this study showed the highest rates of fledging success in areas of high (rocky; internest distance = 3–4 m) and low (puffin; internest distance = 8–9 m) nest density, and the lowest rate at intermediate nest density (meadow; internest distance = 6–7 m; Pierotti 1982, table 9).

Similarly, Burger concludes that rates of aggression in Herring Gulls are highest at high and low densities and lower at intermediate densities (1984, fig. 28b). She further argues that rate of intrusion by non-neighbors increases with increasing territory size (1984, fig. 29). My study demonstrates, however, that factors other than simple nest density may be responsible for these patterns. In all of these studies rates of aggression are highest where egg and chick production is greatest and fledging success is least. Burger (1984) notes this relationship, but characterizes it as “the most aggressive pairs fledged the fewest young

(pg 74),” and presents data to show high levels of aggression at high and low nest densities. From my results it can be seen that birds that lose young become more aggressive, and that the habitat with the lowest density of nests also has the lowest rates of aggression, probably because intrusion rates are low and chicks are not attacked in this habitat.

Also in contrast to Burger (1984), in this study intrusion rate was greatest in the highest density (rocky) habitat. This habitat was preferred for nesting and therefore attracted the most intruders. Ewald et al. (1980) came to a similar conclusion after noting that small territories had the highest rates of intrusion in the Western Gull, and Coulson and Thomas (1983) noted that clutches were initiated earlier and rates of intrusion were higher in areas of high nest density in colonies of Kittiwakes, *Rissa tridactyla*.

These results suggest that the conclusions drawn by Burger (1984) are not of general applicability, and that the relationship between rate of aggression, territory size, and fledging success is best understood on a case-by-case basis. In the Herring Gulls on Great Island fledging success appears to be most strongly influenced by predation, and relatively independent of territory size. Similarly, rate of aggression appears to be independent of territory size, and the relationship between breeding success and aggression appears to take the form of an increase in aggression by birds that have lost offspring to predation or are under threat of predation. Therefore, predation on eggs and young, either by conspecifics or by other species, e.g., Great Black-backed Gulls, may be a key factor determining time budgets and reproductive output in Herring Gulls on Great Island.

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