

SIGNIFICANCE OF THE PATTERN OF NEST DISTRIBUTION IN THE PIGEON GUILLEMOT (*CEPPHUS COLUMBA*)

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ABSTRACT.—We studied nest distribution in the Pigeon Guillemot (*Cephus columba*), and three possible selective factors that influence it: nest predation, the use of nest groups as information centers for food finding, and spatial variation in nest-hole quality. Quadrat surveys in 2 yr suggested that nests were dispersed randomly with respect to the distribution of suitable holes, but on a larger spatial scale, holes on the south shore were preferred to those on the north. Predation intensity was largely independent of nest density. This was true whether egg predation alone, chick predation alone, or total predation was considered. Nesting close to other birds, however, had a slight advantage on a very local scale. Reduced predation on south-shore nests seemed to be due to their being better protected from predators rather than to specific advantages to aggregation. Neither chick feeding rates nor chick growth rates increased with nest group size, indicating that nest groups did not serve as information centers for food finding. We conclude that the observed clumping of nests was due to a clumped distribution of suitable sites and spatial variation in nest-hole quality. Received 18 February 1988, accepted 3 October 1988.

COLONIAL nesting is a highly conspicuous pattern of breeding in birds, and many studies have been devoted to understanding its adaptive significance (see Wittenberger and Hunt [1985] for review). Lack (1968), in a major comparative study, found that coloniality was disproportionately common in species that eat aquatic prey, seeds, or fruit, and that it is often associated with flock feeding. He suggested that the main advantage of coloniality, at least for species that feed in flocks, was an increased efficiency of food exploitation. Ward and Zahavi (1973) argued explicitly that many bird species used breeding colonies as "information centres" for food finding. Several studies have supported Ward and Zahavi's hypothesis (Horn 1968, Siegfried 1971, Krebs 1974, Emlen and Demong 1975, Erwin 1978, Loman and Tamm 1980, Ydenberg et al. 1983), but Bayer (1982) argued that other hypotheses explained equally well much of the data, and Andersson et al. (1981) found that Black-headed Gull (*Larus ridibundus*) colonies did not appear to serve as information centers. However, De Groot (1980) showed unequivocally that captive *Quelea quelea* learned the location of food or water from

knowledgeable roost mates, and recently Brown (1986), Greene (1987), and Waltz (1987) provided strong evidence that Cliff Swallow (*Hirundo pyrrhonota*), Osprey (*Pandion haliaetus*), and Common Tern (*Sterna hirundo*) colonies serve as information centers.

A second major explanation for the evolution of coloniality is that predation pressure decreases as nest density increases (Patterson 1965, Robertson 1973, Parsons 1976, Hoogland and Sherman 1976, Birkhead 1977, Götmark and Andersson 1984, Robinson 1985). Several mechanisms have been invoked to explain this fact, although alternatives are often difficult to separate in the field. First, predator mobbing often increases with colony size or nesting density (Patterson 1965, Tenaza 1971, Balda and Bate-man 1972, Hoogland and Sherman 1976, Götmark and Andersson 1984, Robinson 1985). Increased mobbing may drive off predators or lower their hunting success. Second, the *per individual* probability of being caught decreases as colony size increases through a prey dilution effect (Bertram 1978). Third, a "selfish herd" effect may operate (Hamilton 1971). Fourth, predator satiation may occur if prey are sufficiently abundant. Support for this last mechanism comes from studies that show that the proportion of individuals killed decreases during the peak of the breeding season (Patterson 1965, Nisbet 1975, Daan and Tinbergen 1979,

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Findlay and Cooke 1982, Nisbet and Welton 1984).

A third possible influence on the pattern of nest distribution is spatial variation in site availability. Birds may nest in clumps because suitable sites are limited and patchily distributed (Lack 1968, Snapp 1976), or because high-quality sites are clumped even though suitable sites are not limited.

Most studies of coloniality have concentrated on highly colonial species (e.g. Patterson 1965, Tenaza 1971, Parsons 1976, Hoogland and Sherman 1976, Birkhead 1977). Loosely colonial species (those that nest in smaller, less dense aggregations) have received less attention, but the factors that influence their nest-distribution patterns may be very different. Studies of loosely colonial species may also help to illuminate the problem of the *evolution* of coloniality, because their nest-distribution patterns are probably similar to those on which selection once acted in species that are now highly colonial. Thus one can partially avoid the argument that by studying highly colonial species one can demonstrate only the selective factors that *maintain* coloniality. We studied the Pigeon Guillemot (*Cephus columba*) because it nests at a wide range of densities, from solitary individuals to loose aggregations and even dense colonies in some high arctic regions (Nettleship and Evans 1985). Our purpose was to determine the factors responsible for the nest-distribution pattern of this species.

STUDY AREA AND METHODS

The Pigeon Guillemot is a medium-sized (400 g) alcid that breeds on the coasts of the northern Pacific. It nests in holes under boulders and rock tumbles on the lower shore, in crevices in rock faces, in driftwood piles, and in a variety of similar locations (Drent et al. 1964), including man-made sites (Campbell 1977). It is unusual among the alcids because it nests largely in small, loose aggregations, feeds mainly on inshore, benthic organisms, and lays normally two eggs instead of one (Storer 1952, Thoreson and Booth 1958, Drent 1965, Koelink 1972, Kuletz 1983).

The study was done on Mitlenatch Island, British Columbia (49°57'N, 125°00'W), a small (35.5 ha) rocky island at the northern end of the Strait of Georgia, in 1984 (between 20 April and 24 August) and 1985 (between 20 April and 18 August). The island is composed largely of basaltic rock that forms two low hills (<60 m) and a series of rocky bluffs. The south shore consists of low, vertical cliffs up to 20 m in height.

The north and east shores are much lower and more gently sloping. Exfoliation of the rocks is most extensive on the east and south shores, where there are a number of boulder tumbles below the cliffs, and here the majority of the guillemots breed. Details about the island are given in Butler (1974, 1980) and Brooke et al. (1983). Thomson (1981) provides detailed information about the oceanography of the Strait of Georgia.

Approximately 200 pairs of Pigeon Guillemots nest on Mitlenatch. We determined their breeding distribution by systematically searching the island shore for nests and mapping their locations onto a 50 m² quadrat system. (We did not search the cliffs on the south shore to avoid disturbing breeding cormorants.) We found nests during the egg-laying period, or occasionally later in the season, by observing food deliveries to chicks. We searched all quadrats for unoccupied but apparently suitable nest holes. We measured the height and width of the entrance hole, the distance from the hole entrance to the nest, the height and width of the nest chamber, and the distance from the hole entrance to the rear of the chamber. We scored concealment of the hole entrance on a scale of one to five, and complexity of the nest chamber on a scale of one to six. Holes were considered suitable if the measurements fell within the range of the same measurements of occupied holes. Birds might have used other criteria to decide whether a hole was suitable or not. Although our criteria might have led to an under- or overestimation of the total number of suitable holes, it is unlikely that we created a systematic bias in the data.

To look for nonrandom patterns of nest distribution, we plotted nest density per quadrat against suitable-hole density and compared the fitted slope to the slope expected if nests were distributed randomly. A random distribution of nests implies that the same proportion of suitable holes is occupied at all hole densities, so the expected slope has a value equal to the overall proportion of occupied holes. If birds chose to nest colonially, proportionately more holes than expected would be occupied at high hole densities and proportionately fewer holes than expected would be occupied at low hole densities. The fitted slope would then be steeper than expected. Conversely, if birds were territorial, the fitted slope would be shallower than expected. The data were transformed before analysis because nest density per quadrat is binomially distributed (a hole is either occupied or unoccupied). Its variance therefore increases as suitable hole density increases. Homogeneity of variances was obtained by dividing both sides of the regression equation by the square root of the independent variable: the regression was transformed from $N = bS$ to $N/\sqrt{S} = b\sqrt{S}$, where N = nests per quadrat and S = suitable holes per quadrat. Because b is the same in both cases, the slope fitted to the transformed data can still be compared directly to the expected

slope. One potential problem with this analysis is the appropriate choice of quadrat size. We arbitrarily chose 50 m², and although a random distribution cannot be made to appear clumped by adjusting quadrat size, a clumped distribution could appear random if the quadrat size chosen were too small. We therefore pooled data from adjacent quadrats and repeated the analysis on the new quadrat size of 50 × 100 m. We used the same method to look for variation in predation intensity with nest density.

We visited all occupied nests every 1–5 days throughout the breeding season and recorded their fates. The major causes of nest failure were predation, desertion, and failure of the eggs to hatch. A small number of chicks died in the nest each year.

We used discriminant function analysis to separate nests into depredated and nondepredated groups on the basis of the hole measurements listed above plus three extra variables: size of the entrance hole (height × width), the ratio of entrance width to nest depth (i.e. depth to the nest), and the ratio of entrance-hole size to nest depth. We used the last two variables to allow for the conflicting effects of nest depth and entrance-hole size on predation risk: i.e. a nest with a large entrance hole might be well-protected if the nest were deep inside, while a shallow nest might be protected if it had a narrow entrance hole. All variables were log_e transformed before analysis; but even after transformation, nest-chamber height showed a strong positive skew and was therefore dropped from the analysis.

We weighed chicks with 0–100 g and 0–500 g Pesola scales until they fledged, died, or were eaten. Weighings were done in the afternoon, every 3–5 days in 1984 and every day in 1985.

We observed feeding rates to nests from a blind, or from locations distant or concealed from the nest group. Observation periods lasted 2 h. We recorded the number of pairs in the nest group that fed chicks, the number of food deliveries to each nest, the time at the start of each observation period, and the state of the tide during the period. We chose starting times so that the tidal height halfway through the period was either 0.75 m, 2.30 m, or 3.85 m. These were classified as low-, mid-, and high-tide periods, respectively. We also kept records of the number of chicks in each nest in the nest group.

We used the BMDP statistical software programs (Dixon 1985) for all analyses. We calculated fledging masses of chicks by fitting logistic equations to the growth curves of individual chicks and using the asymptotic mass parameter *A* as a measure of fledging mass (Ricklefs 1967). Because nestling guillemots reach their maximum mass at fledging, *A* is a reasonable measure of fledging mass. The mass on the last day in the nest was not a good measure because masses varied considerably (up to 30–40 g) from day to day during the final part of the fledging period. We calculated growth rates as mass increases in g/day by

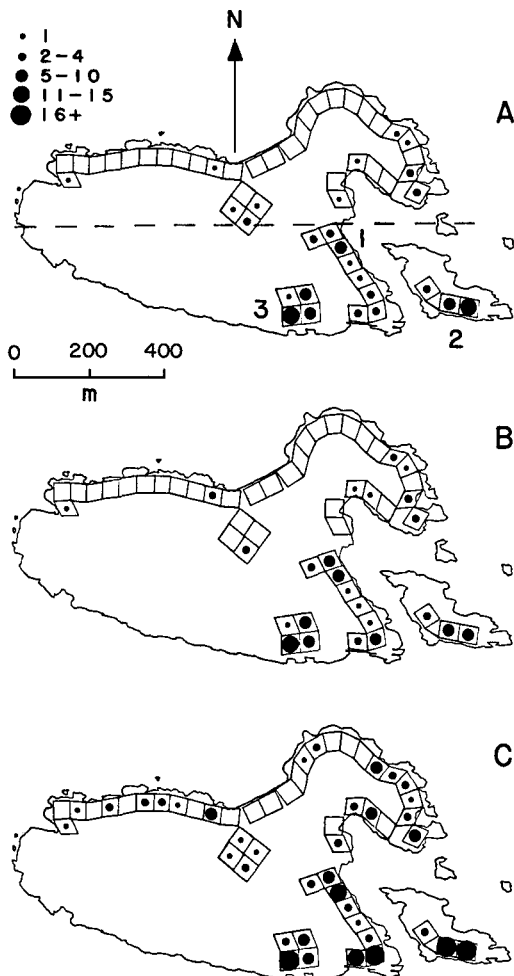


Fig. 1. Mitlenatch Island, showing the distribution of (A) guillemot nests in 1984; (B) guillemot nests in 1985; (C) total number of suitable holes. Quadrat size is 50 m². The size of the dot in each quadrat indicates the number of nests or suitable holes. In (A), the dotted line shows north-south division of the island, 1 = Camp Bay; 2 = F-Island; 3 = West Hill.

fitting linear regressions to the linear phase of growth, when chicks were 5–20 days old. This is preferable to using the growth curve constant *K* of the logistic equation, as recommended by Ricklefs (1967), because *K* is a measure of the speed with which the asymptote is reached and can therefore give misleading results if comparisons are made between chicks reaching different asymptotes (Hussel 1972, Gaston 1985).

We mostly used parametric statistics, transforming the data to obtain normal distributions where appropriate. We used nonparametric statistics if normal distributions could not be obtained by transformation.

TABLE 1. Fitted and expected slopes for regressions of nests per quadrat vs. total number of suitable holes per quadrat. Analyses were done on transformed data; *t*-tests are two-tailed.

Year	Slope		<i>t</i>	<i>n</i>	<i>P</i>
	Fitted ± SE	Ex-pected			
50 m² Quadrat					
1984	0.547 ± 0.113	0.464	0.735	37	>0.40
1985	0.700 ± 0.110	0.495	1.860	37	>0.05
50 × 100 m Quadrat					
1984	0.638 ± 0.112	0.468	1.520	22	>0.10
1985	0.750 ± 0.091	0.503	2.710	22	<0.05

RESULTS

The distribution pattern of nests.—In both 1984 and 1985, nests were clumped into three main areas: Camp Bay, F-Island, and West Hill (Fig. 1A, B), but suitable holes were also clumped (Fig. 1C), and in neither year was the distribution of nests within 50 m² quadrats significantly different from that expected if birds chose nest holes randomly (see Study Area and Methods). The same result held for 50 × 100 m quadrats in 1984, but in 1985 the fitted slope was significantly steeper than expected, indicating that occupied holes were more clumped than suitable holes (Table 1). On a larger scale, birds preferred holes on the south side of the island in both years (1984: 74/136 vs. 16/58; $\chi^2 = 11.75$, $P < 0.001$; 1985: 81/138 vs. 15/58; $\chi^2 = 17.60$, $P < 0.001$).

The effect of spatial variation in nest-hole quality.—Several nest-hole characteristics affected the risk of predation. Deeper nests, nests with small and concealed nest entrances, and those with

TABLE 3. Predation on individual nests in 1984 and 1985. Only nests whose complete fates were known in both years were used. Nests that were depredated in 1984 were likely to be depredated in 1985. $\chi^2 = 9.12$, $P < 0.01$.

	Depredated (1985)	Not depredated (1985)
Depredated (1984)	18	2
Not depredated (1984)	8	10

deep and complex nest chambers were somewhat better protected from predators (Table 2), but for none of the measures of predation did the same characteristics enter the analysis in both years. In addition, the percentage of correct classifications of nests into depredated and nondepredated groups was never very high (64.9–73.2%). Thus, the probability of a nest being depredated cannot be predicted with much confidence from measurements of the nest hole. However, nests that were depredated in 1984 were also highly likely to be depredated in 1985 (Table 3).

The differences in nest-hole vulnerability shown by the discriminant function analyses were partially reflected in the choice of nest holes by breeding pairs. Over the island as a whole, used holes were more complex (\bar{x} : 3.09 vs. 2.45; $n = 218$, $t = 3.55$, $P = 0.0005$) and had smaller ratios of entrance size to depth to nest cup (11.55 vs. 13.98; $n = 216$, $t = -2.35$, $P = 0.02$) than unused holes. Suitable holes on the south shore were better concealed (2.25 vs. 1.75; $n = 223$, $t = 3.79$, $P = 0.0002$) and had more complex chambers (3.05 vs. 2.28; $n = 217$, $t = 4.18$, $P < 0.0001$) than those on the north shore.

TABLE 2. Discriminant function analyses separating nests into depredated and nondepredated groups on the basis of nest-hole characteristics. Means and standard errors are for raw data, but data were log_e transformed before analysis. See text for the complete set of predictor variables.

Grouping variable	Significant predictor variables	Depredated nests ($\bar{x} \pm SE$)	Nondepredated nests ($\bar{x} \pm SE$)	<i>n</i>	<i>F</i> -value	<i>df</i>	Correct cases (%)
Total predation 1984	—	—	—	71	—	—	—
Total predation 1985	Depth to nest	43.34 ± 24.83	48.44 ± 20.46	77	5.86	1, 75	64.9
Egg predation 1984	Concealment	1.67 ± 1.05	2.26 ± 0.69	70	4.95	1, 68	68.6
Egg predation 1985	Complexity	2.06 ± 1.08	2.92 ± 1.00	82	10.30	2, 79	73.2
Chick predation 1984	Depth to nest	34.00 ± 14.53	44.91 ± 18.90	48	7.53	1, 46	62.5
	Entrance size/depth to nest	9.71 ± 4.56	14.96 ± 8.44				
Chick predation 1985	—	—	—	33	—	—	—

TABLE 4. Fitted and expected slopes for regressions of depredated nests per quadrat vs. number of nests per quadrat. Analyses were done on transformed data; *t*-tests are two-tailed.

Predation intensity estimate	Slope		<i>t</i>	<i>n</i>	<i>P</i>
	Fitted ± SE	Expected			
1984					
Upper	0.686 ± 0.123	0.614	0.585	27	>0.50
Lower	0.584 ± 0.121	0.545	0.322	27	>0.70
1985					
Upper	0.424 ± 0.164	0.479	-0.335	25	>0.70
Lower	0.275 ± 0.142	0.396	-0.852	25	>0.40

Occupied holes were also better concealed on the south shore (Mann-Whitney *U*-test, *P* = 0.014), but there were no significant differences between unoccupied holes in the south and occupied holes in the north. None of the other nest-hole characteristics differed between groups in any of the analyses.

The effect of nest density on predation intensity.—The two main predators of guillemot eggs and chicks on Mitlenatch were Northwestern Crows (*Corvus caurinus*) and garter snakes (*Thamnophis elegans*). Crows were probably responsible for all egg predation, because it is unlikely that even the largest garter snake could swallow guillemot eggs (Campbell 1969, P. W. Gregory pers. comm.). Conversely, chick predation was probably almost exclusively by snakes, although crows sometimes took young chicks from very exposed nests.

We plotted the number of nests depredated per quadrat against the total number of nests per quadrat and compared the fitted slope to that expected if predation were occurring randomly. For some nests we were uncertain whether predation had occurred, so we did separate analyses for upper and lower estimates of predation intensity. The number of quadrats for which we had useful data was small, so we were

unable to pair quadrats and repeat the analyses on the large quadrat size of 50 × 100 m.

In neither 1984 nor 1985 were the fitted and expected slopes significantly different (Table 4), suggesting that predation pressure was independent of nest density. We also analyzed egg predation alone and chick predation alone, because eggs and chicks were taken largely by different predators, but found no consistent effects of density (Tables 5, 6). In only one of the eight analyses—egg predation in 1985 using lower estimates of predation—was there a significant effect. The slope was shallower than expected, indicating that clumped nests suffered less predation.

We found no consistent differences in the risk of predation to nests on the north and south shores (Table 7). In 1984 the only significant effect was a higher egg predation on the north shore when lower estimates of predation were used. In 1985 both egg predation and total predation were higher on the north shore. No analyses of chick predation were done in 1985 because no birds on the northern shore hatched their eggs.

One problem with the above analyses was that the number of nests per quadrat reveals little about the proximity of nests within quad-

TABLE 5. Fitted and expected slopes for regressions of depredated nests per quadrat vs. number of nests per quadrat for egg predation only. Analyses were done on transformed data; *t*-tests are two-tailed.

Predation intensity estimate	Slope		<i>t</i>	<i>n</i>	<i>P</i>
	Fitted ± SE	Expected			
1984					
Upper	0.248 ± 0.121	0.264	-0.132	27	>0.80
Lower	0.153 ± 0.122	0.230	-0.631	27	>0.50
1985					
Upper	0.051 ± 0.130	0.266	-1.654	24	>0.10
Lower	-0.066 ± 0.1280	0.213	-2.180	24	<0.05

TABLE 6. Fitted and expected slopes for regressions of depredated nests per quadrat vs. number of nests per quadrat for chick predation only. Analyses were done on transformed data; *t*-tests are two-tailed.

Predation intensity estimate	Slope		<i>t</i>	<i>n</i>	<i>P</i>
	Fitted ± SE	Expected			
1984					
Upper	0.852 ± 0.186	0.600	1.355	19	>0.10
Lower	0.690 ± 0.191	0.533	0.822	19	>0.40
1985					
Upper	1.083 ± 0.208	0.636	2.149	12	>0.05
Lower	0.753 ± 0.205	0.455	1.454	12	>0.10

rats. Spacing nests on a very local scale is advantageous if predators show area-restricted searching (Tinbergen et al. 1967; Croze 1970; Smith 1974a, b; Zach and Falls 1977). Area-restricted searching requires that predators take more than one prey item at a time. Although snakes probably do not do this, crows certainly do (Verbeek pers. obs.). Spacing nests is also advantageous if predators return to areas where they were successful in the past. We strongly suspected that both crows and snakes did this. We analyzed the frequency of predation on nearest neighbors of depredated nests for two arbitrary distance categories, 0–10 m and 10–20 m. If predators showed area-restricted searching, or returned to areas where they had been successful, nests close to depredated neighbors should have suffered more predation than those farther away. In 1984 there was no significant effect (9/16 vs. 5/7; Fisher's Exact Test, $P = 0.657$), but in 1985 the observed effect was opposite to that predicted. Nearest neighbors 10–20 m away from a depredated nest were more likely to be depredated than those 0–10 m away (10/13 vs. 2/13; Fisher's Exact Test, $P = 0.005$).

Nest groups as information centers for food finding.—We tested the information center hypothesis indirectly through feeding rates and chick growth rates. If nest groups serve as information centers, the amount of information available to unsuccessful foragers should increase with nest-group size. Consequently, both feeding rates to nests and chick growth rates should increase with nest-group size. When we controlled for date, time of day, tidal state, chick age, and number of chicks per nest in a multiple regression analysis, nest-group size did not significantly affect feeding rates to nests ($b = -0.008 \pm 0.005$, $t = -1.69$, $P = 0.091$, $n = 524$). Chick growth parameters did not differ between years, so data from 1984 and 1985 were pooled. Nest-group size had no effect on either growth rates or fledging mass (Fig. 2).

DISCUSSION

The pattern of nest distribution.—*Cephus guillemots* nest in small colonies or loose aggregations (Belopol'skii 1957; Preston 1968; Cairns 1980, 1981). This pattern was found on Mitle-

TABLE 7. Predation intensities on north and south shore nests. *P*-values are for Fisher's Exact Test. No tests were done for chick predation in 1985 because no birds on the north shore hatched eggs.

Predation measure	Proportion of depredated nests					
	Lower estimate			Upper estimate		
	North	South	<i>P</i>	North	South	<i>P</i>
1984						
Total	10/16	38/72	0.584	10/16	44/72	1.000
Egg	7/16	13/71	0.046	7/16	16/71	0.116
Chick	4/8	28/52	1.000	4/8	32/52	0.702
1985						
Total	10/15	28/81	0.024	11/15	34/81	0.046
Egg	9/14	11/80	0.0002	9/14	16/80	0.0015
Chick	—	—	—	—	—	—

natch, presumably due to a clumped distribution of suitable holes which birds are occupying at random. However, the evidence was somewhat equivocal. In one of the four surveys (50 × 100 m quadrats in 1985), nests were significantly more clumped than expected. In addition, holes on the south shore, where total hole density was much higher, were preferred to those on the north shore in both years. There are two possible explanations for the north-south effect. First, birds benefit from nesting colonially, and they do this only on the south shore, where holes are sufficiently dense. Second, south shore holes are better than north shore holes for reasons unassociated with aggregation.

The information center hypothesis.—Guillemots on Mitlenatch did not appear to use their nesting groups as information centers. An information center is only of value if food is distributed unpredictably in space and time (Ward and Zahavi 1973). Although the distribution pattern of the inshore, benthic fish on which *Cephus* guillemot chicks feed is not well-known, it is probably relatively uniform and predictable (Cairns 1984). Kuletz (1983) provided evidence that food is predictably distributed: individual parent guillemots had preferred foraging areas to which they returned regularly within a season and faithfully from year to year, and from which they may have excluded other birds. On Mitlenatch, foraging birds always flew east from the island. This suggested that they knew where to find food. Food could be distributed unpredictably on a very local scale, but then birds could find it by locating flocks of foraging individuals on the feeding grounds rather than by getting information at the colony (Bayer 1982). Theoretically the benefits of using colonies as information centers decline as foraging range decreases and inshore feeders such as Pigeon Guillemots should have little use for information centers (Waltz 1982). In a comparative study of six tern species, Erwin (1978) found that colony size was positively correlated with both foraging range and gregariousness when feeding. It seems, therefore, that Pigeon Guillemots have no need to obtain information about the location of good feeding sites from conspecifics at the breeding site. Cairns (1984) argues similarly.

Predation pressure.—Predation only weakly influenced the distribution of nests through variation in predation intensity with nest density. The quadrat surveys showed that predation

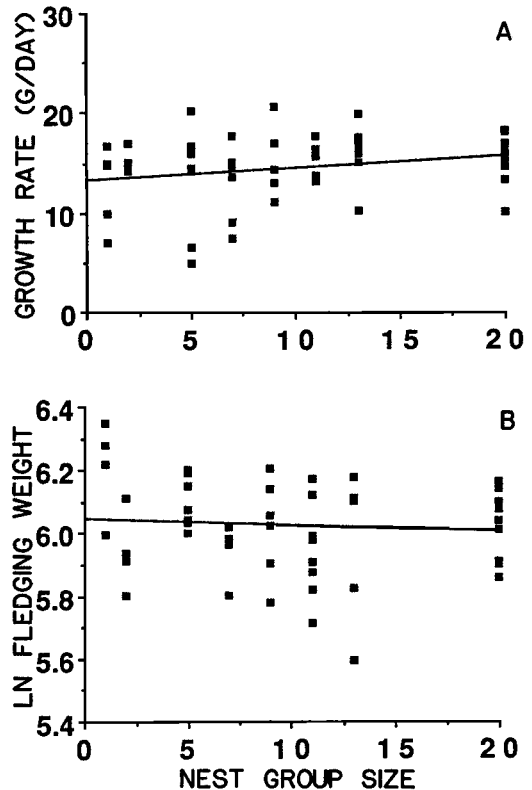


Fig. 2. The effect of nest-group size on (A) chick growth rate: $y = 0.122x - 13.37$, $r^2 = 0.055$, $P = 0.094$; (B) fledging weight (\log_e transformed): $y = -0.002x + 6.05$, $r^2 = 0.007$, $P = 0.563$.

intensity was generally independent of nest density, and only in 1985 did nests close to depredated neighbors suffer less predation than those farther away. The latter effect may be due to satiation of snake predators (Emms and Morgan in press). However, there was significantly more predation on the north shore of the island in 1985. This could imply an advantage to nesting colonially because the density of nests in the north was much less than in the south. However, we believe that the effect was due to variation in nest-hole quality.

Variation in nest-hole quality.—Nest holes could differ in quality in two ways. First, the microclimate could be different on the two sides of the island. The south shore is sunnier, and holes there may be slightly warmer. The south shore is less sheltered, especially early in the breeding season when the prevailing winds (which often bring strong rain) are from the southeast. Storey

and Lein (1985) found that the temperature inside an artificial Manx Shearwater (*Puffinus puffinus*) burrow on the leeward side of Middle Lawn Island, Newfoundland, was slightly higher than inside a similar burrow on the windward side. Most occupied burrows were on the leeward side of the island. Holes could also vary in the degree of protection from predators. South shore nests were significantly better concealed and had more complex chambers than north shore nests. Both these factors had some effect in reducing predation risk.

South shore nests are both more clumped and of better quality than north shore nests, and either clumping or quality could be responsible for the reduced predation. We believe that the association between predation on individual nests in 1984 and 1985 shows nest-hole quality to be the important factor. If clumping were responsible for the benefit, those nests depredated within clumps should be random. Individual nests within clumps should not be especially vulnerable, unless there was a center-edge, or some other sort of position, effect. The degree of clumping of nests on Mitlenatch was not sufficiently great to allow us to assign nests to "center" and "edge" categories, but nests that were depredated in both years were not significantly farther from their nearest neighbor (\bar{x} : 22.22 m vs. 23.17 m; $n = 15, 10$; $P = 1.000$, Mann-Whitney U -test), nor did they have significantly fewer nests in their quadrat (4.60 vs. 6.20; $n = 15, 10$; $P = 0.262$, Mann-Whitney U -test), than those that were not depredated in both years. However, sample sizes were small.

Cairns (1980) also addressed the pattern of nest distribution in guillemots. Black Guillemots (*Cepphus grylle*) on Brandypot Island, St. Lawrence River estuary, nested colonially, but the birds did not use their colonies as information centers, nor was predation important on Brandypot (Cairns pers. comm.).

One explanation for Cairns's observations (and for our data that birds preferred south shore nests) is that first-time breeders searched for nest holes near to established birds because this was the most efficient way of finding a suitable site. Guillemots are social birds early in the breeding season, display in groups, and aggregate on the sea and the lower shore. First-time breeders are probably attracted to these aggregations. After pairing, the quickest way to find a nest hole may be to search where other birds

are already nesting, because if there are some suitable sites in the area, there are probably others.

Lack (1968) argued that many island-nesting seabirds nest in groups primarily because of a shortage of suitable nesting habitat. We believe that, even when suitable sites are *not* limiting, nests can be clumped because of a clumped distribution of sites and spatial variation in site quality. Thus, to show *true coloniality* (i.e. that birds choose to nest close to other birds), one must show that nests are clumped significantly more than suitable sites and that the clumping of nests is not due to a clumping of high-quality sites. Wittenberger and Hunt (1985) argue similarly. It may be easier to show true coloniality for species (like guillemots) that occupy discrete natural cavities than for open-nesting species, or for hole nesters that dig their own burrows. Even so, showing that birds nest in tighter clumps than would be predicted from the spatial distribution of sites of varying quality poses substantial difficulties. The null hypothesis for such a test is that during colony formation birds occupy sites in order of decreasing intrinsic quality, irrespective of local site density. Comparing data with this null hypothesis is complicated by such factors as nest-site fidelity and the effect of age and experience on breeding date.

Of course, the fact that a species does not choose to nest in "true colonies" does not mean that there are no benefits to group nesting. During the initial evolution of coloniality in species that are now highly colonial, selection presumably acted on groups brought together for reasons unrelated to the advantages of group living. For example, there must have been some initial variation in nesting density on which selection could work. The distribution of guillemot nests on Mitlenatch is largely random with respect to the distribution of suitable nest holes, but variations in the local density of nests are produced because of variations in the distribution of suitable holes and spatial variation in nest-hole quality. It was possible that birds exploited these variations by using nest groups as information centers or benefited from reduced predation at certain densities. Selective pressures could have acted in opposite directions. One possibility is increased efficiency of food exploitation by using colonies as information centers, while higher predation on dense

aggregations was another reason for territorial behavior. In fact, none of these alternatives was true, but there was no a priori reason to prefer one of them over the others simply on the basis of the distribution pattern of nests. All potential selective pressures should be considered to understand patterns of breeding dispersion.

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