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NESTING DENSITY, HABITAT STRUCTURE AND HUMAN DISTURBANCE AS FACTORS IN BLACK GUILLEMOT REPRODUCTION

DAVID CAIRNS

Seabirds probably choose inaccessible islands and cliffs for breeding sites to counteract predation, but colony size and distribution are related more closely to food habits (Lack 1967). Thus, species of seabirds which feed inshore tend to form small colonies, while species which feed offshore often form large concentrated colonies, less often along the coast. The Black Guillemot (*Cepphus grylle*) differs from most alcids in feeding inshore, and its colonies are generally small and dispersed. But unlike other inshore feeders, guillemots nest in crevices which protect their clutches from avian predation at least. Breeding dispersion in other inshore feeders is affected by predation, so this protection may permit guillemots to respond to other selective pressures affecting nest spacing.

Breeding success of the Black Guillemot has been related to habitat quality and nesting density (Divoky et al. 1974, Preston 1968). In the latter case, low breeding success and a high rate of intraspecific aggression in 1 high density nesting area suggested that the Black Guillemot is not well adapted for colonial nesting.

The purpose of this study was to investigate the relations among habitat structure, nesting density, breeding success and behavior in the Black Guillemot. I also evaluated the possible influence of observer interference on breeding success, such as has been documented for Common Murres (*Uria aalge*) (Johnson 1938), Double-crested Cormorants (*Phalacrocorax auritus*) (Ellison and Cleary 1978) and gulls (*Larus* spp.) (Hunt 1972, Robert and Ralph 1975, Gillett et al. 1975).

STUDY AREA AND METHODS

This study was conducted on Brandypot Island (47°52′N, 69°41′W) in the estuary of the St. Lawrence River in 1976, and on the St. Mary's Islands (50°18′N, 59°39′W) on the north shore of the Gulf of St. Lawrence in 1977. Brandypot Island comprises 3 wooded islets underlain by quartzite and conglomerate bedrock. In quartzite areas the shores are generally smooth and regular, but the conglomerate shores are fissured deeply with cracks and caves and in several places are fronted by cliffs or jumbles of large boulders. On the St. Mary's Islands vegetation is limited to tundra-like communities and on wide bands around the islands' peripheries the metamorphosed igneous bedrock is exposed. The shorelines of St. Mary's West and Middle islands, where the study was carried out, vary from stepped terraces and low cliffs to gently sloping beaches of bare or stone-covered bedrock.

Common Murres, Razorbills (*Alca torda*) and Atlantic Puffins (*Fratercula arctica*) nested in small colonies throughout the St. Mary's study area, and Razorbills bred in small numbers on Brandypot. Detailed physical and avifaunal descriptions of these islands can be found in Reed (1973) for Brandypot, and Bédard (1969) for St. Mary's.

I found nests through repeated ground searches. I checked nests every 1–5 days on Brandypot, and daily (in the heavily disturbed zone) or every 4 days (in the lightly disturbed zone) on St. Mary's. In assessing the effect of my visits I considered a "visit" to be whenever I passed within 15 m of a nest.

Measurements of the types listed below were taken on all occupied nests, and on unoccupied holes on Brandypot which seemed to be suitable for nests.

(1) Particle size—the longest dimension of the largest particle on the surface of the nest cup.

(2) Nest diameter—the smallest dimension of the nest cavity, measured either vertically or horizontally.

(3) Nest depth—the distance between the nest bed and nest entrance. The nest entrance was defined as the deepest point able to be reached by a disc 25 cm in diameter oriented perpendicular to the nest.

(4) Overall shelter—the ratio of luminosity in the nest cavity to ambient exterior luminosity. Readings were taken with a Gossen Luna-pro meter (Berkey Marketing Co., Woodside, New York), equipped with a remote release. Measurements were made on overcast days so that the ambient light would be diffuse and uniform.

(5) Neighbor distance—mean distance between nests and their nearest neighbors.

(6) Nest density—number of nests per 50 m of coast. On Brandypot densities were determined from a continuous transect system set up from a randomly determined point of departure. Densities on St. Mary's were established from transect systems set up separately for each subcolony because the coast was irregular and nests were clumped.

Unoccupied holes on Brandypot were considered arbitrarily as potential nest-sites if their physical measurements fell within the central 90% of the frequency distributions of measurements of occupied sites for that island (except for particle size). In the case of particle size, the smallest 90% of measurements were included.

Hatching dates were determined by nest checks or estimated from growth curves of weight and wingspan (Cairns 1978). Behavioral observations on Brandypot were made in the morning when the birds assembled on the rocks during the rising tide, between 23 May and 23 June. The frequency of agonistic behavior was expressed as the number of agonistic interactions per bird-min. Agonistic interactions were defined as encounters in which the behavior of 1 bird induced the retreat of another.

RESULTS

I located 165 Black Guillemot nests on Brandypot and 143 on St. Mary's; these probably represent nearly all the nests in the study areas. My data on breeding success are complete for 90 and 122 nests in the 2 areas, respectively.

Nesting on Brandypot was restricted to areas of conglomerate bedrock. Nesting occurred in vertical and oblique fissures, under rock overhangs, under boulders and in earth-lined holes with ceilings of tree roots or rock. All occupied sites were bedded with either soil, small stones, or organic matter.

On St. Mary's most guillemots nested in natural crevices in the bedrock, although nests were also found among the small boulders of raised beach-

TABLE 1

SITE CHARACTERISTICS OF BLACK GUILLEMOT NESTS, AND THEIR CORRELATIONS WITH BREEDING SUCCESS

			St. Mary's			
	Brandypot N = 90		Lightly disturbed N = 72		Heavily disturbed N = 50	
Characteristic	$\bar{x} \pm$ SD	t^a	$\bar{x} \pm$ SD	t	$\bar{x} \pm$ SD	t
Particle size (mm)	11.8 ± 11.4	-0.21^b	19.3 ± 12.0	0.16	21.4 ± 12.2	−0.003
Nest diameter (cm)	14.5 ± 5.0	−0.042	13.4 ± 3.6	−0.037	15.2 ± 12.1	−0.074
Nest depth (cm)	102 ± 51.6	−0.095	75.1 ± 27.8	0.092	79.7 ± 26.4	0.062
Overall shelter (ratio)	0.0072 ± 0.018	−0.087	0.040 ± 0.041	−0.032	0.045 ± 0.048	-0.34^c
Neighbor distance (m)	6.3 ± 11.2	0.094	32.1 ± 46.2	−0.13	16.9 ± 14.6	−0.016
Nest density (nests/50 m)	16.7 ± 11.9	0.005	3.44 ± 2.25	0.081	6.0 ± 1.6	0.16

[a] Kendall's rank-order coefficient of correlation between breeding success, ranked on a 1–6 scale, and site characteristics.

[b] $P \leq 0.01$.

[c] $P \leq 0.002$.

TABLE 2

BLACK GUILLEMOT NESTING SUCCESS IN 3 HABITATS

		St. Mary's	
	Brandypot N = 90	Lightly disturbed N = 72	Heavily disturbed N = 50
Eggs laid/nest	1.79[a]	1.94[a]	1.96
Eggs hatched/nest	1.11	1.31[b]	0.64[b]
Chicks fledged/nest	0.64	0.97[c]	0.38[c]
Eggs hatched/eggs laid	0.59	0.66[d]	0.32[d]
Chicks fledged/chicks hatched	0.59	0.71	0.61

[a] $P < 0.025$, G = 8.7.

[b] $P < 0.005$, G = 16.2.

[c] $P < 0.01$, G = 14.3.

[d] $P < 0.005$, G = 16.5.

es, under rock slabs and blocks splintered from the bedrock, and in earth-lined holes under boulders. As on Brandypot no eggs were found laid on bare rock, and fine gravel was the most common nest-bed material.

Mean values of nest characteristics are presented in Table 1. The most consistent parameter was nest diameter, its mean varied only from 13.4–15.2 cm in the 3 areas. Particle size of nest-bed material was larger on St. Mary's than on Brandypot, although nest-bed particles on Brandypot tended to be more sharp-edged and jagged than the rounded pebbles of St. Mary's. In general, nest-sites on Brandypot were more sheltered than those on St. Mary's, as indicated by their greater depth and lower light penetration.

Razorbill and guillemot nests were interspersed on Brandypot, but the Razorbills used crevices that were much less sheltered and I only once found eggs of the 2 species in the same hole. On St. Mary's the alcid dispersion pattern was not uniform, and nests were grouped by species and habitat. The highest densities were those of Common Murres nesting in large crevices and caves, and puffins nesting in burrows on turf slopes. Razorbills and crevice-nesting puffins tended to nest together, with large holes being occupied by Razorbills and smaller ones by puffins. Black Guillemot pairs nested individually and in small groups along the coast, and were generally absent from areas occupied by other alcids.

Nest density was considerably higher on Brandypot than on St. Mary's (Table 1). Potential nest-sites were available in excess in both study areas, but they were mapped and measured only on Brandypot. This was because puffins occupied many such sites on St. Mary's and tended to nest deep within them where they could not be detected. The Brandypot colony was divided into high and low density areas in order to give equivalent sample

TABLE 3

MEAN PARTICLE SIZE AND OVERALL SHELTER OF BLACK GUILLEMOT NEST-SITES, ACCORDING TO BREEDING SUCCESS OF NESTS

	Nests with clutch of:		Nests with hatching success of:			Nests with fledging success per hatched chick of:		
Variable and study area	1	2	0	0.5	1	0	0.5	1
Particle size (mm) Brandypot	13.5	11.1[a]	16.8	12.1	7.6[b,c]	7.2	4.4	11.4[d]
Overall shelter (ratio) St. Mary's heavily disturbed	0.034	0.049[e]	0.073	0.015	0.026[f]	0.025	0.0038	0.028[g]

[a] $P > 0.05$, F = 0.66.

[b] $P < 0.005$, F = 5.99.

[c] Values not significantly different are underscored (*a priori* test).

[d] $P > 0.05$, F = 2.34.

[e] $P > 0.05$, F = 0.18.

[f] $P < 0.025$, F = 4.25.

[g] $P > 0.05$, F = 0.54.

TABLE 4

DENSITY, REPRODUCTIVE VARIABLES AND FREQUENCY OF AGONISTIC BEHAVIOR IN 2 BLACK GUILLEMOT SUBCOLONIES ON BRANDYPOT ISLAND

	Subcolony	
	Aggregated	Dispersed
Number of nests	38	13
Density (nests/50 m of coast)	54.5	6.0
Occupation rate of potential sites	86%	76%[a]
Young fledged/nest	0.52	0.83[b]
Hatching date: $\bar{x}$	28 June	27 June
SD	±11.9	±13.4[c]
Agonistic interactions/bird-min	0.0312	0.0218[d]
Mean number of birds under observation	7.6	11.1
Total observations (bird-min)	4437	4078

[a] $P > 0.05$, $G = 0.29$.

[b] $P > 0.05$, $G = 1.3$.

[c] $P > 0.05$, $F = 1.27$.

[d] $P < 0.01$, $G = 6.87$.

sizes in the 2 density categories. The occupancy rate of available sites was significantly higher in areas of high site density than in areas of low site density (84 vs 58%, $P < 0.005$, $G = 18.8$).

Overall nesting success was highest in the St. Mary's lightly disturbed area where 0.97 young per nest fledged (Table 2). This value was not significantly different from the success rate on Brandypot (0.64 chicks fledged per nest), but was significantly higher than the 0.38 young produced per nest in the St. Mary's heavily disturbed zone. Most of the difference between production rates in the St. Mary's heavily vs lightly disturbed areas was due to lowered hatching success in the heavily disturbed area; differences between the 2 areas were large and significant for eggs hatched per nest and eggs hatched per egg laid, but the difference between rates of chicks fledging per chick hatched was small and not significant (Table 2).

The relation between breeding success and observer disturbance on Brandypot was examined with a Kendall rank-order correlation between the number of nest visits and a ranked scale of breeding success. The scale assigned values of from 1–6 according to success achieved (i.e., 1 or 2 eggs laid, 1 or 2 eggs hatched, 1 or 2 chicks fledged). The Kendall coefficient was non-significant ($t = -0.08$, $P > 0.05$).

The same scale of breeding success was used to examine the relationship between site characteristics and success (Table 1). Only 2 significant relationships emerged: on Brandypot breeding success diminished with increasing particle size, and in the St. Mary's heavily disturbed area success was reduced in holes with decreasing overall shelter. In order to break down the influence of these site variables on each stage of nesting, I calculated their mean values according to the breeding success of the nest (Table 3). No significant difference in site characteristics was found for nests of varying clutch-size or fledging success per hatchling, but sites with different hatching successes differed significantly in their particle size (Brandypot) and overall shelter (St. Mary's heavily disturbed).

In order to determine the effects of observer interference on the condition of chicks at fledging, I calculated maximum weights attained and wingspans at fledging of chicks in the St. Mary's lightly and heavily disturbed habitats. Chicks in the heavily disturbed area were heavier, but did not have broader wingspans than chicks in the lightly disturbed zone (412 vs 370 g, $P < 0.001$, $F = 21.4$; 516 vs 508 mm, $P > 0.05$, $F = 1.8$).

Mean hatching dates were 26 June on Brandypot, and 14 and 18 July in the 2 St. Mary's zones. To examine the relation between breeding synchrony and nest dispersion, I calculated Pearson correlations between deviations from mean hatching dates, and neighbor distances and nesting densities. No statistically significant relations were found.

A comparison between rates of agonistic interactions between 2 Brandypot subcolonies with high and low nesting densities is presented in Table 4. Agonistic behavior was significantly more frequent in the aggregate subcolony, but there were no significant differences between hatching dates, breeding synchrony or breeding success.

DISCUSSION

Reproductive success of Black Guillemots nesting in the part of the St. Mary's colony subjected to daily visits was much lower than in the part visited once every 4 days. Unfortunately, the possibility that observer disturbance might have a detrimental impact on breeding success was not suspected during planning of the fieldwork, and the 2 St. Mary's study areas are not strictly comparable, as the nesting density in the heavily disturbed zone is much higher than in the lightly disturbed zone (Table 1).

There are good reasons to believe, however, that high nesting density could not be responsible for the drastic difference in productivity between the areas. In the first place, no significant relation between density and breeding success was detected (Tables 1 and 4). If high density reduces breeding success, then the Brandypot colony should have a success rate lower than that of the St. Mary's heavily disturbed area, since its density is much greater (Table 1). However, this is true neither for the Brandypot colony as a whole (Table 2), nor for a subcolony whose density is 9 times that of the St. Mary's heavily disturbed area (Tables 1 and 4).

A depressing effect of density on success seems to be absent in the colonies, so observer disturbance is the most probable cause of the low breeding performance in the St. Mary's heavily disturbed area. Most of the reproductive failure in this area was due to a reduced hatching rate, possibly induced through decreased incubation attentiveness, damage to eggs during panic departures from the nest, nest abandonment, or some combination of these. None of these factors was measured directly, because nest abandonment generally could not be confirmed until the normal incubation period was exceeded, by which time the eggs were too decayed to determine the cause of their death.

The significant negative correlations between particle size and overall shelter, and breeding success (Table 1) may also have been observer-induced. On Brandypot most nest beds were lined with conglomerate pebbles with sharp-edged concave faces, and it can be assumed that the larger the nest-bed particles, the greater the chances that eggs would be damaged by a bird departing suddenly. Breeding success was greatest in the darker, better sheltered holes in the St. Mary's heavily disturbed area. Birds in these sites may have been less inclined to flush in panic when an observer entered the area (observer presence was usually signalled by gull alarm calls). In the case of both particle size on Brandypot and overall shelter on St. Mary's, the main effects on breeding success occurred during the egg stage, since the means of these variables differed for nests with varying levels of hatching success, but not for nests of differing clutch-size and fledging success per hatchling (Table 3).

Despite the depression in success rates associated with observer interference, maximum weights attained by fledglings were considerably higher in the St. Mary's heavily disturbed area than in the lightly disturbed area. Those birds which succeeded in hatching their eggs in the face of daily disturbance may have been more attentive or more experienced as parents than the average successful nester in the lightly disturbed area. Robert and Ralph (1975) found a similar situation in a colony of Western Gulls (*Larus occidentalis*), where hatching success dropped with increasing disturbance, but chick survivorship rose.

Previous studies of the effects of human interference on seabird reproduction indicate that disturbance lowers breeding success by raising the susceptibility of eggs or young to intra- or interspecific predation (Johnson 1938, Hunt 1972, Gillett et al. 1975, Ellison and Cleary 1978). The directly harmful effects on parental care induced by human interference have been documented poorly in colonial seabirds, although the possibility of such effects has been suggested by several authors, including Bergman (1971) for Black Guillemots, and Nettleship (1975) for Gannets (*Morus bassanus*).

On both Brandypot and St. Mary's suitable nest-sites were available in excess. In other North American guillemot colonies studied by Preston (1968) and Divoky et al. (1974), lack of suitable habitat forced many birds into marginal sites where they suffered heavy nest losses. The fact that the Brandypot guillemots, when given a choice of habitat, tended to nest in a clumped distribution suggests that the species shares the gregarious nesting tendencies of other alcids, although this effect could have come about through colony tradition (Lack 1967).

Preston (1968) found breeding success to be lower in a guillemot subcolony with high nesting density, and concluded that higher aggression rates in the dense area were the cause. In this study agonistic behavior was more frequent in a high density subcolony, but no evidence for a relation between density and breeding success was found.

SUMMARY

Breeding success, breeding synchrony and condition of young at fledging were measured in 2 Black Guillemot colonies. Nest productivity was lower, but maximum chick weights were higher, in an area disturbed daily than in an area disturbed once every 4 days. Intraspecific agonistic behavior was more frequent in a high density subcolony, but nesting density was uncorrelated with breeding success and synchrony. No relationship was found between habitat structure and breeding success. The occupancy rate of available sites was greater in high density zones, suggesting a gregarious tendency in Black Guillemot nesting.

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LITERATURE CITED

BÉDARD, J. 1969. Histoire naturelle du gode, *Alca torda*, L., dans le golfe Saint-Laurent, province de Québec, Canada. Can. Wildl. Serv. Rep. no. 7.

BERGMAN, G. 1971. Gryllteisten *Cepphus grylle* in einem Randgebiet: Nahrung, Brutresultat, Tagesrhythmus und Ansiedlung. Commentat. Biol. Soc. Sci. Fenn. 42:1–26.

CAIRNS, D. 1978. Some aspects of the biology of the Black Guillemot (*Cepphus grylle*) in the estuary and the Gulf of St. Lawrence. M.Sc. thesis, Université Laval, Québec, Québec.

DIVOKY, G. J., G. E. WATSON AND J. C. BARTONEK. 1974. Breeding of the Black Guillemot in northern Alaska. Condor 76:339–343.

ELLISON, L. N. AND L. CLEARY. 1978. Effects of human disturbance on breeding of Double-crested Cormorants. Auk 95:510–517.

GILLETT, W. H., J. L. HAYWARD AND J. F. STOUT. 1975. Effects of human activity on egg and chick mortality in a Glaucous-winged Gull colony. Condor 77:492–495.

HUNT, G. L. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology 53:1051–1061.

JOHNSON, R. A. 1938. Predation of gulls in murre colonies. Wilson Bull. 50:161–170.

LACK, D. 1967. Interrelationships in breeding adaptations as shown by marine birds. Proc. XIV Int. Ornithol. Congr. 3–42.

NETTLESHIP, D. N. 1975. A recent decline of Gannets, *Morus bassanus*, on Bonaventure Island, Quebec. Can. Field-Nat. 89:125–133.

PRESTON, W. C. 1968. Breeding ecology and social behavior of the Black Guillemot, *Cepphus grylle*. Ph.D. thesis, Univ. Michigan, Ann Arbor, Michigan.

REED, A. 1973. Aquatic bird colonies in the Saint Lawrence estuary. Serv. de la faune du Québec, Bull. 18.

ROBERT, H. C. AND C. J. RALPH. 1975. Effects of human disturbance on the breeding success of gulls. Condor 77:495–499.

DÉPARTEMENT DE BIOLOGIE, UNIVERSITÉ LAVAL, QUÉBEC, QUÉBEC G1K 7P4, CANADA. (PRESENT ADDRESS: MACLAREN MAREX INC., BOX 9493, POSTAL STATION B, ST. JOHN'S, NEWFOUNDLAND A1A 2Y4 CANADA.)
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