# THE NESTING OF THE CRESTED, LEAST, AND PARAKEET AUKLETS ON ST. LAWRENCE ISLAND, ALASKA

JEAN BÉDARD[1]

Department of Zoology
University of British Columbia
Vancouver 8, British Columbia

Among the North Atlantic marine birds only one species fills the plankton-feeding niche (*Plautus alle*, Alcidae), while in the North Pacific and adjacent seas it is occupied by no less than five alcids. A comparison of the feeding and nesting habits was made in order to understand how the food resources and nesting habitat are partitioned among three of these species, the Crested Auklet (*Aethia cristatella*), the Least Auklet (*A. pusilla*) and the Parakeet Auklet (*Cyclorrhynchus psittacula*). This article is concerned with one aspect of the study, the utilization of the nesting space by these three species.

While the two congeneric species differ markedly in size (*A. pusilla*, 90 g; *A. cristatella*, 290 g), the Crested and Parakeet Auklets are of equivalent body size. All are extremely able to walk, run, and climb along near-vertical boulder edges. If differences are observed in the micro-distribution of these species, they are not attributable to different locomotory abilities.

The birds arrive in the vicinity of the breeding grounds four to six weeks before laying and take up nest sites which they presumably defend. Available evidence also indicates that the three species studied are comparable to other alcids in that they show pronounced faithfulness to the nest site (Sealy 1968). During this study, laying occurred in the last days of June and the first 10–12 days of July. Birds of these species do not accumulate nest material, and a single egg is deposited under the shelter of jumbled rocks on appropriate slopes (in *Aethia*) at the angle of contact of two or more boulders. The case of *Cyclorrhynchus* will be discussed separately. Both parents take part in incubating the egg and caring for the nestling.

All three species are diurnal. As with other alcids, a number of immature birds are found in the colonies during most of the breeding season and can be recognized by plumage characteristics, behavioral attitudes, or both. In July, at their peak attendance, these immature birds comprise 30–35 per cent of the total number present.

## METHODS

This study was conducted on St. Lawrence Island, Alaska, between 1964 and 1967. Background information on the geography, fauna, and ecological conditions prevalent on the island may be found in Fay and Cade (1959) (see also fig. 1).

The two species of *Aethia* make use, for nesting purposes, of the layer of rock debris that covers the slopes. Thirty quadrats, 14.2 m to a side, were marked out on the slopes of Sevuokok Mountain (17) and Kongkok Basin (13). The 14.2 m dimension proved the most adequate for covering the stripe-like stretches of nesting habitat and provided an easy-to-handle surface value of 200 m$^2$.

In Sevuokok, censuses had to be conducted from a vantage point in order to have a plain view of the quadrat. The vantage point was always more than 40 m from the quadrat to minimize possible disturbances. This meant elimination of total randomness in selecting the quadrat location. In Kongkok, the observation site was centrally located with the tilted walls of the cirque and the painted boundaries of the quadrats in plain view. All censuses were conducted between 05:00 and 08:00 during the few days preceding laying, coinciding with a minimum daily attendance of immature birds in the colony and maximum activity of breeding birds on the surface of the slope. Much courtship activity takes place on the nest site itself, out of sight of the observer. Tallies were made every 30 min during the 3 hr period, on three successive days. Between 5 and 20 tallies per species were available for each quadrat.

Late in the breeding season, every quadrat was surveyed. Among the most important characteristics measured were: bearing to water-line, altitude, angle of slope, percentage of stoniness, percentage of the quadrat used by the birds, sphericity of the particles, thickness of the layer of rubble or mantle (20 spot measurements), and particle size. The latter was measured by stretching a string across the

---

[1] Present address: Départment de Biologie, Faculté des Sciences, Université Laval, Québec 10, Province of Québec, Canada.

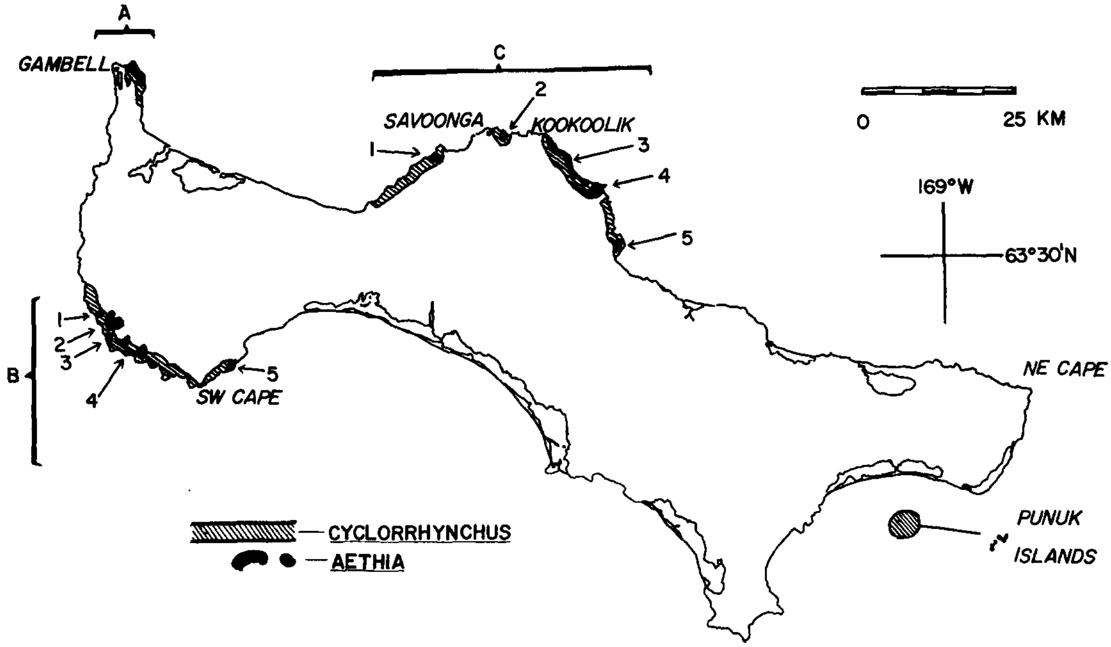

FIGURE 1. Location map showing St. Lawrence Island with the names of places mentioned in the text and the location of all known colonies of *Aethia* spp. and concentrations of *Cyclorrhynchus psittacula.* A = Sevuokok Mountain. B 1 = Omwalit Mountain; B 2, Kongkok; B 3, Iveekan; B 4, Tupurpuk and Sitiilekk; B 5, Powooiliak (reported). C 1 = Kineeghit (reported); C 2, Savoonga; C 3, Kookoolik-Ataakas; C 4, Ataakas Camp; and C 5, Reindeer Camp (reported).

quadrat and recording the three dimensions for every reachable particle intersected by the string. In Sevuokok, seven such intersect lines were made in each quadrat but this number was reduced to five in Kongkok. The validity of this procedure rests on the assumption that the layer of rocks used as nesting habitat is vertically homogeneous. Although, normally, small particles would be expected to accumulate at the lower levels, evidently, mass-wasting processes, frost, and other factors contribute so much to the mixing of the material in this layer of rock debris that the assumption is quite acceptable.

Most of the colonies were visited and figures on nesting area (measured by pacing), sketches of colony extent, and estimates or measurements of the relative abundance of the two *Aethia* species were obtained. These measurements were transferred to large scale maps (Army Map Service, Q-801, 1951; 1:25,000) for an evaluation of the nesting area used by *Aethia.* A few colonies were reported by the residents of the island but could not be visited. Most of these are reputedly small in extent and their location, as well as approximate area, was derived from multiple interviews.

Fowling, an age-old tradition, is still conducted on a moderate scale in the Sevuokok colony. Unfortunately it was discovered too late that a few quadrats were located in the midst of traditional fowling areas. The Kongkok colony has been left undisturbed for at least a decade.

In a few quadrats prominent boulders protruding above the surface were used as landing spots by birds nesting beyond the quadrat boundaries. After a disturbance an abnormally high tally was obtained in such quadrats. For this reason, the standard procedure in averaging census values was to ignore the highest count in each quadrat, thus correcting for the aberrant series of counts without affecting the normal ones. It is also obvious that low census figures do not have as much importance as the high ones since partial or complete disturbances were common during the censuses (passage of a gull, a fox, etc.). The average density figures given in table 1 were obtained by averaging the second, third, and fourth highest census figures for each quadrat. To render values of density comparable between quadrats, the average densities had to be corrected for two unrelated variables affecting them: (1) percentage of the quadrat occupied by the birds, with correction to 100 per cent occupancy whenever needed, and (2) thickness of the mantle of rocks on the slope, with correction to a uniform depth of one meter.

Frequency distributions were obtained for

TABLE 1. Corrected census figures and selected slope characteristics in the quadrats of Sevuokok and Kongkok colonies of *Aethia pusilla* (P) and *Aethia cristatella* (C).

| Quadrat no. | Rock diameter (dm) | | Altitude (m) | Angle of slope | % of occupancy | Density/200 m² | | Total | Relative abundance[a] |
|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | SD | | | | P | C | | |
| Sevuokok | | | | | | | | | |
| 1 | 7.29 | 5.75 | 115 | 39.5 | 100 | 22.31 | 11.28 | 33.59 | 66.42 |
| 2 | 7.23 | 5.92 | 120 | 30.0 | 80 | 69.42 | 23.35 | 92.77 | 74.83 |
| 3 | 6.74 | 4.77 | 90 | 32.5 | 100 | 17.99 | 23.10 | 41.09 | 43.78 |
| 4 | 5.02 | 3.19 | 105 | 32.5 | 80 | 59.72 | 20.83 | 80.55 | 74.14 |
| 5 | 10.03 | 7.39 | 40 | 18.5 | 100 | 11.39 | 12.37 | 23.76 | 47.95 |
| 6 | 6.08 | 4.12 | 75 | 35.0 | 100 | 52.08 | 39.93 | 92.01 | 56.60 |
| 7 | 4.87 | 3.40 | 105 | 27.0 | 65 | 73.07 | 11.52 | 84.59 | 86.38 |
| 8 | 3.74 | 2.68 | 75 | 33.0 | 80 | 120.00 | 10.00 | 130.00 | 92.31 |
| 9 | 6.14 | 4.48 | 55 | 28.0 | 45 | 62.68 | 44.61 | 107.29 | 58.42 |
| 10 | 9.87 | 6.12 | 5 | 16.0 | 65 | 25.02 | 10.50 | 35.52 | 70.44 |
| 11 | 6.93 | 4.22 | 5 | 9.0 | 70 | 42.48 | 14.84 | 57.32 | 74.11 |
| 12 | 6.31 | 5.01 | 75 | 28.5 | 100 | 31.38 | 19.72 | 51.10 | 61.41 |
| 13 | 9.57 | 6.03 | 15 | 10.5 | 100 | 11.73 | 28.18 | 39.91 | 29.39 |
| 14 | 4.12 | 2.93 | 20 | 9.0 | 100 | 91.04 | 59.70 | 150.74 | 60.40 |
| 15 | 4.18 | 2.54 | 20 | 6.0 | 100 | 112.03 | 98.61 | 210.64 | 54.19 |
| 16 | 4.95 | 3.39 | 35 | 19.5 | 80 | 51.51 | 22.41 | 73.93 | 69.68 |
| 17 | 5.49 | 4.06 | 30 | 17.0 | 55 | 54.45 | 14.02 | 68.47 | 79.52 |
| Kongkok | | | | | | | | | |
| 18 | 3.26 | 1.49 | 105 | [b] | 100 | 67.95 | 15.81 | 83.76 | 81.13 |
| 19 | 3.37 | 1.60 | 130 | | 100 | 58.21 | 9.38 | 67.59 | 86.12 |
| 20 | 3.22 | 1.53 | 120 | | 100 | 60.87 | 12.55 | 73.42 | 82.91 |
| 21 | 3.26 | 1.47 | 150 | | 90 | 68.23 | 5.17 | 73.40 | 92.96 |
| 22 | 3.49 | 1.69 | 165 | | 100 | 74.31 | 18.03 | 92.34 | 80.48 |
| 23 | 6.72 | 3.94 | 110 | | 100 | 1.21 | 50.17 | 51.38 | 2.38 |
| 24 | 4.90 | 2.74 | 110 | | 100 | 11.97 | 31.45 | 43.42 | 27.57 |
| 25 | 4.09 | 2.23 | 165 | | 100 | 28.47 | 37.86 | 66.33 | 42.92 |
| 26 | 4.46 | 2.47 | 115 | | 100 | 20.53 | 28.87 | 49.40 | 41.56 |
| 27 | 3.21 | 1.30 | 105 | | 100 | 68.53 | 12.68 | 81.21 | 84.39 |
| 28 | 3.29 | 1.35 | 110 | | 100 | 81.69 | 15.69 | 97.38 | 83.89 |
| 29 | 4.94 | 2.97 | 215 | | 100 | 9.25 | 46.82 | 56.07 | 16.50 |
| 30 | 5.73 | 4.09 | 180 | | 100 | 5.26 | 44.36 | 49.62 | 10.60 |

[a] Relative abundance expressed as (*pusilla* density/total density) × 100.

[b] Angle of slope not measured in Kongkok.

the linear measurements of the particles using the three linear dimensions obtained in the field. Statistical procedures employed in comparing bird populations with various slope characteristics are simple linear and curvilinear correlations and regressions. Corrected census figures and selected habitat characteristics are presented in table 1.

## THE NESTING HABITAT AND NUMBERS OF AUKLETS

### LEAST AND CRESTED AUKLETS

The location of all known auklet colonies on St. Lawrence Island is shown in figure 1. The complete absence of *Aethia* from the southeastern half of the island has been attributed to the combined effects of absence of suitable habitat in the form of maritime bluffs and to the presence of unfavorable hydrographic conditions, known to differ sharply from those found along the western and northwestern coasts (Bédard 1969b). Figure 1 illustrates the patchy nature of the distribution of *Aethia* as opposed to the linear aspect of the distribution of *Cyclorrhynchus*. This obviously reflects their habitat preferences, the latter being at ease in almost any type of precipitous bluff, while the other two species are nearly restricted to talus slopes. On talus slopes, *Aethia* uses the covering of cobbles and boulders for nesting. This mantle is a volumetric entity, generally not over 5 m thick. Its lower limit is the unfractured parent rock or, more often, the result of the accumulation and settling of fine to very fine particles with the production of a flat and relatively uniform surface.

*Talus slopes.* Talus slopes are actively formed in areas of periglacial conditions and are the product of weathering of cliffs by such processes as frost-heaving on the cliff face, tumbling by gravity of the detached blocks, and accumulation and settling of the debris by slow mass-wasting processes such as creep and solifluction.

There are two major types of talus slopes:

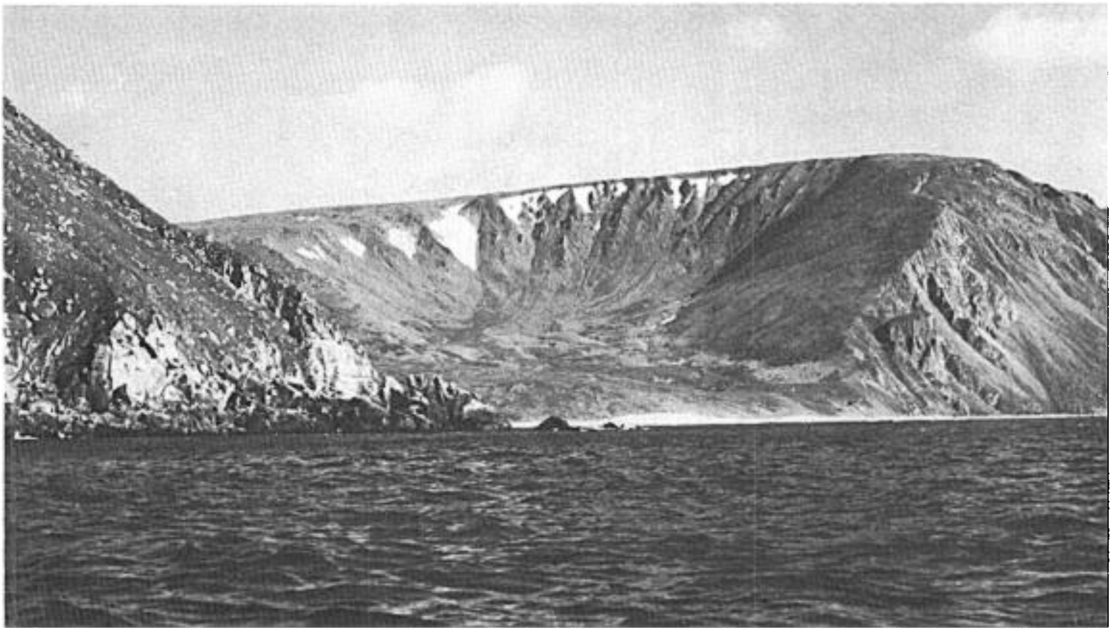

FIGURE 2. The glacial cirque of Kongkok, on the southwestern coast of St. Lawrence Island. The sloping walls and the moraine floor of the cirque are used as nesting habitat by *Aethia* spp., but not the gently sloping ground between the beach and the center of the floor. The distance between the upper rims of the cirque is slightly over one km; the highest altitude (on the right) is approximately 475 m. Within the cirque periphery, only a few pairs of *Cyclorrhynchus* were found nesting on the ridges of the rear wall. The scree slopes on the extreme right are also used by nesting auklets.

inland slopes, as found at Kongkok Basin (fig. 2), and maritime slopes. Since in the former there is no agent for the continuous removal of material from the base, heaving and disintegration act on the same material somewhat longer and the inland slopes are covered with a mantle of much finer particles. For the same reason, the combined action of creep and solifluction usually produce a concave profile. The presence of fine particles is often followed by soil development and invasion by vegetation. Inland slopes are more stable than maritime slopes.

A number of factors influence the nature, appearance, and stability of the maritime slopes exposed to wave action. Lithology, orientation of the diaclases or joints in the rock, presence or absence of littoral shelf, etc., all modify the end result and may create a large variety of slopes. In one type, exemplified by Sevuokok Mountain, the rock is massive and poorly jointed and wave action does not remove the large blocks at the foot of the bluff. This gives the geomorphic processes of wedging and heaving an opportunity to proceed unchecked, and the talus slope retreats upwards. Sea action, however, contributes to the removal of fine particles from the base of the slope, maintaining a slightly greater angle of repose in the lower reaches of the bluff and giving it a slightly convex profile (fig. 3). The lowest portion of the slope is subject to more rapid processes such as slumping and mud-flows, is noticeably less stable, and is seldom inhabited by auklets.

When the rock is soft and jointed, even moderate wave action effectively removes material from the base of the bluff. This results in another type of slope characterized by a greater degree of activity and a slightly higher angle of repose. Gravity, therefore, plays a dominant role in its modification. This type of slope is found in numerous places along the island's north coast. Here, suitable places for *Aethia* colonies are found only in sheltered coves or on the top of bluffs where talus formation is not checked by the removal of material by the sea. Along the coastline between Savoonga and Ataakas Camp, the auklets are found in an almost continuous colony and although few of them are found on the small unstable talus slope itself, they nest abundantly along the rim of the bluff and inland from it, sometimes for distances of almost one km. The terrain in such colonies is generally horizontal or slopes gently seawards (fig. 4) and I refer to it as "cliff-top" habitat. In a geomorphic sense, it is a true talus slope produced because of the friability of the basalt that covers the area. As nesting habitat, it is

FIGURE 3. View of one section of the colony of Sevuokok Mountain. Notice the slight increase in the angle of repose in the lowermost levels. The lack of sorting in particle size with altitude is evident, as well as the more or less patchy nature of the nesting habitat. Altitude at the rim is approximately 150 m. The Parakeet Auklet nested in abundance in cracks in the vicinity of the needle-like projections in the upper center and in the weathered ridge at the left center of the photograph.

undistinguishable from the true talus slopes of Sevuokok. It is not homologous with the flattish rocky terrain found further inland nor can it be compared to inland talus slopes such as Kongkok.

In the above ways, slope morphology may have important effects upon the nesting of auklets. The nature of the geomorphic processes, while affecting the size of the particles, the slope stability, the development of vegetation, etc., also determine the presence or absence of the birds and the degree of their occupancy.

*Population estimate.* Table 2 presents an estimate of the populations of auklets in the colonies of St. Lawrence Island. In the colonies of Sevuokok and Kongkok a series of actual figures on density were obtained in the quadrats, and the population estimate was obtained by using average density (all quadrats combined) and measured nesting area (table 1). In the other colonies, however, a less direct procedure was followed. In all cases, uncorrected census figures were used, for the aim was to obtain an estimate of absolute density and not to determine the effects of various variables.

For field use, I established four categories of nesting terrain, ranging from one extreme in which large boulders dominate and where fine material is scarce, to the other extreme in which the material of the mantle has been reduced to a fine condition and where large boulders are absent. In the former, *A. cristatella* was by far the most abundant bird, while in the latter *A. pusilla* was virtually the only bird present. A colony was assigned to one of the four categories, enabling me to calculate total auklet populations and relative abundance on the basis of the relationship shown in figure 5. This relation indicates, in effect, that an increase in the representation of *pusilla* means a decrease in the total abundance of the two species. Apparently this occurs because primitive habitats where large boulders dominate afford more nesting opportunities than do the more stable slopes covered with fine particles and some vegetation. Whatever the real cause for the relationship, for any of the four easily recognized types of terrain, it is possible to calculate a pair of density figures for the two auklets that fall within a resonable margin of error ($\text{SE} = 21.7$).

The averages obtained at Sevuokok have been applied to the Savoonga colony where

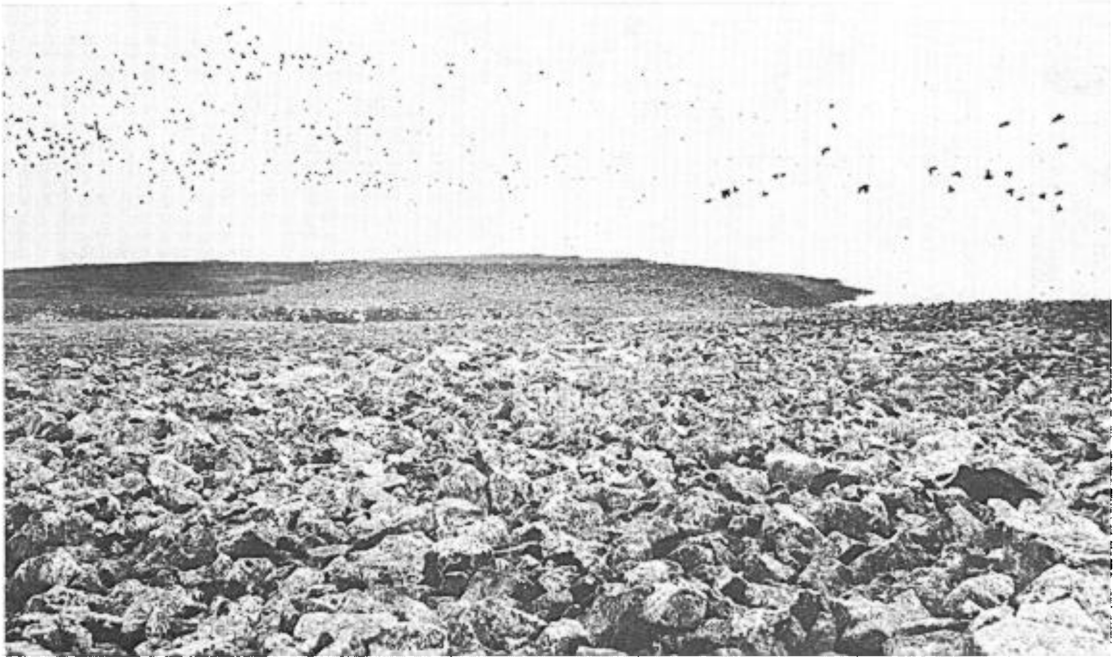

FIGURE 4. "Cliff-top" colony in the vicinity of CapeMyaughee (between Kookoolik and Ataakas Camp). Notice the continuity of the mantle from the talus to the terrace. Only the Least and Crested Auklets are found in such habitat.

overall habitat characteristics and conditions of human exploitation are comparable. Similarly, the averages obtained at Kongkok were applied to Iveekan Mountain because of habitat similarities. Raw averages calculated from figure 5 were applied to the other colonies. The population density estimates given in table 2 are probably low for two reasons: the censuses could not be completed before some laying had occurred, which probably reduced the potential number of observable breeders, and the nesting grounds, when measured on the maps, were treated as flat areas, although gullying and surface irregularities add to the total nesting area.

PARAKEET AUKLET

In the Aleutian Islands, the Parakeet Auklet is said to nest "among large boulders on the beach, and in crevices in rocky cliffs, also on slopes where the rocks are partly covered with vegetation" (Murie 1959:194). In the Commander Islands, Stejneger (1885:43) saw them nesting "in steep, cracked and inaccessible

TABLE 2. Estimates of total populations of *Aethia pusilla* (P) and *Aethia cristatella* (C) in the colonies of St. Lawrence Island.

| Colony | Area (m²) of nesting habitat | Density of breeding birds/200 m² | | Total no. breeding birds[a] | | Total no. birds, breeding and non-breeding | | No. birds in colony[a] |
|---|---|---|---|---|---|---|---|---|
| | | P | C | P | C | P | C | |
| Reindeer Camp | 100,000[b] | 25.3 | 47.1 | 13,000 | 24,000 | 20,000 | 37,000 | 57,000 |
| Ataakas Camp | 445,000 | 37.4 | 4.0 | 83,000 | 9,000 | 128,000 | 14,000 | 142,000 |
| Ataakas-Kookoolik | 1,160,000 | 35.7 | 19.2 | 207,000 | 111,000 | 318,000 | 171,000 | 489,000 |
| Savoonga | 185,000 | 36.0 | 23.6 | 33,000 | 22,000 | 51,000 | 34,000 | 85,000 |
| Kineeghit | 50,000[b] | 35.7 | 19.2 | 9,000 | 5,000 | 14,000 | 8,000 | 22,000 |
| Sevuokok | 400,000 | 36.0 | 23.6 | 72,000 | 47,000 | 111,000 | 72,000 | 183,000 |
| Omwalit SW | 31,000 | 35.7 | 19.2 | 5,000 | 3,000 | 8,000 | 5,000 | 13,000 |
| Kongkok | 715,000 | 34.4 | 29.9 | 123,000 | 107,000 | 189,000 | 165,000 | 354,000 |
| Iveekan | 94,000 | 34.4 | 29.9 | 16,000 | 13,000 | 25,000 | 20,000 | 45,000 |
| Tupurpuk & Sitiilekk | 275,000 | 35.7 | 19.2 | 49,000 | 26,000 | 75,000 | 40,000 | 115,000 |
| Powooiliak | 50,000[c] | 35.7 | 19.2 | 9,000 | 5,000 | 14,000 | 8,000 | 22,000 |

[a] Figures are rounded to the nearest 1000.

[b] Colony has not been visited. Its precise location and extent, here derived from interviews with the residents, remain to be determined.

[c] No informant had visited the colony in the vicinity of Powooiliak in recent years and its present existence is questionable.

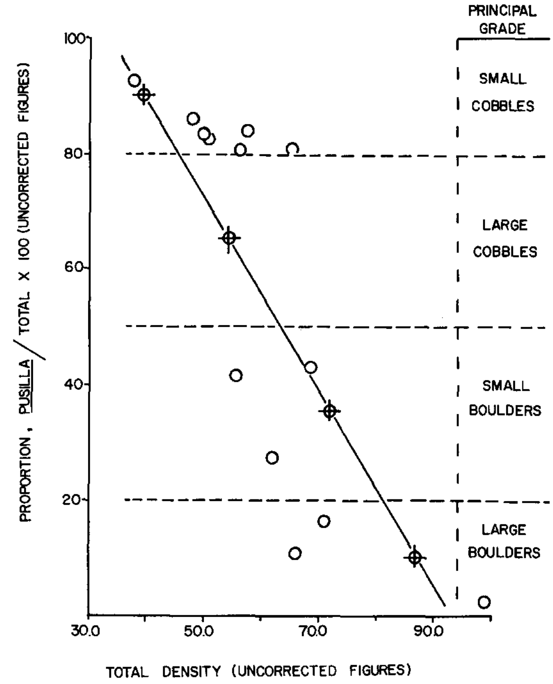

FIGURE 5: Relationship between total density and relative abundance of the two species of *Aethia* for each quadrat of the Kongkok Basin (open circles). The four categories were designed for field use and enabled one, once a colony had been visited and characterized as to the principal grade, to derive pairs of population density figures (circles with crosses) used in computing the estimates of table 2.

rocks." On St. Lawrence Island, *Cyclorrhynchus* occupies the same type of habitat as described by these writers. It is generally found in the cliff areas of the southwestern coast between Omwalit Mountain and at least as far as Southwest Cape (fig. 1). It is present in small numbers in Kongkok Basin, restricted to the ridges that cross the walls of the cirque. It is also common and locally abundant along the north-central coast of the island. In all these areas it is in company with puffins (*Lunda* and *Fratercula*) and the Pigeon Guillemot (*Cepphus columba*), sharing with the latter traits of ubiquitous distribution and of moderate to low numbers.

The Parakeet Auklet is abundant on Sevuokok Mountain where it is concentrated along the rim of the bluff and appears on the slope wherever weakly weathered outcrops break through the mantle. However, it also appears occasionally on the talus slope itself where it is associated with grassy stretches and where it will nest underneath large boulders or in the mantle below the sod cover. Finally, the few nests found in the rocky mantle in company with *Aethia* accounted for less than 5 per cent of all the nests observed.

In fact, *Cyclorrhynchus* barely overlaps *Aethia* in nesting requirements. It is primarily a scarp-face nester, and when it appears on talus slopes, it is always on grassy stretches or in areas where the mantle is covered with turf. There is no reason to suspect that *Cyclorrhynchus* is "pushed" into these habitats by the more abundant *A. cristatella*. Rather, the two birds have distinct habitat preferences and corresponding behavioral correlates (Sealy 1968).

The Parakeet Auklet does not form dense aggregations, and the largest groups seen in the best sections of the bluffs were smaller than 50 individuals. The total population of this species (all age categories) on Sevuokok Mountain was placed at 2000 birds. If only suitable habitat is considered, this gives a density estimate of one bird for 200 $m^2$. Suitably enclosed cracks in rocky outcrops or in vertical cliffs, by far the most important type of nest site for *Cyclorrhynchus*, are less available than the extremely numerous crannies and interstices among jumbled boulders preferred by *Aethia*.

## HABITAT FACTORS AFFECTING NUMBERS

Factors other than mortality and predation that could control density locally are physical factors, such as particle size, angle of slope, and thickness of the mantle, or overt conflict between the two species for nesting space, a biological factor not easily measured. Birds of the two species of *Aethia* are observed to display, and generally live amiably, on the same boulders. Social dominance between the individuals of the two species, which seems to depend upon body size differences, is frequently expressed in mild forms of aggression during which *pusilla* consistently withdraws. This set of influences will be examined later.

### DENSITY OF *A. PUSILLA*

The density of this species is compared to the average particle size in figure 6. The relationship for both observation areas is curvilinear, but in Sevuokok the rock material in the mantle is much coarser and this is accompanied by higher population densities. Coefficients of correlation ($r$) for log transformations of these two sets of data are −0.865 and −0.993 respectively; both are significant at the 0.001 level of confidence.

There is a very close relationship between the average particle size ($\bar{x}$) and the SD of particle size, the trend being for areas with large boulders to be very homogeneous in size

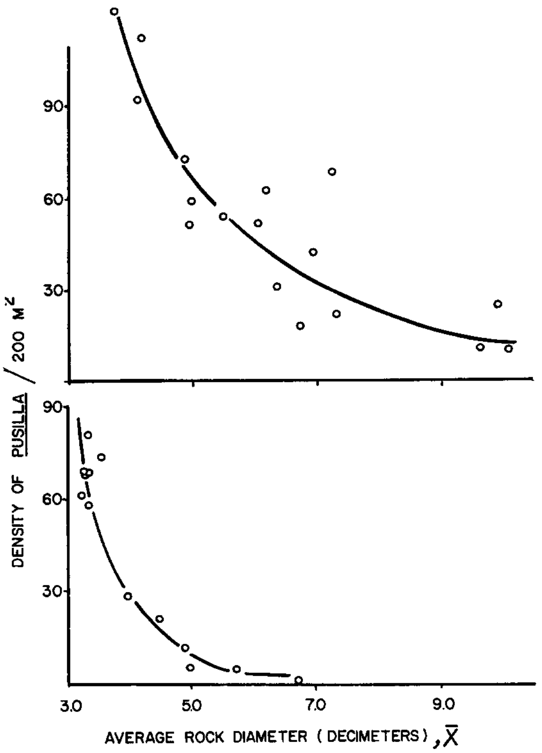

FIGURE 6. Relationship between the density of *Aethia pusilla* and the average rock diameter in the Sevuokok Mountain (above) and Kongkok colonies. For Sevuokok, the equation of the fitted line for transformed data is: log $D_{pusilla} = 2.52 + (-0.139)\bar{x}$, and 74.8% of the variation in the density of *pusilla* is explained. For Kongkok, the equation is: log $D_{pusilla} = 3.46 + (-0.49)\bar{x}$, and explains 98.6% of the variation in the density of *pusilla*.

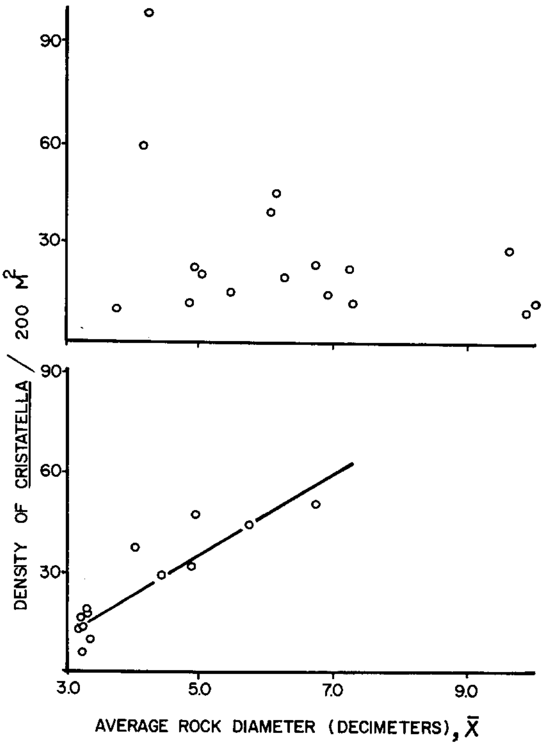

FIGURE 7. Relationship between the density of *Aethia cristatella* and the average rock diameter in the Sevuokok Mountain (above) and the Kongkok (below) colonies. The equation of the regression line for Kongkok is: $D_{cristatella} = 12.35\bar{x} + (-25.97)$.

composition (in Kongkok, the coefficient of correlation between $\bar{x}$ and SD is 0.975 and in Sevuokok, 0.944, both highly significant). This eliminates the necessity of dealing jointly with the two characteristics. For all practical purposes, the relationship between homogeneity of particles and the density of auklets reflects the relationship between mean particle size and density.

Evidently the relationship between the density of *pusilla* and the average particle size depends on control of the number of suitable nest sites. This number increases with diminishing particle size up to a point when cobbles become so small that the interstices they produce cannot accommodate *pusilla*.

### DENSITY OF *A. CRISTATELLA*

The relationship between the density of breeding birds of this species and the average particle size is shown in figure 7. The scatter diagram for Sevuokok is not very enlightening, but the lack of similarity between the two series (see *pusilla* above) is attributed to predation by the native hunters. This predation, although probably not amounting to more than a few thousand birds per year (approximately nine *cristatella* are taken for every *pusilla*), is a continuous influence. The fact that in known undisturbed environments, such as Kongkok, the species varies in abundance according to the average particle size ($r = 0.908$, $P < 0.001$) indicates that the Sevuokok series is not natural. Only replication of these observations in other disturbed and undisturbed areas would allow us to reach this conclusion with confidence, but there are, unfortunately, very few such areas. It may be that predation does not sufficiently account for the situation in Sevuokok. Basic differences may exist in the nature of the mantle between stabilized and "old" talus slopes, such as Kongkok, and relatively active slopes, such as Sevuokok.

### TOTAL DENSITY

Only the Kongkok series is used to establish this relationship since it has been noted earlier that figures for *cristatella* in Sevuokok can hardly be used. There is a slight curvilinear

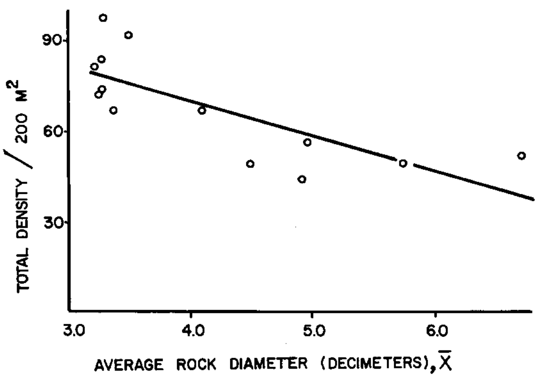

FIGURE 8. Relationship between the total density of *Aethia pusilla* and *A. cristatella* and the average rock diameter. The regression line equation is: $D_{total} = 116.96 + (-11.78)\ \bar{x}$. Of the variation in $D_{total}$, 59% is explained, and $r = -0.768$ $(P < .01)$.

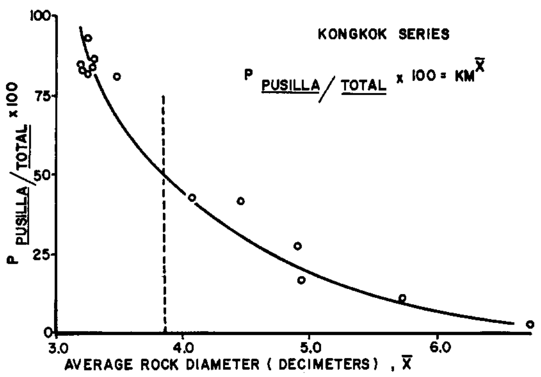

FIGURE 9. Relationship between the average rock diameter and the relative abundance (P) of the two species of *Aethia*. The broken line indicates the value of $\bar{x}$ at which both species are in equal abundance. The equation is: $\log P_{pusilla/total} \times 100 = 3.32 + (-.414)\ \bar{x}$.

trend in the data of figure 8 but the increased amount of explained variance by a curvilinear fit is not statistically significant ($F = 0.85$, $P > 0.20$).

### OTHER HABITAT CHARACTERISTICS

No meaningful relationship was detected between the density of *pusilla*, the density of *cristatella*, or their total density and the major habitat characteristics for which quantitative information was available. Altitude appears to have no direct effect upon the density of either species, nor upon their combined density. Yet Fay and Cade (1959) observed an altitudinal sorting, claiming that *pusilla* occupied the highest levels of the talus slopes. This relation, however, is only an indirect one. Smaller particles are generally found at the rim or crest of talus slopes, apparently because gravity and mass-wasting processes tend to accumulate more large particles in the lowest reaches of the slope. But this is not the case in all colonies. Figure 3, for instance, indicates that there is no obvious pattern in the distribution of various-sized particles with altitude. It seems clear, on the contrary, that the proximity to crests, or ridges, or, more generally, to sources of rock material determines the presence of large rock fragments. This type of altitudinal sorting of particles is found in Kongkok and can also be seen on the scree slope at the extreme right of figure 2. Even there, dense groups of *cristatella*, sometimes outnumbering *pusilla*, were found wherever areas of large boulders existed, up to the southeastern rim of the cirque at an altitude of some 400 m.

Observed features such as angle of slope, stabilization by vegetation, and size of the particles are all interdependent characteristics of a whole and integrated structure. However, the explained variation in the density of auklets by the use of a single dominant factor, mean rock diameter, does give enough predictive power and a fair enough description of the effect of slope morphology that other possible factors can be neglected.

### RELATIVE ABUNDANCE OF THE TWO *AETHIA*

Relative abundance has been expressed as $P_{pusilla/total} \times 100$ and varies between 2.36 and 92.96 (table 1). The scatter diagram together with the regression line for the value of P versus the average particle size ($\bar{x}$) for the Kongkok series is given in figure 9. The dominance of one species over the other, when P passes through 50.0, can be calculated to take place at a value of the independent variable equal to 3.8 dm. Fitted to a curvilinear regression of the type $Y = KM^{\bar{x}}$, a very small standard error of the estimate is produced; the amount of explained variation is very high ($r^2 = 0.966$, or 96.6 per cent) and affords a remarkable predictive power.

As I have mentioned above, P increases with altitude in some colonies but this is merely a consequence of geomorphic sorting of particles. No other habitat factor studied affected the relative abundance (P) of the two auklets.

## SEGREGATION BETWEEN THE TWO *AETHIA*

By using the census figures for Kongkok Basin, and with the help of qualitative observations, it is possible to illustrate the patterns of partitioning of the nesting habitat between the two

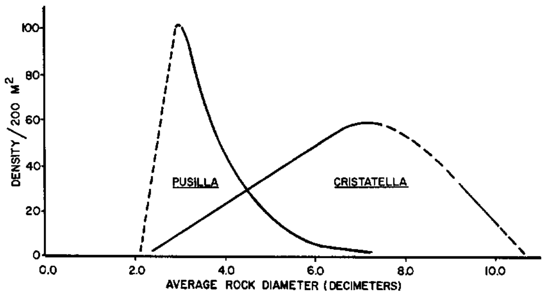

FIGURE 10. Generalized model showing the segregation between *Aethia cristatella* and *A. pusilla* on the nesting slopes according to the average rock diameter. Those parts of the curves shown by a broken line are inferred from qualitative observations.

species of *Aethia*. In figure 10, the left part of the curve for *pusilla* falls very abruptly after reaching a maximum rock-size diameter of about 3.0 dm. This part of the curve has not been documented but has been drawn from qualitative observations. A decrease in the average size of the particles is generally accompanied by a clogging of the interstices, soil formation, and increasing vegetation. Such conditions develop rapidly between $\bar{x}$ values of 3.0 and 2.0 dm. At the other extreme of the graph, in the domain of *cristatella*, there is likewise an obvious limit to talus formation with particles exceeding $\bar{x}$ value of 10.0 dm. In the colonies examined, such large blocks accumulated at the base of the talus slope to form the "rubble." This habitat is usually occupied by other alcids such as the Pigeon Guillemot and often the Horned Puffin. Furthermore, the increase in particle size above a certain limit brings about a great decrease in the possible number of interstices and, consequently, nest-sites, which probably accounts for most of the drop in the abundance of *cristatella* between average particle size values of 7.0 and 10.0 dm.

## DISCUSSION AND CONCLUSIONS

Radiation in feeding habits and, more generally, in feeding adaptations has no doubt been the major and most stringent element in the evolution of the family Alcidae (Bédard 1969a). But to some extent radiation has also resulted in the full use of a limited choice of nesting situations. It is appropriate to recall that eight species of alcids can be found in some colonies of the Bering Sea, in a simplified environment whose main and only feature is rock in various stages of disintegration. The full biological implications of this diversification are far from understood and will hopefully be easier to grasp after more knowledge has been acquired of the anatomy, social behavior, and ecology of the species concerned.

A number of ecological investigations require a sound and repeatable technique for assessing levels of density. To my knowledge, the present work represents the first attempt to establish this parameter in colonies of auklets. The catalogue of colonies in itself may also be useful since it becomes increasingly evident that alcid colonies do not have the permanency and stability of numbers often implied in the literature. Variations in abundance and distribution are, in my opinion, rather the rule. Censuses and catalogues may eventually provide means of recognizing patterns in changes in density levels and dispersion.

There can be no doubt that the local density of both *A. cristatella* and *A. pusilla* is markedly influenced by physical characteristics and that the average diameter of the rocks in the nesting habitat bears an important relationship to density. As much as 98.6 per cent of the variation in the density of one species can be accounted for by this factor alone.

Reliable predictions cannot be made about the density of *cristatella* in the colony of Sevuokok Mountain. I have also indicated that *pusilla* maintains in the latter colony higher densities per unit area than in Kongkok. Since the latter species, because it is small, is not eagerly sought by hunters, its higher density in Sevuokok may be a result either of peculiar habitat conditions, or of the decrease in the abundance of *cristatella*. Habitat measurements obtained by standarized procedures reveal no differences in the nature of the mantle to support the former hypothesis. But what evidence would support the proposition that *pusilla* fills the vacuum created by the decrease of *cristatella* in Sevuokok?

First, a comparison of the relationship between the density of the Least Auklet and the average particle size in the two colonies (fig. 6) shows that in Sevuokok, the slope of the regression line is not as steep, and population densities at sites with intermediate rock sizes are more variable than in the case of Kongkok. Furthermore, the relative abundance decreases in a logarithmic fashion in Kongkok but linearly in Sevuokok (fig. 11). This is taken as another indication that the reduction in the numbers of its large congener favors *pusilla*.

Brief reference was made earlier to the dominance of *cristatella* during the mild conflicts observed between the two species. Wherever *cristatella* is abundant, it "stakes out" all the large boulders as displaying areas and *pusilla*

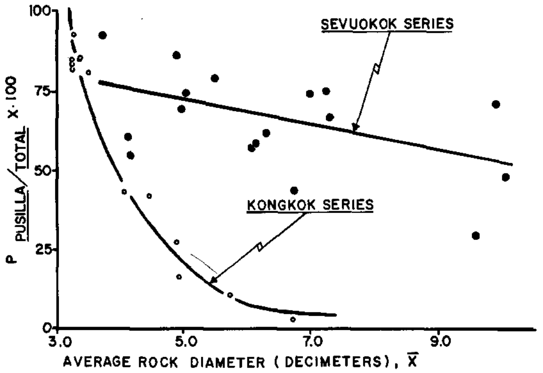

FIGURE 11. Comparison of the relationship between the average rock diameter and the relative abundance (P) of the two species of *Aethia* in the colonies of Sevuokok and Kongkok. The values of the equation parameters are given in figure 9. For the Sevuokok colony, the equation of the regression line is: $P_{pustlla/total} \times 100 = (-4.01)\,\bar{x} + 90.34$ and the coefficient of correlation ($r$) between the two sets of data is –0.498, $P < 0.05$.

seldom engages in courtship activities in this immediate vicinity. Areas of dense aggregations of Crested Auklets are attractive to large numbers of immature individuals which attempt to engage in courtship with the adult birds. But, when a small census figure is given for *cristatella*, it generally represents a few pairs limited to a small section of the quadrat, and small groups of that type seldom attract immature birds in their neighborhood. Although I have not quantified the relationship, it appears that the amount of social interaction and inteference between *cristatella* and *pusilla* will increase in an exponential fashion with an increase in the density of adult (breeding) *cristatella* per unit area.

To show conclusively that *pusilla* benefits from the decrease in *cristatella*, it would be necessary to show that the curvilinear relationship between density of *pusilla* and size of rocks disappears following removal of *cristatella* from experimental plots, or that in comparable terrain where *cristatella* is naturally absent, the relationship is linear rather than curvilinear.

In short, the degree of structural control upon the density of auklets is remarkable considering all the possible sources of error in censusing, measuring the habitat and applying correction factors. The local density of *cristatella* seems to be a direct function of the average particle size although the local density of *pusilla* appears to be a function of both the average particle size and the presence of its large congener.

Since the density of the birds is so dependent upon simple measurable habitat characteristics, it should be possible to determine whether there is ever a shortage of nest-sites, or whether a ceiling could be imposed upon a population through a shortage of nest sites. On the scale of the quadrat, it is quite clear that most if not all of the suitable nest sites are actually utilized; otherwise the relationships described above would not emerge with such clarity. But on the scale of a nesting colony, the question becomes intractable. There is, as yet, no way to discriminate between usable and non-usable nesting habitat. Some parts of talus slopes are inexplicably left uninhabited, yet do not differ in any measurable respect from adjacent nesting areas. And the question, though of ultimate importance, is inappropriate, for even if it were possible to decide which area is nesting area and which is not, we would still have to show conclusively, among other things, that the shortage of nest sites has dynamic effects upon the population, or a part of it, through preventing otherwise mature breeders from breeding, or through lowering the breeding efficiency of breeders forced into nest sites of inferior quality. The second alternative would be equivalent to showing that plasticity in selection of nest sites is very low. Such demonstrations are arduous and were not even attempted. The available data do not enable me to risk even a tentative answer.

Can physical factors in the nesting habitat affect the distribution and the relative abundance of the two species within their geographic range? The spectrum of sampled conditions is too small to enable me to say much about patterns of distribution or patterns of absolute density. There is indication that the proportion of *pusilla* increases with the age of the talus slope. On inland talus slopes, we know that the climatic factors break down the debris of the mantle to a much finer condition. This is the case in Kongkok, and on the southwestern wall, for instance, the proportion of *pusilla*:*cristatella* is 15:1. *Cristatella* is abundant in Kongkok, but in localized areas such as the moraine floor of the cirque and the lowest parts of the northern wall. Fay and Cade (1959) report a ratio of 20:1 in the colony of Singikpo Cape (herein called Ataakas Camp); ratios of 4:1 to 9:1 were obtained there by me during 1967. This colony is established on a gently sloping terrace that reaches inland for over one km. The mantle there is made of finely fractured and highly porous volcanic material (scoria) and the slope conditions are even more "stabilized" than in Kongkok.

This is also the case on St. George Island in the Pribilof Archipelago. Hopkins and Einarsson (1966) remarked that creep and solifluction dominated frost riving. On this island, the exposed surfaces of basalt have been reduced to loose rubble during past intervals of more severe climate. The main auklet colony is located on an inland knoll about one km from the coast and reputedly contains *pusilla* exclusively (M. G. Thompson, in litt.). On this island at least, *cristatella* is limited to the base of maritime bluffs (Thompson, in litt.; Preble and McAtee 1923) where talus slopes are still in earlier stages of formation. Thus, available evidence tends to support the proposition that physical factors, particularly the size of the boulders in the nesting habitat, exert much influence in determining the overall proportion of the two species of *Aethia* within the overlapping parts of the range.

Finally, the fact that segregation occurs amidst the nesting grounds in such a marked and predictable fashion is merely a reflection of the large differences in body size between the two species. This, however, does not preclude the existence of habitat segregation at a biological level and important adaptive differences may exist between the species, for instance, in the degree of tolerance of the chicks to hypothetical factors of the micro-habitat or in adults' preferences for different substrates, etc.

Owing to its small size, *pusilla* is able to occupy a wider range of nesting situations than *cristatella*. It has access to a broader choice of nest sites and there is evidence that it makes use of this ability whenever possible. It is also a more versatile nester and can be found in isolated pairs on pinnacles and ridges, and it regularly nests on sheer cliffs in company with murres (*Uria* spp.), puffins and cormorants (*Phalacrocorax*).

In nesting as in feeding (Bédard 1969b), the two species of the genus *Aethia* have basically the same type of requirements. But between the genera *Aethia* and *Cyclorrhynchus* there are differences in the very nature of these requirements. Brief mention was made earlier of the fact that the Parakeet Auklet, when compared to the Least and the Crested, makes use of nest sites which are much less abundant. This fact is more fully appreciated with the knowledge that this situation parallels what has been observed in feeding segregation between the two genera ( Bédard 1969b). In that case, *C. psittacula* was found largely to restrict its feeding to prey types that were much less abundant in the environment (for instance, pelagic amphipods) while the two *Aethia* made use of superabundant zooplankters (for instance, copepods and euphausids). The abundance and availability of the latter prey types are known to vary widely while it can safely be said that the stocks of carnivorous zooplankton which are the mainstay of *C. psittacula* are less variable.

## SUMMARY

This study represents an attempt to determine the modalities of segregation in nesting among three species of auklets (*Aethia cristatella*, *A. pusilla*, and *Cyclorrhynchus psittacula*). The study was carried out on St. Lawrence Island, Alaska, between 1964 and 1967.

A catalogue of the auklet colonies on St. Lawrence Island follows a detailed description of the nesting habitat. Estimates of total populations of *A. cristatella* and *A. pusilla* in these colonies are also given, the former varying from 5,000 to 171,000 and the latter from 8,000 to 318,000 individuals. Only fragmentary observations are available in the case of *Cyclorrhynchus*, but its populations are of a much smaller order of magnitude.

The local density of the two species of *Aethia* is clearly affected by a single principal slope characteristic, the size of the rocks on the talus slopes used as nesting habitat. This factor seems to operate in a direct fashion by regulating the number of interstices usable as nest sites. Although there is an upper ceiling to the number of birds that can nest in a given geographic area, the evidence that such a maximum has been reached could not easily be gathered.

Segregation on the nesting grounds between *Aethia pusilla* and *A. cristatella* is achieved in the following way: *pusilla* dominates in areas where the average rock size is small while *cristatella* is almost the only one represented in areas where the slope is made of large boulders. *Pusilla* becomes less abundant with the increasing average rock size, and this is attributed to the presence of its large congener. In other words, *cristatella* seems to respond directly to the increasing rock size by increasing its density; the increase in the density of *pusilla* depends not only on this physical element but also on the density of its congener.

*Cyclorrhynchus psittacula* nests in semi-decomposed or shattered pinnacles, ridges, or cliffs and in vegetation-covered talus slopes. In a geomorphic sense, both situations are adjacent to talus slopes and represent stages which are anterior or posterior to the habitat used by *Aethia* spp.

There is some evidence that the size of the rock debris on talus slopes strongly influences

the relative abundance of the two species of *Aethia.* The average rock diameter diminishes with increased stability of slope or age (frost has a chance to act longer on the same material in the absence of removal agents at the base). This would account for observed dominance of *Aethia pusilla* on inland talus slopes.

Compared to *Aethia, Cyclorrhynchus* depends upon nest sites which are much less available, and also has less gregarious habits. Also, the Parakeet Auklet principally eats prey organisms which are less abundant and not subject to wide oscillations in availability. These characteristics seem to be related to a lowering of its biomass (or its lower density per unit area than *Aethia*). As a whole, the amount of overlap in nesting between the three species studied is very small.

## ACKNOWLEDGMENTS

This work was supported by a grant from the National Research Council of Canada to M. D. F. Udvardy who, together with I. McT. Cowan, supervised the study and helped in many ways. I am grateful to D. Chitty, I. McT. Cowan, P. LeBlond and the late Henri Talbot who assisted in gathering the data or in commenting on the manuscript. I owe special thanks to D. M. Hopkins for his expert comments on slope morphology and to F. H. Fay for his unfailing interest and stimulating discussions.

## LITERATURE CITED

Bédard, J. H. 1969a. Adaptive radiation in Alcidae. Ibis 111:189–198.

Bédard, J. H. 1969b. Feeding of the Least, Crested and Parakeet Auklets around St. Lawrence Island, Alaska. Can. J. Zool., in press.

Fay, F. H., and T. J. Cade. 1959. An ecological analysis of the avifauna of St. Lawrence Island, Alaska. Univ. California Publ. Zool. 63:73–150.

Hopkins, D. M., and T. Einarsson. 1966. Pleistocene glaciation on St. George, Pribilof Islands. Science 152:343–345.

Murie, O. J. 1959. Fauna of the Aleutian Islands and Alaska Peninsula. N. Amer. Fauna, no. 61.

Preble, E. A., and W. L. McAtee. 1923. Biological survey of the Pribilof Islands, Alaska. Part I. Birds and mammals. N. Amer. Fauna, no. 46.

Sealy, S. G. 1968. A comparative study of breeding ecology and timing in plankton-feeding alcids (*Gyclorrhynchus* and *Aethia* spp.) on St. Lawrence Island, Alaska. M. Sc. thesis. University of British Columbia, Vancouver.

Stejneger, L. 1885. Results of ornithological explorations in the Commander Islands and Kamchatka. U. S. Natl. Mus. Bull. 29:7–362.

Accepted for publication 20 March 1968.