INFLUENCE OF SNOW ON EGG-LAYING IN AUKLETS

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IN many high northern regions, optimum conditions for nesting exist for only a short time. Consequently most bird species have restricted breeding seasons and start nesting at about the same time each year (see Immelmann 1971, 1973). The timing of restrictive breeding involves two major problems: the phylogenetic aspect, which includes the development of species-specific and population-specific breeding seasons through natural selection (the "ultimate" factors), and the current physiological aspect, which involves the precise adjustment of the individual to the phylogenetically determined reproductive season (the "proximate" factors).

Each spring Least Auklets (*Aethia pusilla*), Crested Auklets (*A. cristatella*), and Parakeet Auklets (*Cyclorrhynchus psittacula*) return about mid-May to their nesting slopes on Sevuokuk Mountain, St. Lawrence Island, Alaska. Although the nesting slopes at this time are still covered with snow, with yearly variations in extent and depth, the auklets begin to visit and settle on these slopes each day. Here courtship activities take place while their previous pair bonds are renewed and strengthened; meanwhile the snow melts and the nesting crevices among the boulders immediately below become available to the birds.

During studies of breeding ecology of these auklets (Sealy 1968, Sealy and Bédard 1973) it became evident that snow on the nesting slopes influenced the timing of egg-laying and productivity within the auklet population, particularly in 1967 when the snow melted early. Bédard (1969a) demonstrated that food supply is an important ultimate factor controlling the general timing of these auklets' breeding on St. Lawrence Island. The present paper examines the role of snow cover and the sudden emergence of the nest sites as proximate factors.

METHODS

I spent the 1966 and 1967 nesting seasons (mid-May to mid-September) on Sevuokuk Mountain (Fig. 1) on the northwest cape of St. Lawrence Island, Bering Sea, studying the breeding ecology of auklets. I arrived in May before the auklets' return in 1966 and shortly after their return in 1967. The nesting and marine environments of these auklets on and near St. Lawrence Island have been described elsewhere (Fay and Cade 1959; Sealy 1968, 1973; Bédard 1969a, 1969b; Sealy et al. 1971).

Snow cover and its disappearance from the nesting slopes were recorded photographically (Fig. 2) and estimated by the ratio of bare ground to snow-covered ground (Fig. 3) in the same eight randomly selected plots (five on the west slope and three

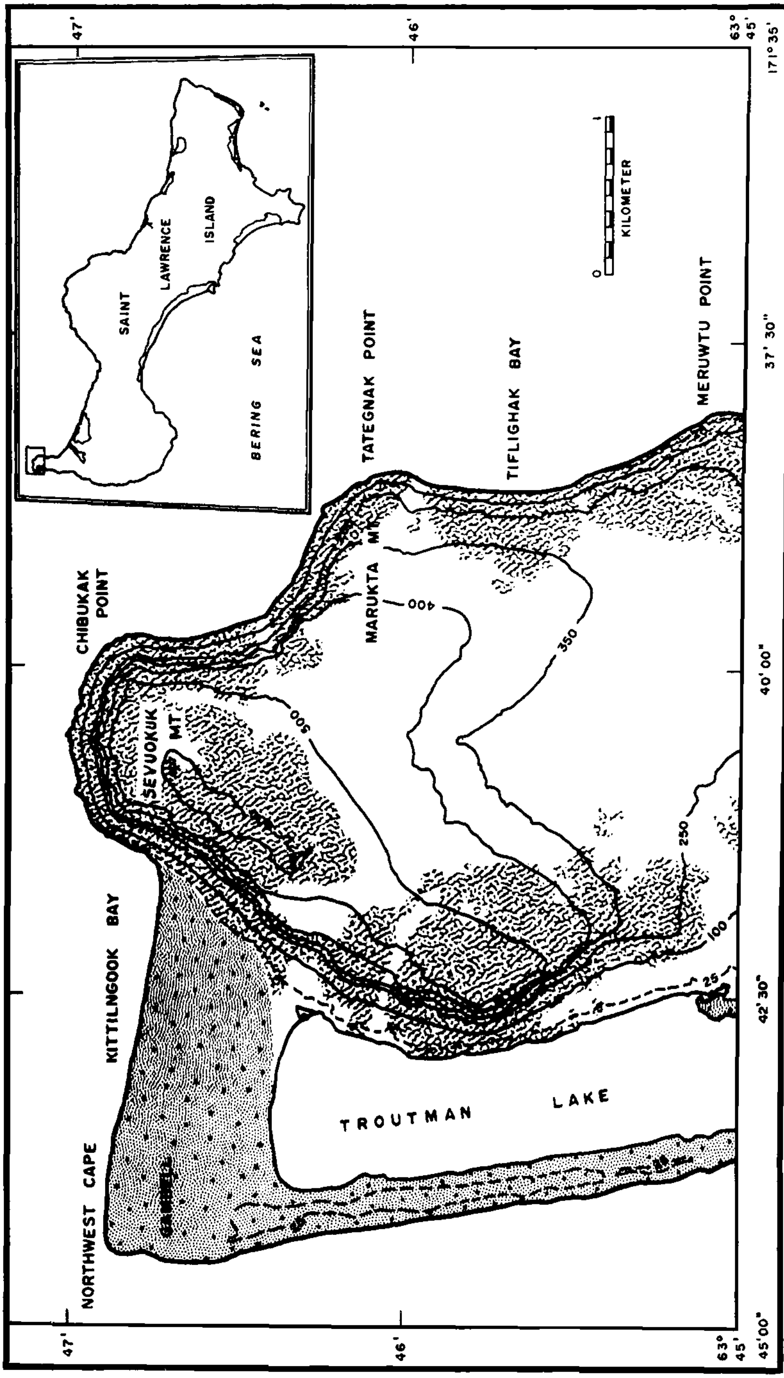

Fig. 1. Sevuokuk Mountain and vicinity, St. Lawrence Island, Alaska. The stippled portion is a sand bar, shaded parts are rock, and clear spaces tundra. Contour levels are in feet. Drawn from U.S. Army Map Service Q–801.

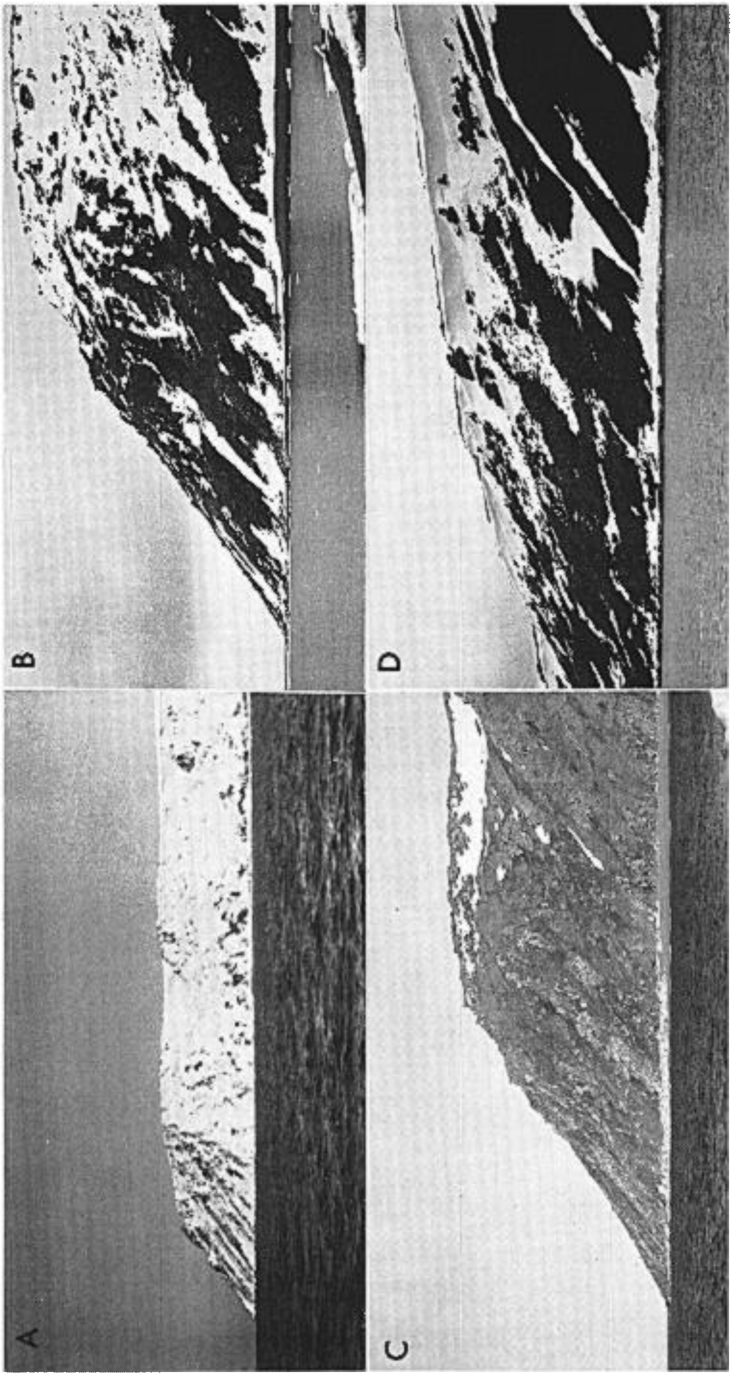

Fig. 2. Snow cover on Sevuokuk Mountain on different dates in 1966 and 1967 showing the different amounts of snow and the earlier melt in 1967. A, 5 June 1966; B, 2 June 1967; C, 23 June 1967; D, northeast slope on 11 June 1967 showing accumulation of snow along the brow of the mountain.

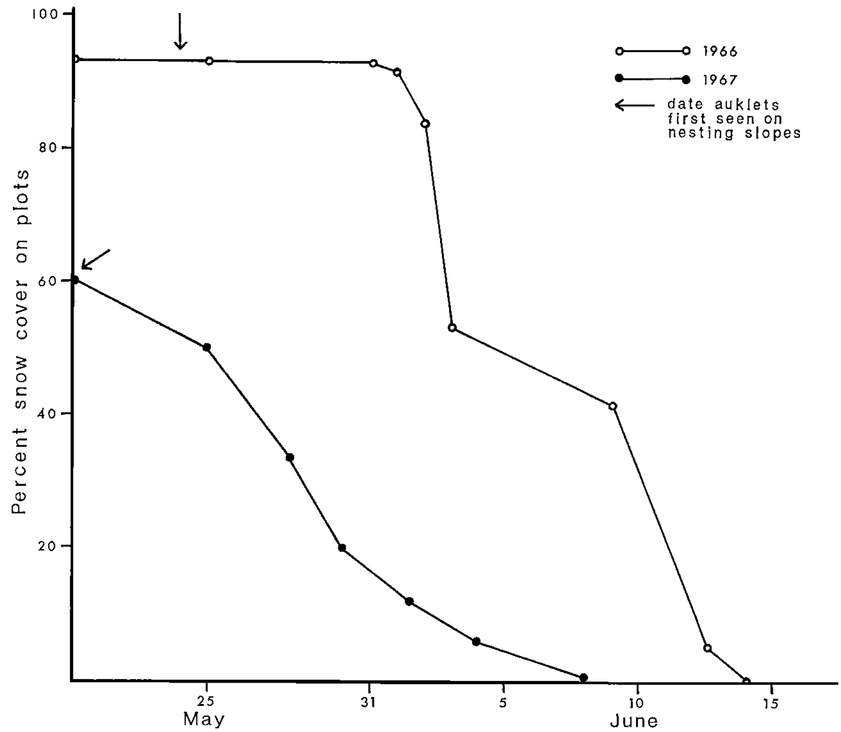

Fig. 3. Pattern of snowmelt on Sevuokuk Mountain in 1966 and 1967. Each point represents the mean value of estimated snow-free nesting habitat from each of 8 plots. Value of 0 indicates snow- and ice-free nesting crevices.

on the northeast slope of Sevuokuk Mountain) in Least and Crested Auklet nesting habitat. In 1966–67 using "noose carpets" (see Berger and Hamerstrom 1962) I live-trapped, banded, and color-marked 17 Least Auklets and 6 Crested Auklets sitting on the snow in one of the plots on the northeast slope of Sevuokuk Mountain.

Reproductive development of birds sitting on bare rocks (rock-sitters) and on the snow (snow-sitters) was studied in 121 specimens collected between 4 June and 11 July 1967, with about 10 individuals being taken from each habitat each week. The ovaries of all females ($n = 56$) were removed, the diameter of the largest follicle was measured to the nearest 0.1 mm, and the presence of a postovulatory follicle or shelled egg in the oviduct was recorded. All gonads were fixed for 24 h in Bouin's fixative and stored in 70% ethanol.

Egg-laying dates of each species were determined by dissection of adult females and by visiting nest sites daily until the single eggs appeared. These visits were made in the late morning or early afternoon when the nest sites were empty and therefore the disturbance did not affect the timing of egg-laying. In 1967 I filled six Least Auklet nests I located in 1966 with snow for up to 6 days after the ice and snow had melted out of the other nest crevices, to prevent the pairs from entering them and laying their eggs. Egg-laying in seven other nests in the same portion of the slope was permitted to proceed normally.

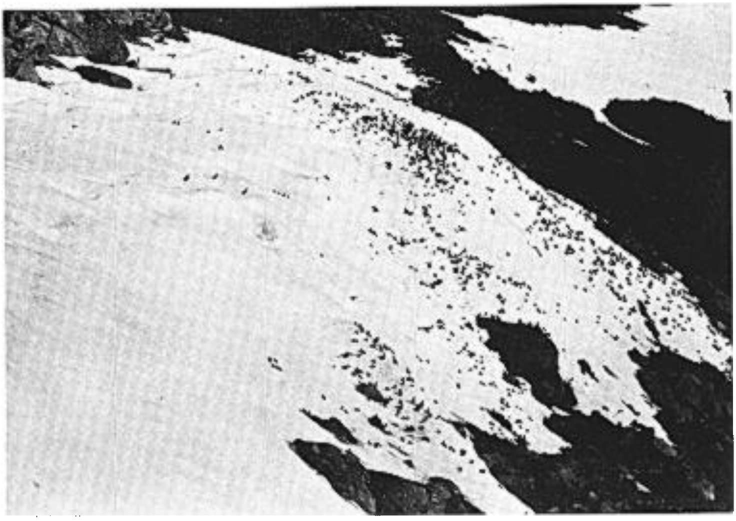

Fig. 4. Crested and Least Auklets sitting on the snow along the brow of the northeast slope of Sevuokuk Mountain, 25 June 1967. Note the nonrandom dispersion of birds on the snow.

RESULTS

Snow and its disappearance from the nesting slopes.—The extent and persistence of snow encountered by the returning and settling auklets on Sevuokuk Mountain differed considerably in 1966 and 1967 (Figs. 2 and 3). In 1966, a late season, snow covered about 95% of the nesting habitat when the first auklets settled on 24 May. In 1967, an early season, it covered only about 60% when the first Least Auklets settled on 20 May. The mean temperature at Gambell (3 km west of Sevuokuk Mountain) was –1.0° C from 21 May to 15 June 1966 and 7.0° C from 26 May to 15 June 1967. Thus most of the snow, except that along the brow of the mountain (Fig. 2C), melted earlier in 1967. Despite the earlier overall melting of the snow on the lower reaches of the slope in 1967, the total snow cover when the first eggs were laid in both years was about the same.

The snow melted at different rates on different parts of the slope depending upon the exposure and elevation, leaving some portions covered with snow (Figs. 2C and 4) while other parts were bare. In both years, snow persisted along the brow of the northeast slope of Sevuokuk Mountain until about 12 July despite the difference in the general phenology of snow melt those years. Fig. 4 shows the snow on the brow of the mountain covering much auklet nesting habitat.

Fig. 5. Least and Crested Auklets settled on the rocks (the rock-sitters) and snow (the snow-sitters) on the northeast slope of Sevuokuk Mountain, 25 June 1967. Note fidelity of birds to snow-covered rocks despite adjacent snow-free rocks.

Timing of egg-laying.—In 1966 egg-laying in nests studied on the lower reaches of the slope spanned the period 24 June to 7 July. Those auklets faithful to nest sites covered by snow along the brow have access to snow-free nesting habitat a few days later and therefore are able to lay their eggs at that time. Thus egg-laying was essentially synchronized within the entire population in 1966.

In 1967 egg-laying spanned 13–25 June for those nests studied on the lower snow-free portions of the slope that were completely free of snow by 8 June (Fig. 3). In 1967 the snow persisting on the brow prevented birds there from reaching their nest sites. On 22 June Least and Crested Auklets began to lay their eggs on this snow. These eggs were subsequently destroyed either by rolling down the slope and breaking on the exposed rocks below or were taken by Herring Gulls (*Larus argentatus*). No attempt was made by the birds to incubate eggs that were laid on the snow. These individuals did not renest.

During the pre-egg stage, the auklet population (particularly Crested and Least Auklets) is divided into two groups, those settling and courting on the rocks and actually entering nest sites and those courting on the snow and unable to enter the nest sites (Fig. 5). The dispersion of auklets settling on the snow-covered slope was not random (Fig. 4). These birds, unclassified as to experienced or inexperienced breeders, were apparently familiar with the nesting slope, and their acute sense of

TABLE 1
BANDING AND SUBSEQUENT OBSERVATIONS AND/OR RECAPTURES OF LEAST AND CRESTED AUKLETS IN 1966 AND 1967[1]

Species	Date banded	Date observed	Activity
Least Auklet	15 June 1966	5 July 1966	Incubating egg
" "	15 June 1966	9 July 1966	Incubating egg
" "	19 June 1966	3 August 1966	Carrying food to chick
" "	19 June 1966	10 August 1966	Carrying food to chick
Crested Auklet	15 June 1966	4 August 1966	Carrying food to chick
" "	12 June 1967	15 July 1967	Incubating egg
" "	12 June 1967	3 August 1967	Incubating egg
" "	12 June 1967	21 August 1967	Carrying food to chick

[1] Each adult was live-trapped on top of the snow in a plot at about the 20-m contour on the northeast slope of Sevuokuk Mountain and seen later at the same spot.

location was borne out by the banded and color-marked birds captured on the snow that subsequently occupied the nest sites below (Table 1). The auklets exhibit mate retention and nest site tenacity (Sealy 1968).

General timing of egg-laying in auklets on Sevuokuk Mountain in 1966 and 1967 is presented in Fig. 6. Egg-laying started 10 days earlier in 1967 in all species. The mean laying date in seven Least Auklet nests in a sector of nesting habitat with early snow melt was 17 June 1967. The six nests in the same sector of the slope that were plugged with snow for 6 additional days had a mean laying date of 28 June. The interval between absence of snow in places where it melted early to the mean egg-laying date was 20 days in 1966 ($n = 36$) and 10 days in 1967 ($n = 28$). Where the snow cover was prolonged this interval averaged 4 days ($n = 3$) in the Parakeet Auklet, 3.1 days ($n = 4$) in the Crested Auklet, and 3.6 days ($n = 9$) in the Least Auklet.

Gonadal development.—Gonadal development in male snow-sitting and rock-sitting Least Auklets was examined elsewhere (Sealy 1968). There was no relationship between testicular development, as indicated by the weight of the left testes, and whether or not the birds were able to enter snow-free nest sites. Follicular maturation in adult female Least Auklets from rock and snow areas is summarized in Fig. 7; the

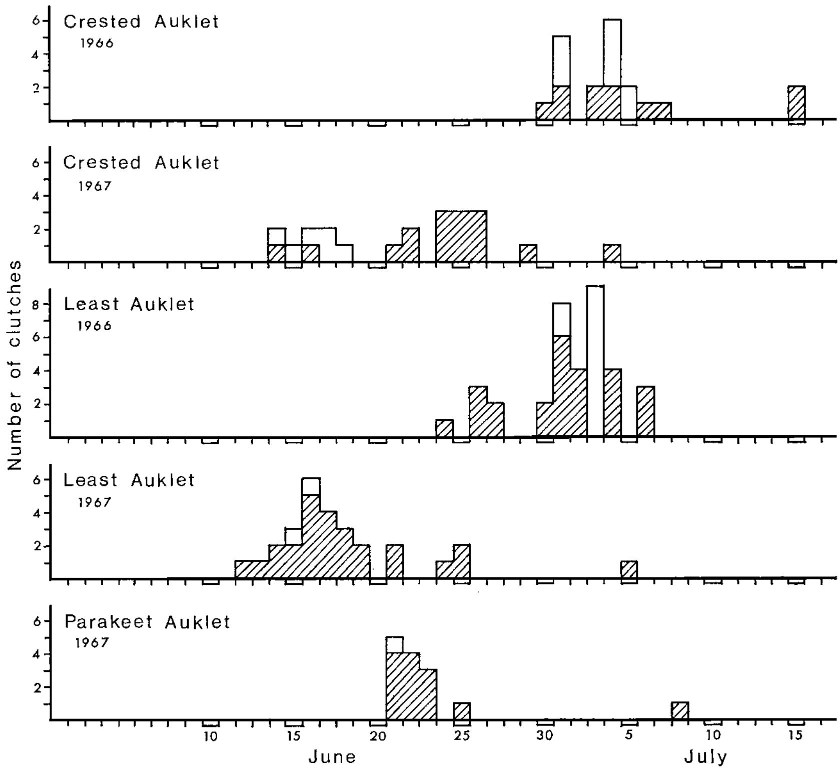

Fig. 6. Egg-laying in the Parakeet, Crested, and Least Auklets on Sevuokuk Mountain, 1966 and 1967. Shaded blocks show egg-laying dates obtained by direct observations in nests, open blocks dates obtained by dissection of fully shelled eggs from the oviduct.

more rapid (earlier) maturation of ova of females taken on sites that became free of snow earlier is evident. No atretic follicles were found in any of the females collected.

Discussion

The effects of prolonged snow cover in delaying egg-laying or even preventing nesting in certain years has been amply documented. Barry (1962) demonstrated the effects of late seasons on Brant (*Branta bernicla*) where fewer young are produced in some seasons than in others; in fact no young are produced in some years. Although Brant return to their breeding grounds on the same date each year, they must wait for the snow to melt and uncover nesting habitat. If the snow persists, energy reserves are depleted and follicular astresia occurs, which Barry

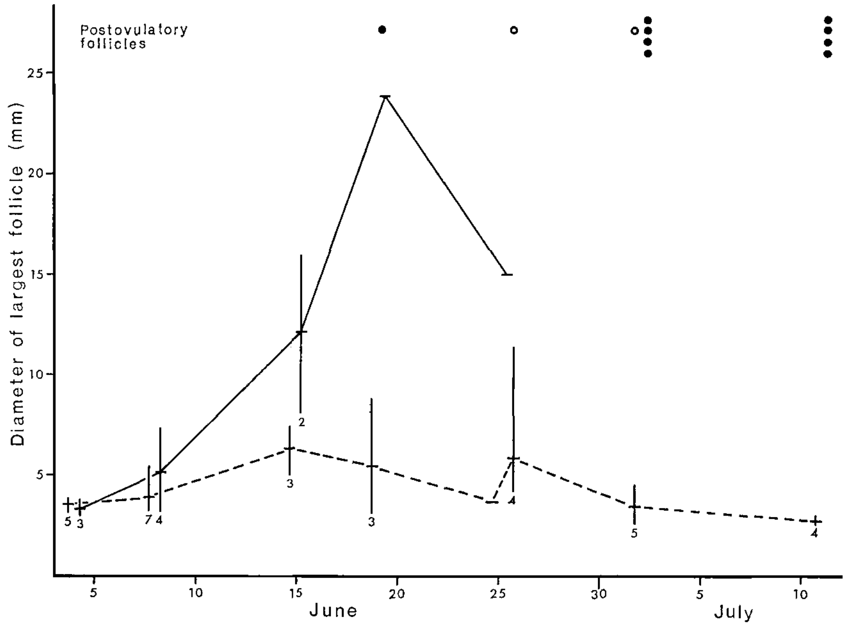

Fig. 7. Follicular maturation of snow-sitting and rock-sitting Least Auklets as indicated by the diameter of the largest follicle. The solid line and circles indicate rock-sitters; the dashed line and open circles indicate snow-sitters. The horizontal lines indicate mean and vertical lines the extremes; numbers beneath extremes are the sample sizes.

argues is an effort to retain nourishment as their food is unavailable under the snow. If the snow persists too long, the entire clutch is resorbed. Besides providing nourishment, the follicular atresia prevents extremely late nesting, which would jeopardize the entire population by allowing too little time to complete nesting activities and molt and regain the power of flight before freezeup.

Lack (1933) found that Arctic Terns (*Sterna paradisaea*) in northern Norway laid their eggs on different dates in different places as the nesting spots successively became available after the snow melted. He suggested that the delayed availability of nest sites coupled with the inability of the gonads to remain in breeding condition may combine to make reproduction impossible in a particular year.

Holmes (1966) noted that the timing of arrival of Dunlins (*Calidris alpina*) and most other arctic nesting shorebirds differs each season and is correlated with year-to-year differences in climatic events that either prolong or accelerate snowmelt, thereby influencing the availability of snow-free tundra. Once the Dunlins return, vigorous activity ensues with territories being established and defended on the patches of tundra as they become available.

The situation in the auklets differs from those described above. In auklets the final production of eggs and egg-laying is at least partially controlled by the proximate environmental stimulus of a snow-free nest site. Rock-sitters presented with this stimulus sooner than snow-sitters will lay earlier. The auklets appear unable to halt their follicular maturation in response to prolonged unavailability of nesting habitat, and lay their eggs on the snow. In geese and shorebirds, the food supplies and the nest sites lie beneath the snow. The longer snowmelt is prolonged, the longer the birds must do without food. Hence the follicles cannot develop or, if development has progressed, atresia results. The auklets make regular trips to sea to feed and therefore have the energy necessary for egg production readily available.

Manniche (1911) attributed the nonbreeding of aquatic birds in a late season in Greenland to the lack of food because ice remained in the inlet all summer. Arctic Terns laid eggs on the snow, which suggests that their gonads developed as usual, and that they probably obtained food by flying to open water.

Parakeet Auklets return in spring before Crested and Least Auklets, which lay their eggs earlier (see Fig. 6). Most of the 2000 breeding pairs of Parakeet Auklets (Bédard 1969b) on Sevuokuk Mountain use crevices among splintered parent rock (Sealy and Bédard 1973), which is largely distributed along the brow of the mountain where the greatest accumulation of snow occurs (Fig. 2D) and melts last. Parakeet Auklets, by nesting later, are able to use these nest sites that are unavailable 7–10 days earlier when the Crested and Least Auklets have begun egg-laying. In 1967 the Parakeet Auklets nested successfully along the brow of the mountain after the Crested and Least Auklets had laid their eggs on the snow.

Acknowledgments

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Summary

Egg-laying in relation to snowmelt in a population of Crested, Least, and Parakeet Auklets on Sevuokuk Mountain, St. Lawrence Island, Alaska, is examined. In 1966 the snow melted late and egg-laying was synchronized throughout the population. In 1967 individuals faithful to nesting habitat from which the snow melted early laid their eggs earlier than individuals faithful to portions of the slope where snowmelt was prolonged. Crested and Least Auklets faithful to nesting habitat along the brow of the mountain where the snow remained until mid-July laid their eggs on the snow, which caused nesting failure in about 5% of the population. Snow cover as a proximate factor influencing timing of egg-laying on an individual basis is discussed.

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