Pacific Science (1973), Vol. 27, No. 2, p. 99–119
Printed in Great Britain

Breeding Biology of the Horned Puffin on St. Lawrence Island, Bering Sea, with Zoogeographical Notes on the North Pacific Puffins[1]

SPENCER G. SEALY[2]

THE HORNED PUFFIN (*Fratercula corniculata*) is one of six species of alcids which regularly nest on Sevuokuk Mountain, 3 km east of Gambell on St. Lawrence Island, Alaska (Fig. 1). During the summers of 1966 and 1967, I conducted on this island a study of the breeding ecology of three of these species, the Parakeet Auklet (*Cyclorrhynchus psittacula*), Crested Auklet (*Aethia cristatella*), and Least Auklet (*A. pusilla*) (see Sealy, 1968). During these summers some observations on the breeding biology of the Horned Puffin were obtained and are reported here. The only life history study of this species which spans the entire breeding season is that of Swartz (1966) in the Cape Thompson region, Alaska, some 560 km north of St. Lawrence Island (Fig. 2).

Numerous studies of the biology of the congeneric Common Puffin (*Fratercula arctica*) of the Atlantic and Arctic oceans are available (e.g., Lockley, 1953; Belopol'skii, 1957; Uspenski, 1958; Myrberget, 1959, 1961, 1962; Kartaschew, 1960; Nettleship, 1972; and others) and some of these will be utilized here for comparative purposes. When available, comparative observations on the breeding biology of the other Pacific puffins, the Rhinoceros Auklet (*Cerorhinca monocerata*), which is actually a puffin (Storer, 1945), and the Tufted Puffin (*Lunda cirrhata*) will also be included.

DISTRIBUTION

The breeding distribution of the Horned Puffin has been mapped recently by Udvardy (1963: 105). Briefly, in North America this species breeds from Cape Lisburne on the Arctic Ocean coast south through the Bering Sea, the Aleutian Islands, Shumagins and Semidis (Gabrielson and Lincoln, 1959). Along the Aleutian chain, Murie (1959: 202) found it on "all suitable islands, from Kodiak to Attu, including the Shumagins and Sanak." In southeastern Alaska it has been reported breeding on Kodiak Island (Friedmann, 1935), St. Lazaria Island (Willett, 1912) and south to Forrester Island (Heath, 1915; Willett, 1915). This species has not been recorded breeding in British Columbia (Drent and Guiguet, 1961) but it was observed regularly in the springs and summers of 1968, 1969, and 1971, some 70 km south of Forrester Island near Langara Island, Queen Charlotte Islands (Sealy and Nelson, in press). It has also been observed in British Columbia, mostly during the nonbreeding season, near the Queen Charlotte Islands and Vancouver Island (Brooks and Swarth, 1925; Sealy and Nelson, in press).

On the Asian side of the Pacific Ocean, the Horned Puffin occurs as a breeding species from Wrangel Island, Kolyuchin Island, along the Chukotskiy Peninsula, and along the eastern coast of Kamchatka Peninsula (Kozlova, 1957). It breeds on the Commander Islands (Johansen, 1961), the Kurils (Austin and Kuroda, 1953), and Sakhalin (Gizenko, 1955).

Gabrielson and Lincoln (1959) stated that Horned Puffins apparently winter at sea from the limit of open water south. In the southwestern Bering Sea, Shuntov (1961), on the other hand, observed it on open sea only during May and June while Arnold (1948) and Jaques (1930) did not record it far from shore along the Aleutian chain and in northern Alaska, respectively, in late summer. Contrary to these observers, Swartz (1967) commonly sighted Horned Puffins far from shore in the Chukchi Sea, also in late summer, and Hamilton (1958) observed several individuals on the open sea in the North Pacific in June 1955.

[1] Manuscript received 16 November 1972.

[2] Museum of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A. Present address: Department of Zoology, University of Manitoba, Winnipeg, Manitoba, Canada.

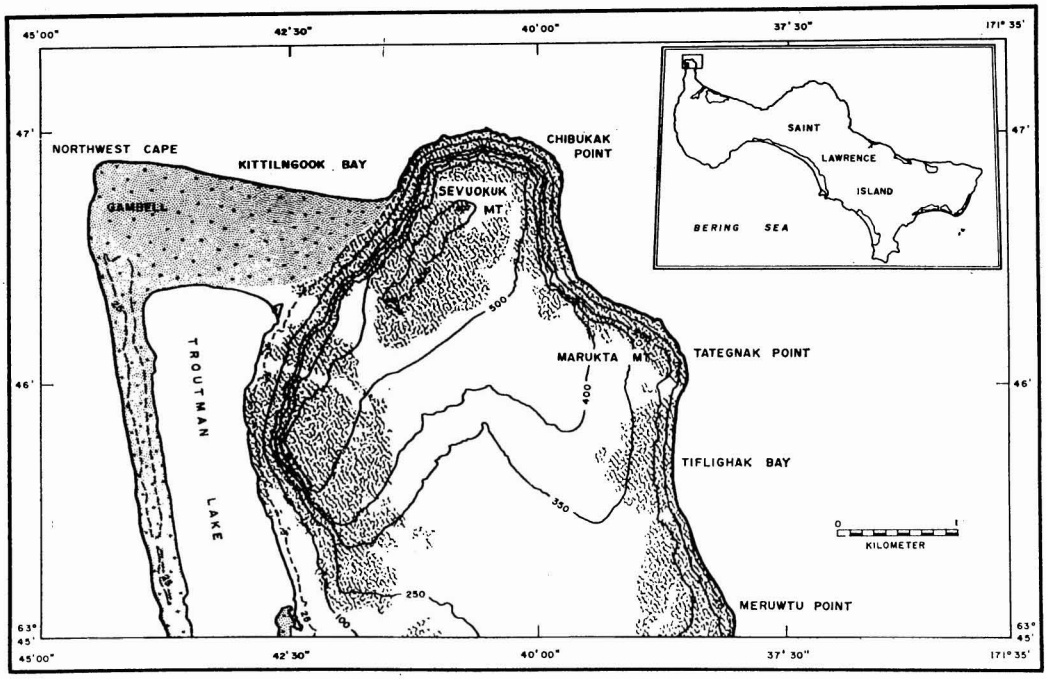

FIG. 1. Sevuokuk Mountain and vicinity, St. Lawrence Island, Alaska.

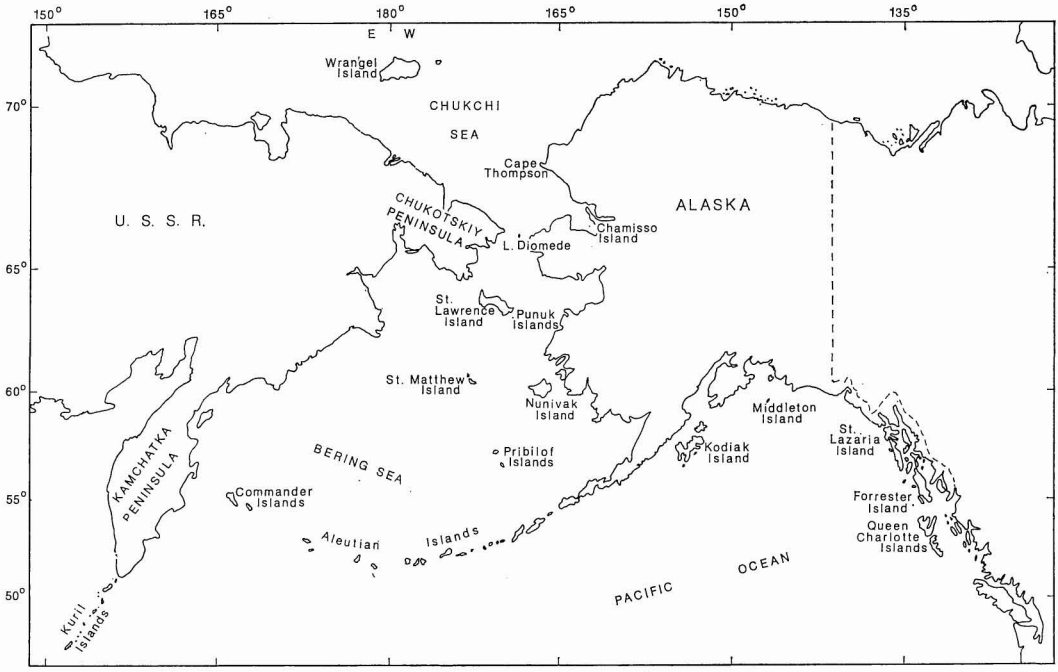

FIG. 2. Map of the North Pacific Ocean showing areas inhabited by breeding Horned Puffins.

TABLE 1

POPULATION ESTIMATES OF BREEDING HORNED AND TUFTED PUFFINS IN SOME AREAS OF SYMPATRY IN ALASKA

LOCALITY*	YEAR	BREEDING HORNED PUFFINS (PAIRS)	BREEDING TUFTED PUFFINS (PAIRS)	SOURCE
Cape Thompson	1961	1,902	36	Swartz (1966)
Little Diomede Island	1958	2,500 to 5,000	250 to 500	Kenyon and Brooks (1960)
Chamisso Island	1898	"immense numbers"	6	Grinnell (1900: 6)
St. Lawrence Island (Sevuokuk Mountain)	1967	1,500	500	this study
Middle Punuk Island	1964	none	breeding	Thompson (1967)
St. Matthew Island	1966	275	225	Klein (1959: 43)
Nunivak Island	1927	"breeding colonies"	"noted but twice"	Swarth (1934: 40–41)
Kodiak Island	1893	"common"	"rare"	Bretherton (1896: 48–49)
Pribilof Islands (St. George)	ca. 1910	"abundant summer resident"	"abundant summer resident"	Preble and McAtee (1923: 18–19)
Middleton Island	1956	none	breeding	Rausch (1958)
St. Lazaria Island	1912	12	2,000	Willett (1912)
Forrester Island	1913	2,000 to 3,000	35,000	Heath (1915)

* Localities, shown in Fig. 2, are listed from north to south.

According to Murie (1959), Horned Puffins winter throughout the Aleutian chain. It has been observed farther south in late winter particularly along the northern shore of the Queen Charlotte Islands but also near Vancouver Island, British Columbia (Sealy and Nelson, in press), and along the coasts of Washington state (Jewett et al., 1953), Oregon (Gabrielson and Jewett, 1970), and California (Grinnell and Miller, 1944).

The marine bird family Alcidae shows a center of differentiation in the Bering Sea region (Udvardy, 1963). The genus *Fratercula* is considered a late Tertiary immigrant to the Atlantic from the North Pacific Ocean where its close relative *Lunda* is distributed (Johansen, 1958). After *Fratercula* evolved into a boreal species it became sufficiently isolated into *corniculata* and *arctica* (Udvardy, 1963), which Johansen (1958) considers a vicarious species pair. The range of *arctica* eventually split up into a high arctic and boreal refuge, and subspecific separation subsequently occurred (see Salomonsen, 1944; Myrberget, 1963).

Udvardy (1963) has reasoned that, since there are present-day breeding records of *F. corniculata* as well as some other alcids from parts of the Okhotsk Sea coasts, these areas were probably part of their range during the last glaciation, and probably also during the previous ones, together with the central and eastern Aleutians and the islands of the Bering Sea (or, if these were part of the land bridge, then the coasts of same).

Horned and Tufted puffins are sympatric throughout about half of their breeding ranges (see Udvardy, 1963); however, their relative population numbers in areas of sympatry vary greatly with the Horned outnumbering the Tufted in the northern portions of their ranges (Table 1). Although the degree of confidence of the estimates in Table 1 is not known, absolute population numbers are not necessary in the ensuing discussion.

The differences between the numbers of breeding Horned and Tufted puffins and their apparently differing nesting habits were recognized early. On the Commander Islands, Stejneger (1885: 62) stated "The Horned Puffin is not very common on the islands as compared with the Tufted Puffin...probably because suitable breeding places are scarce, as they require rather deep holes in rocks or between stones....As stated above, the nest-holes are found in the rocks, and I never saw a single pair breeding in a hole dug out of the soft ground, as is often the case with *F. arctica*, and invariably, so far as my experience goes, with

Lunda cirrhata." More recently on the Commander Islands, Johansen (1961: 45–46) also observed that, although Horned Puffins are common breeders there, the Tufted Puffin is "one of the most common breeders... where [he] counted about 100,000 pairs."

Murie (1959: 203) found the Horned Puffin less abundant than the Tufted throughout most of the Aleutian chain, "in whose company it generally nests. The fact that it has a different nesting habit may account for its smaller numbers, for its particular habitat may be less available than that of the tufted puffin. While the latter burrows in the sod, the horned puffin seeks a crevice among large boulders or a cliff." Only on Kodiak Island (Bretherton, 1896) and Chamisso Island (Grinnell, 1900) has the Horned Puffin been observed to dig its own burrow; on both of these islands breeding Tufted Puffins were scarce at the time of these authors' visits.

In the ensuing analysis, some data, speculations, and avenues of future research will be discussed which it is hoped will stimulate more work on the population biology of puffins.

METHODS

The Horned Puffin work was concomitant with field research on the breeding ecology of the plankton-feeding auklets to which I devoted most of my efforts. The main auklet colony in which I worked was located at Tategnak Point on Marukta Mountain (Fig. 1) near Gambell, St. Lawrence Island, Alaska. I moved between Gambell and Tategnak Point almost daily from 9 June to 14 September 1966 and 26 May to 9 September 1967. In 1967, I also visited the auklet colony on the west-facing slope of Sevuokuk Mountain, about three times per week, where Horned Puffins and lesser numbers of Tufted Puffins were also nesting. Thus, I was in contact with breeding puffins along the western slope of Sevuokuk Mountain and at Tategnak Point; my studies of Parakeet Auklets in this area especially brought me into close contact with puffin nesting habitat.

Trips by foot were taken on 13 July 1966 and 28 June 1967 along the rim of Sevuokuk Mountain from due east of the northeast corner of Troutman Lake around by Chibukak Point and southeast to the limit of puffin nesting at Meruwtu Point (Fig. 1). Total counts of individuals, visible on the cliffs and boulders, of both puffin species were made on these trips in the afternoon, which is the peak attendance at the colony each day (see Sealy, 1972). Although counts are approximate and I am aware of the shortcomings of this method (see Myrberget, 1959; Brun, 1971; Brooke, 1972), an estimate of 1,500 pairs of Horned and 500 pairs of Tufted puffins breeding in this area was obtained (Table 1).

All body measurements taken in this study or reported upon were taken in millimeters; all weights were recorded on a triple beam balance to the nearest gram. Environmental temperatures were recorded to the nearest 1.0° C with a Bacharach continuous recording thermometer. Body temperatures of adult and young puffins were measured by means of a portable, battery-powered, multichannel, thermistor thermometer manufactured by the Yellow Springs Instrument Company, Yellow Springs, Ohio. Adult body temperatures were measured by gently inserting a vinyl-sheathed probe down the esophagus to the stomach, and read after 1 minute. Brood patch temperatures of incubating adults were measured with "banjo-tipped" thermistors pressed against the bare skin. Chicks were removed from their nest sites and their body temperatures were measured within 30 seconds and then at 10-minute intervals for 50 minutes at ambient temperatures. I am aware of the limitations of this field method (cf. Farner and Serventy, 1959).

The volumes of the left and right testes in cubic centimeters were calculated (and then combined) using the formula for the volume of an ellipsoid:

$$V = 4/3\pi a^2 b,$$

where $a = \frac{1}{2}$ the shorter diameter and $b = \frac{1}{2}$ the longer diameter. Body measurements were taken from birds collected by Jean Bédard in 1964 and myself in 1966 and 1967 on St. Lawrence Island, by Swartz (1966: 650), and from specimens taken on St. Lawrence Island by other collectors and contained in various museums. Measurements from specimens in the University of Alaska Museum of Zoology (UA nos. 1447, 1449, 3024, 3043) were provided by

TABLE 2

BODY MEASUREMENTS OF ADULT HORNED PUFFINS FROM ST. LAWRENCE ISLAND AND CAPE THOMPSON REGIONS, ALASKA

ITEM	ST. LAWRENCE ISLAND*		CAPE THOMPSON†	
	$\bar{x} \pm 2$ S.E. (N)	RANGE	$\bar{x} \pm 2$ S.E. (N)	RANGE
Wing Length (mm)‡	♂♂190.2 ± 5.6 (6)	183.0–200.0	♂♂199.6 ± 8.2 (7)	194–205
	♀♀187.4 ± 2.5 (8)	182.5–193.0	♀♀ 197 ± 22.0 (10)	182–222
Culmen (mm)	♂♂ 51.6 ± 1.9 (8)	47.3–55.9	♂♂ 50.5 ± 4.0 (7)	46.0–52.7
	♀♀ 50.8 ± 1.4 (9)	47.3–53.4	♀♀ 48.4 ± 4.2 (10)	45.2–50.8
Tarsus (mm)	♂♂ 31.7 ± 3.3 (5)	27.0–37.3	♂♂ 32.4 ± 5.2 (7)	27.5–35.6
	♀♀ 29.1 ± 2.7 (7)	25.4–34.4	♀♀ 31.4 ± 3.0 (10)	29.0–34.1

* Data from specimens collected in 1964 by J. Bédard and in 1966 and 1967 by me; also from specimens in UA, UAMZ, UBC.

† From Swartz (1966: 650).

‡ Wing lengths from St. Lawrence Island are of the wing chord; wing lengths from Cape Thompson are of the flattened wing.

L. G. Swartz; in the University of Alberta Museum of Zoology (UAMZ no. 3521) by N. Panter; and the University of British Columbia Museum of Zoology (UBCMZ nos. 2097, 2098) by R. W. Campbell. In addition, weights from 18 adults taken on Nunivak Island in 1954 were available from specimens collected by P. Stettenheim and deposited in the University of Michigan Museum of Zoology skeleton collection (UMMZ nos. 139,965–139,980; 153,546–7).

RESULTS

Sexual Dimorphism

Sexual dimorphism in plumage is not pronounced in the Horned Puffin (see Bent, 1919; Ridgway, 1919) and birds could not be sexed with any success before dissection. Although the males have larger mean dimensions for all characters measured (Table 2), these differences are not significant ($P > 0.05$ in all cases; *t*-tests). Myrberget (1963) found that male Common Puffins in northern Norway are also larger than the females in all of the above characters; however, these differences were also not statistically significant.

Body Weight during the Breeding Season

Body weights of 22 adult Horned Puffins collected throughout the breeding season on St. Lawrence Island are summarized according to sex in Table 3. Included in this table are weights from 17 adults collected at Cape Thompson in 1960 by Swartz (1966: 650) and 18 adults collected on Nunivak Island in 1954 by P. Stettenheim. Males from all three areas averaged slightly heavier than females during the breeding season but the differences in body weight between the sexes are not significant ($P > 0.05$ in all cases; *t*-tests). Also, the differences in body weights between individuals from the various localities are not significant ($P > 0.05$ in all cases; *t*-tests).

As is shown later, egg-laying in the Horned Puffin generally occurs from the middle of June through the first week of July in the northern Bering Sea region. Thus, the timing of breeding is similar among the various colonies there and, therefore, energy-demanding processes such as egg-laying, chick-rearing, etc., are probably met at a similar time by individuals in these colonies. Therefore, the body weights of adults of both sexes collected at Cape Thompson, St. Lawrence Island, and Nunivak Island were combined and are presented in Fig. 3.

From Fig. 3, it is evident that the loss in body weight throughout the breeding season relative to their weight on arrival in spring amounts to less than 5 percent. Extreme leanness (0 and 1 on a subcutaneous fat scale of 0 to 4) was never encountered in the Horned Puffin specimens examined by me on St. Lawrence Island. Such leanness was also not observed in 142 adult Common Puffins examined during the breeding

TABLE 3

BODY WEIGHTS OF ADULT MALE AND FEMALE HORNED PUFFINS FROM THE NORTHERN BERING SEA REGION

LOCALITY	MALES		FEMALES	
	$\bar{x} \pm 2$ S.E. (N)	RANGE	$\bar{x} \pm 2$ S.E. (N)	RANGE
St. Lawrence Island*	609 ± 30.2 (13)	531–754	589 ± 36.3 (9)	499–691
Cape Thompson†	648 ± 58.6 (7)	610–669	618 ± 94.6 (8)	507–674
Nunivak Island‡	629 ± 40.9 (7)	553–680	581 ± 29.1 (11)	500–636
All areas	625 ± 16.3 (27)	553–754	594 ± 19.1 (28)	499–691

NOTE: Data from specimens collected throughout the breeding season. All weights are in grams.
* Data from specimens collected on St. Lawrence Island in 1964 by J. Bédard and in 1966 and 1967 by me.
† From Swartz (1966: 650).
‡ From specimens in UMMZ.

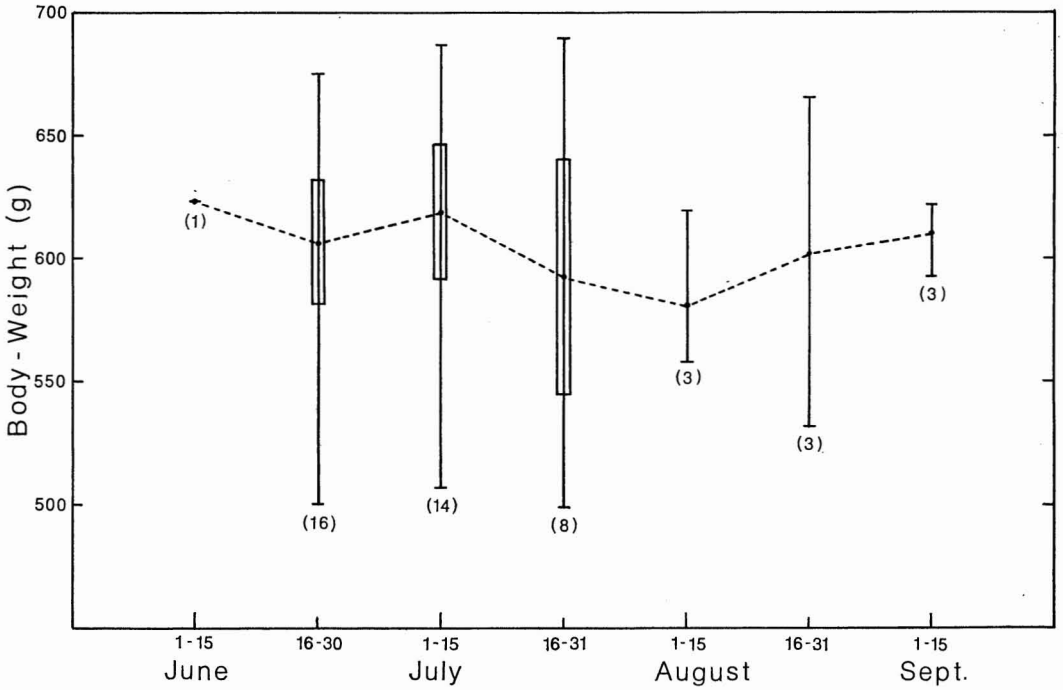

FIG. 3. Body weights of adult Horned Puffins in the northern Bering Sea region. Weights from St. Lawrence Island (1966 and 1967), Cape Thompson (1960, from Swartz, 1966), and Nunivak Island (1954, from specimens in UMMZ) are combined. Mean weights for each 15-day time interval are represented by the dots; the vertical lines denote range; and the bars a distance twice the standard error on each side of the mean.

season by Belopol'skii (1957) in the Barents Sea region.

The seasonal fluctuations in body weight in Common Puffins, among other species, during the breeding season in the Barents Sea region were studied by Belopol'skii (1957: 84–91). The main points resulting from his observations were: (1) male body weights averaged 7.5 percent greater than female body weights, (2) the greatest body weight was recorded in June after arrival, (3) body weight fluctuated 10.8 percent during the breeding season, and (4) a continuing weight loss occurred through the breeding season to August.

TABLE 4

SEX RATIOS OF ADULT HORNED PUFFINS IN THE NORTHERN BERING SEA REGION

LOCALITY	MALES	FEMALES	MALES/FEMALES
St. Lawrence Island*	9	8	1.12
Cape Thompson†	7	10	0.70
Nunivak Island‡	7	11	0.63
All areas	25	29	0.86

*Data from 17 specimens collected on St. Lawrence Island, 1966 and 1967.
† From Swartz (1966).
‡ From 18 specimens in UMMZ.

Sex Ratios

Sex ratios of adult Horned Puffins collected near the nesting slopes of three colonies in the northern Bering Sea region are presented in Table 4. A balanced sex ratio is evident.

In the Common Puffin in Norway, Myrberget (1963) found a sex ratio of 1.08 (85 males/79 females) and Uspenski (1958) calculated it as 1.09 (12 males/11 females in each of 3 years) at Novaya Zemlya. In the Barents Sea region, Belopol'skii (1957) found proportionately more females than males in two of three colonies sampled (0.86 at Ainovy Islands and 0.78 at Grbovaya Inlet). He attributed this preponderance of females to his method of collecting—besides being shot, birds were taken from their nests where females predominated.

Nonbreeders

As in other alcids studied (see Marshall, 1952; Tuck, 1961; Drent, 1965; Bédard, 1967; Sealy, 1972), the Horned Puffin does not reach sexual maturity until its 3rd or possibly 2nd year. Ridgway (1919: 789) stated that young Horned Puffins are "similar in coloration of plumage to winter adults but bill very different, being much less deep, the culmen much less arched, the terminal portion of both maxilla and mandible destitute of grooves or ridges, and horn color brownish, without reddish tinge." Ridgway (1919: 789) also stated that yearling Tufted Puffins are distinguishable from adults because they "have a smaller, narrower bill and lack nuptial tufts."

In Common Puffins, Salomonsen (1944) and Lockley (1953) were able to recognize three age groups, excluding nestlings, according to the number of bill furrows. One-year-old birds have no furrow or a single indistinct furrow in their upper mandible while 2-year-olds have one well-developed and often one indistinct furrow. Older birds (adults) have at least two distinct furrows. Myrberget (1962) found that these groups differ in the time of their return to the colonies in spring in Norway and that only birds with at least two distinct furrows were found on nests.

In the present study, subadult Horned and Tufted puffins were observed on the cliffs of Sevuokuk Mountain but no estimate of the proportion of the total population of each species they comprised was obtained. One yearling female Horned Puffin, taken by an Eskimo on 17 July 1967, had the following measurements: body weight, 461 grams; culmen, 35.6 mm; wing chord, 162 mm; largest ovarian follicle, < 1 mm.

Food Habits and Foraging Areas

The proventriculi of 14 of the 17 Horned Puffins collected on Sevuokuk Mountain by me were empty while three contained unidentifiable fish remains. During the chick-rearing stages, Horned and Tufted puffins were observed carrying only fish, several held crosswise in the bill at one time, to the young

Swartz (1966: 671, table 27) examined 17 stomachs of Horned Puffins collected at Cape Thompson; of eight of the stomachs which contained food, the frequency of fish taken was 75.8 percent while the frequency of invertebrates was 62.5 percent. Of two Tufted Puffins examined by Swartz, the frequency of fish was 100 percent while the frequency of invertebrates was 50 percent.

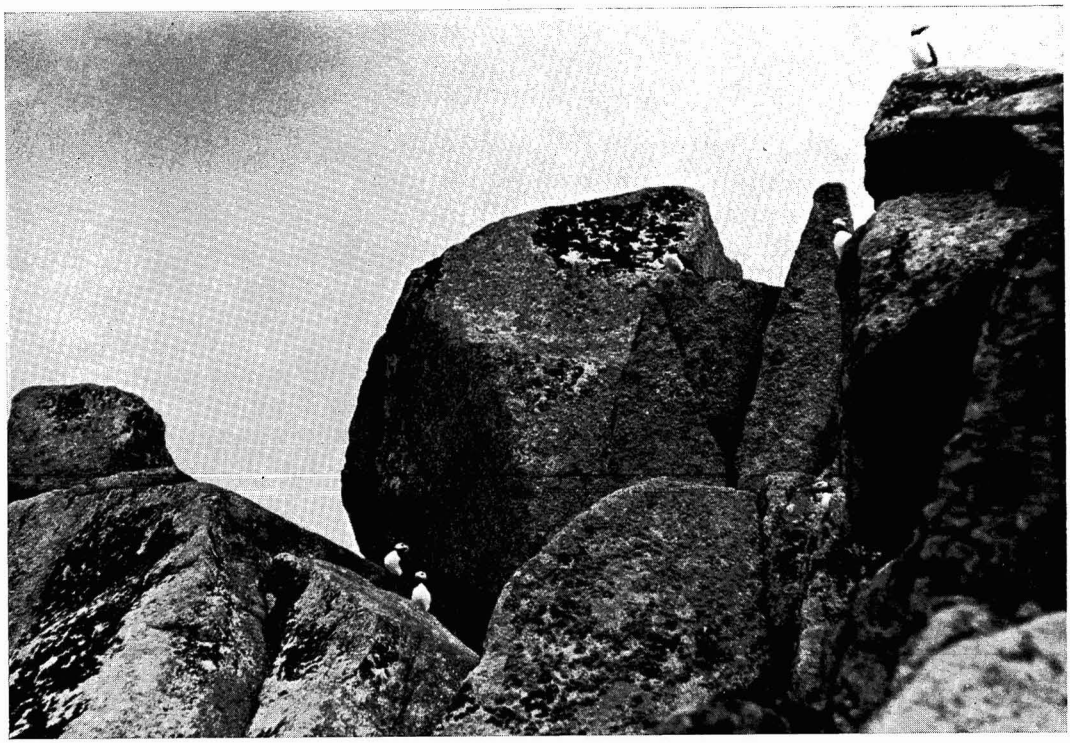

FIG. 4. Nesting habitat of the Horned Puffin; in the "rubble" along the base of Sevuokuk Mountain on St. Lawrence Island, Alaska, 12 July 1967.

Willett (1915: 297) stated that on Forrester Island, "The feeding habits of the Horned Puffin are very similar to those of the Tufted Puffin, but, as a general rule, they seem to feed closer to shore, frequently being seen in small flocks inside the kelp patches." On St. Lawrence Island in 1966 I spent many hours at sea during the latter part of May to early July to the north and west of Sevuokuk Mountain. During these trips feeding Tufted Puffins were encountered at distances up to 15 km from the colony with individuals scattered over a wide area; Horned Puffins, on the other hand, appeared to concentrate their feeding to within 1 or 2 km from the colony. In the Barents Sea region, Belopol'skii (1957) found the Common Puffin to be an inshore feeder.

Although the amount of information on feeding habits of Horned and Tufted puffins is meager, it does appear that adults of both species take invertebrates and fish in their own diets but feed their young exclusively fish. On the basis of morphology, Bédard (1969*a*) pointed out that a comparative study of the feeding ecology of Horned and Tufted puffins, particularly in areas of sympatry, would be worthwhile.

The Nesting Environment

The Pigeon Guillemot (*Cepphus columba*), Parakeet Auklet, Crested Auklet, Least Auklet, and Horned and Tufted puffins nest on the rocky slopes of Sevuokuk Mountain. Even to the casual observer, it soon becomes evident that each of these species is associated during the breeding season with different sectors of the slope. Such differences in habitat selection by these species are related to the different geomorphic features of the slope. Therefore, in order to describe the nesting habits of Horned Puffins it is necessary to understand the nature of the slope morphology which exists there. Bédard (1969*b*) has provided a detailed description of the slope morphologies on St. Lawrence Island; therefore, only a brief summary of that

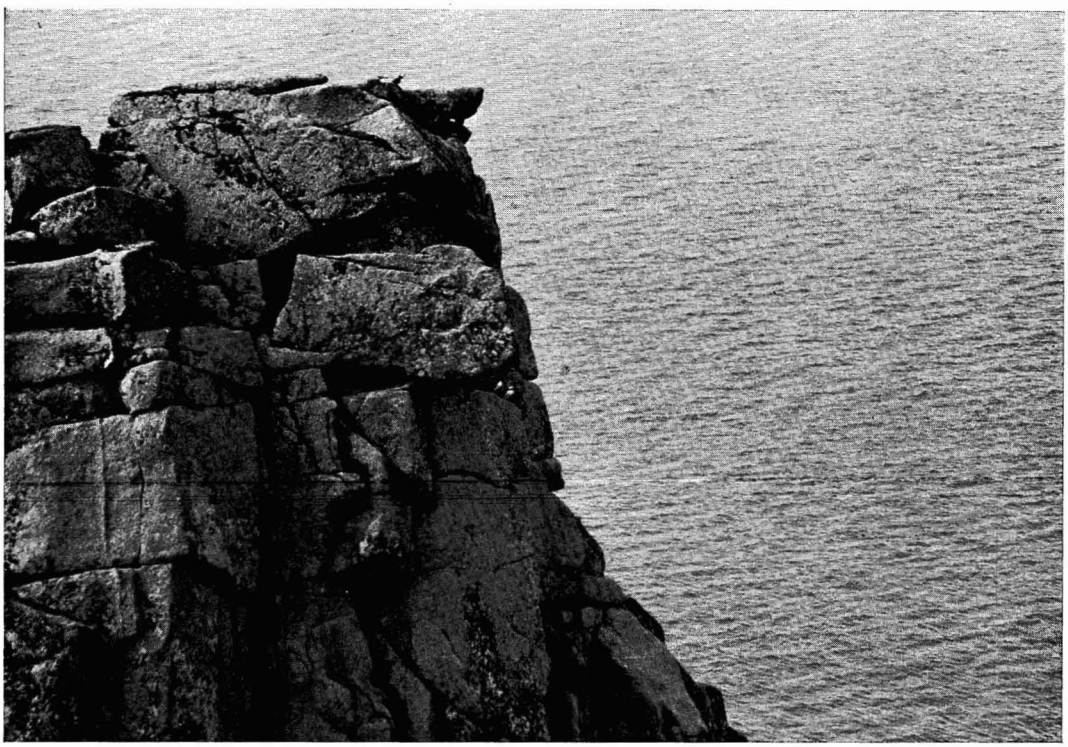

FIG. 5. A typical cliff, along the rim of Sevuokuk Mountain on St. Lawrence Island, Alaska, utilized for nesting by Horned and Tufted puffins, 27 July 1967.

pertaining to Sevuokuk Mountain will be repeated here.

Talus slopes are actively formed in areas of periglacial conditions and are the products of weathering of cliffs by such processes as frost-heaving on the cliff faces, tumbling by gravity of the detached blocks, and accumulation and settling of the debris by slow mass-wasting processes such as creep and solifluction. As Bédard pointed out, Sevuokuk Mountain is an example of a maritime slope where the rock is massive and poorly jointed and wave action does not remove the large boulders which have accumulated at the foot of the bluff forming the "rubble." This gives the geomorphic processes of wedging and heaving an opportunity to proceed unchecked and the talus slope retreats upward.

Crested and Least auklets nest among the boulders on the talus slope, the segregation between the two different sized species being accomplished according to the boulder size (Bédard, 1969*b*). The Parakeet Auklet is concentrated along the rim of the mountain and appears on the slopes wherever weakly weathered outcrops break through the mantle. Pigeon Guillemots, Horned Puffins and, to a lesser extent, Tufted Puffins are found breeding among the "rubble" at the base of the slope (Fig. 4). However, most of the Horned and nearly all of the Tufted puffins are associated with the large cliffs along the rim of Sevuokuk Mountain (Fig. 5).

Descriptions of the nesting habitat of the Common Puffin throughout its breeding range are numerous and have been summarized by Grant and Nettleship (1971) and Nettleship (1972). The latter author provided a detailed description of the nesting habitat on Great Island, Newfoundland, and examined intraspecific habitat selection and its effects on breeding success in this species there. Common Puffins generally nest in self-excavated burrows in turf-covered maritime slopes and level tops of rocky coastal islets. However, Nettleship (1972) pointed out that at high latitudes this

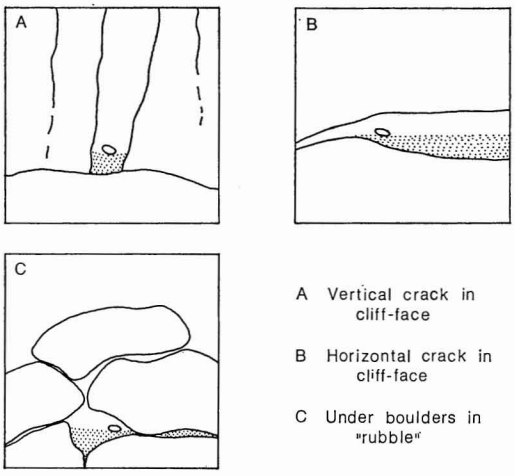

FIG. 6. Cross sections of the three main nest types of the Horned Puffin on Sevuokuk Mountain on St. Lawrence Island, Alaska. Stippling indicates soil; clear portions indicate rock.

species is restricted to rock crevices in cliffs and interstices in talus slopes due to permafrost; exceptions have been found in northern latitudes where Common Puffins dig their own burrows on Novaya Zemlya (Uspenski, 1958) and in the Barents Sea region (Belopol'skii, 1957). Gabrielson and Lincoln (1959) contended that Horned Puffins which breed at high latitudes are also forced to utilize natural crevices because of the frozen ground. However, Horned Puffins utilize, for nesting sites, natural crevices in areas of permafrost (e.g., at Cape Thompson [Swartz, 1966], Little Diomede Island [Kenyon and Brooks, 1960], St. Lawrence Island [this study], St. Matthew Island [Klein, 1959]), in areas with no permafrost (e.g., Kodiak Island [Bretherton, 1896], St. Lazaria Island [Willett, 1912], Forrester Island [Heath, 1915]), and dig burrows in at least one area with permafrost (on Chamisso Island in Kotzebue Sound [Grinnell, 1900]). The Tufted Puffin, although much less numerous than the Horned Puffin in latitudes about 60° N (Table 1), burrows in at least one area affected by permafrost—on the Middle Punuk Island off the southeast cape of St. Lawrence Island (Thompson, 1967).

The Nest

I was able to examine 16 Horned Puffin nests and believe that I encountered all existing types on Sevuokuk Mountain (Fig. 6). In all nests there was an accumulation of grasses on which the egg was laid; in one nest (no. 67–9) several white feathers, possibly from a gull (*Larus* sp.) or the puffin itself, were included in the nest lining. In contrast to the completely sheltered and dark nest sites of auklets (Sealy, 1968), the Horned Puffin nests of types A and B (Fig. 6) were relatively exposed.

THE PRE-EGG STAGE

The pre-egg stage is understood here as the period which extends from the time most of the birds have arrived back at the colony in spring until the first egg is laid.

Return to the Colony

The return of Horned and Tufted puffins to the vicinities of colonies in the northern Bering Sea and Chukchi Sea are tabulated in Table 5. Although the dates of return vary somewhat each year, it appears that these two species return to the vicinity of the colonies at about the same time in spring. A similar situation prevails on the Pribilof Islands where Preble and McAtee (1923) recorded the return of Horned and Tufted puffins at nearly the same time (about the middle of May) for each of 5 years. Occupation of the cliffs occurs about 1 week after their return to the vicinity of the colonies (see Swartz, 1966, for Cape Thompson; Kenyon and Brooks, 1960, for Little Diomede Island; Fay and Cade, 1959, for St. Lawrence Island).

The amount of snow cover and the timing of melting on Sevuokuk Mountain greatly influences the onset of egg-laying in auklets and in some years the breeding success of certain individuals which nest on sectors of the slope where snowmelt is delayed is greatly reduced (Sealy, 1968). All six species of alcids which nest there return in spring before the snow which covers the nesting slopes has begun to melt; the birds, including those Horned and Tufted puffins which nest in the "rubble," land on top of the snow over their future nest sites (this sense of location was borne out by banding in Least Auklets [Sealy, 1968]). Those puffins, on the other hand, which nest on the cliff faces which accumulate less snow which

TABLE 5

SPRING ARRIVAL DATES OF HORNED AND TUFTED PUFFINS IN THE VICINITIES OF NESTING COLONIES ON ST. LAWRENCE ISLAND, CAPE THOMPSON, AND LITTLE DIOMEDE ISLAND

LOCALITY	YEAR	HORNED PUFFIN ARRIVAL DATE	TUFTED PUFFIN ARRIVAL DATE
St. Lawrence Island*	1952	17 May	4 June
	1953	15 May	?
	1954	22 May	?
	1958	?	23 May
	1961	5 May	?
	1966	28 May	23 May
	1967	26 May	26 May
Cape Thompson†	1960	6 June	16 June
	1961	8 June	8 June
Little Diomede Island‡	1953	2 June	2 June
	1958	2 June	26 May

* Data for 1952–1961 from F. H. Fay (personal communication, 1971); for 1966 and 1967 this study.
† From Swartz (1966).
‡ From Kenyon and Brooks (1960).

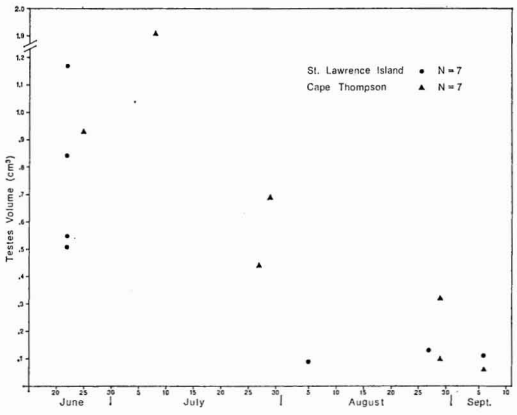

FIG. 7. Reproductive condition of adult male Horned Puffins collected near the breeding colonies on St. Lawrence Island and Cape Thompson (from Swartz, 1966), Alaska, as indicated by the combined volume of left and right testes.

melts sooner, are able to enter their nest sites about a week or 10 days earlier (observations in 1966 and 1967) than those nesting in the "rubble." Whether differential timing of egg-laying between pairs nesting on cliffs or in the "rubble" occurs was not ascertained.

Belopol'skii (1957) presented evidence that microclimatic conditions (i.e., direction slope faces, direction of prevailing winds which facilitate snowmelt) and the phenology of a particular year dictate whether certain populations of the Common Puffin in the Barents Sea region dig their own burrows or seek natural crevices for nesting sites.

Gonadal Development

The reproductive condition of adult male Horned Puffins collected on St. Lawrence Island in 1966 and 1967 and at Cape Thompson in 1960 by Swartz (1966) is shown in Fig. 7. Although the sample size is small, a peak in testicular development is evident around the last week in June and the first week of July. Regression of male gonads occurs rapidly after the middle of July.

One female with a fully shelled egg in the oviduct was collected on Sevuokuk Mountain on 29 June 1966 and one female with one postovulatory follicle was taken on 3 July 1967 and two females each with one postovulatory follicle were taken on 12 July 1967. The presence of postovulatory follicles on the latter dates supports the direct observations (see later) that egg-laying had ceased by the end of the first week of July in 1967.

THE EGG STAGE

Description of the Egg

The egg of the Horned Puffin is ovate in shape with a tendency toward ovate pyriform;

TABLE 6

DIMENSIONS OF PUFFIN EGGS

SPECIES AND LOCALITY	NUMBER	EXTREMES (mm)	MEAN (mm)	SOURCE
Horned Puffin				
St. Lawrence Island	5	70.9 × 44.8	68.9 × 46.2	this study
		68.0 × 50.7		
		66.5 × 46.2		
		68.6 × 44.4		
Bering Sea	38	74 × 50	–	Bent (1919)
		73 × 50.5		
		58 × 43.4		
		61.5 × 41		
Kotzebue Sound	20	–	67.3 × 46.0	Grinnell (1900)
Common Puffin				
Atlantic Ocean	41	–	63 × 44.2	Bent (1919)
Novaya Zemlya	6	–	63.4 × 44.2	Uspenski (1958)
Tufted Puffin				
St. Lazaria Island	20	–	73.7 × 48.5	Grinnell (1900)
Sanak Island	2	–	72.2 × 48.9	UMMZ
Rhinoceros Auklet				
Pacific Northwest	39	–	68.5 × 46.2	Bent (1919)

TABLE 7

WEIGHTS OF FRESH EGGS, BODY WEIGHTS OF ADULTS, AND EGG WEIGHT IN PROPORTION TO ADULT BODY WEIGHT IN PUFFINS

SPECIES	EGG WEIGHT (g)	ADULT BODY WEIGHT (g)	PROPORTIONATE EGG WEIGHT (%)
Horned Puffin*	57.1 (2:56.1–58.1)†	599 (22:499–754)	9.5
Common Puffin‡	55.9 (30:54.5–73.2)	476 (29:407–542)	11.7
Rhinoceros Auklet §	77	518 (10)	14.7
Tufted Puffin‖	91	797 (11:689–920)	11.4

* Measurements obtained on St. Lawrence Island, Alaska, in 1964 by J. Bédard and in 1966 and 1967 by me.

† Number outside the parentheses is the mean value; first number inside the parentheses is the sample size followed by the extremes.

‡ Data from Johnson (1944).

§ Egg weight from Schönwetter (1963); adult body weights from Summers (1970).

‖ Egg weight from Schönwetter (1963); adult body weights obtained on St. Lawrence Island, Alaska, in 1964 by J. Bédard and in 1966 and 1967 by me.

the shell is thick, roughly granulated, and lusterless. The ground color is dull white, dirty white, or creamy white. Conspicuous spots are uncommon but nearly all eggs show faint markings—spots or scrawls—of pale lavender gray or pale olive on buff (Bent, 1919). Some eggs appear spotless but, when they are examined closely, do evince spots. Table 6 gives dimensions of Horned Puffin eggs from St. Lawrence Island with comparative measurements of eggs of other puffins; the variation in size is evident. Table 7 presents weights of fresh eggs and their weight in proportion to adult body weights in puffins.

Clutch Size

Horned and Tufted puffins lay only one egg to a clutch. All 16 Horned and two Tufted puffin nests examined by me on St. Lawrence

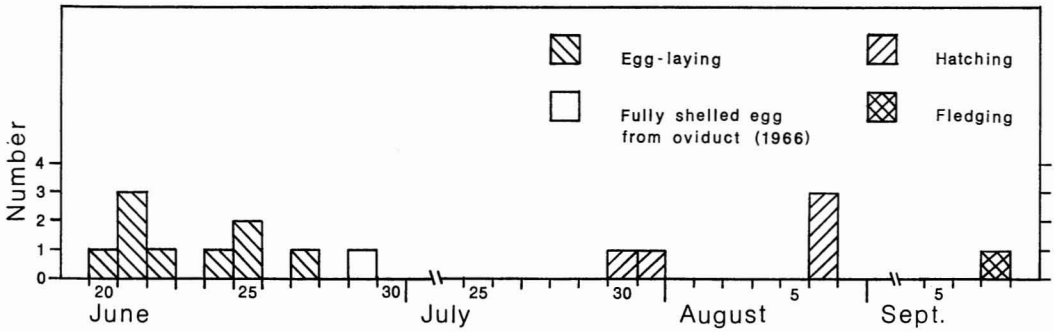

FIG. 8. Egg-laying, hatching, and fledging dates of the Horned Puffin on Sevuokuk Mountain on St. Lawrence Island, Alaska.

Island contained one egg or one young. Swartz (1966) examined 13 Horned Puffin nests at Cape Thompson, each of which contained a single egg or young.

There are rare instances of two-egg clutches in Common Puffins (Kaftanowski, 1951); however, there are no records of their successful hatching (Fisher and Lockley, 1954). Kozlova (1957: 107) stated that "The clutch of Horned Puffins contains one or two eggs"; however, she did not provide details regarding the two-egg clutches. Of 94 nests of the Common Puffin examined by Myrberget (1962), only three contained two eggs. Myrberget did not determine whether two females were involved in each of these clutches but felt that possibly the second eggs were replacement eggs.

Nettleship (1972) conducted twinning experiments with Common Puffins in Newfoundland. He found that no set of twins was reared to fledging. Usually one twin gained weight while the other lost weight. Summers (1970: 13) added a second chick to each of 13 Rhinoceros Auklet nests in British Columbia; of the 26 chicks involved, only eight fledged—in four cases "apparent reaction of the parent to having two chicks resulted in rejection of one or both of them. In the other nine cases one starved."

Timing of Egg-Laying

Egg-laying dates for the Horned Puffin are available in 1966 (one record of a fully shelled egg removed from the oviduct of a female) and in 1967 (Fig. 8). The dates obtained by direct observation in 1967 were from nests first located in 1966; although these adults were not banded, evidence for nest-site tenacity exists. Despite the small sample size, I feel that it is safe to say that egg-laying did not commence prior to 21 June 1967 but could have occurred later than 25 June (as is indicated by still visible postovulatory follicles in females collected up to 12 July 1967). Egg-laying in other alcids was delayed in 1966 on Sevuokuk Mountain due to prolonged snow cover in spring (see Sealy, 1968) and hence 29 June was possibly closer to the peak of egg-laying that year.

On Little Diomede Island, egg-laying in Horned Puffins had not commenced by 25 June 1953 (Kenyon and Brooks, 1960) and at Cape Thompson, Swartz (1966) collected one adult female on 25 June 1960 with one postovulatory follicle which indicates that some egg-laying had occurred by that date. However, the first nests were not located by him until 6 July of that year. In 1961, Swartz located nests with one egg each on 8 July; one of these nests had been empty on 4 July.

Preble and McAtee (1923) summarized egg dates from the Pribilof Islands which indicate that egg-laying in Horned Puffins occurs at least between 19 June and 1 July. In this species' southernmost nesting colony, on Forrester Island, egg-laying apparently occurs during the last 10 days of June (Willett, 1915); however, this author stated (p. 297) that the "first young were noted July 22, but some were probably out several days earlier." In view of the long incubation and fledging periods in this species (see later), it is likely that egg-laying

TABLE 8

LAYING–HATCHING INTERVALS OF THE SINGLE EGGS IN FIVE HORNED PUFFIN NESTS ON ST. LAWRENCE ISLAND, ALASKA, 1967

LAYING DATE	HATCHING DATE	INCUBATION PERIOD
20 June	30 July	40 days
21 June	31 July	40 days
24 June	6 August	43 days
25 June	6 August	42 days
25 June	6 August	42 days
		Mean 41.4 days

begins somewhat earlier there than what Willett suggested.

Accurate egg-laying dates of the Tufted Puffin are lacking. On Middle Punuk Island near St. Lawrence Island, Thompson (1967) found eggs on 12 July 1964 while Fay and Cade (1959) observed downy young there in late August 1953. I located two nests with eggs, one containing a well-developed embryo, on 29 July 1966 at Southwest Cape on St. Lawrence Island. Preble and McAtee (1923: 18) summarized egg dates over several years on the Pribilof Islands which suggest an egg-laying period from the middle of June to early July; in fact, most eggs were "heavily incubated by 1 July." Young birds were recorded there still in nests on 2 October by W. L. Hahn (*in* Preble and McAtee, 1923). Rausch (1958: 236) stated that on Middleton Island "only a few burrows contained eggs on June 5. An egg examined on June 9 contained a small embryo." On Forrester Island, Heath (1915: 29) observed that "eggs were in burrows the third week of June."

Adult Horned and Tufted puffins were first observed in 1967 carrying fish to their young on St. Lawrence Island on 29 July and 2 August, respectively.

Incubation Period

The incubation period of the Horned Puffin on St. Lawrence Island was reported earlier as averaging 41.1 days with extremes of 40 and 43 days (Sealy, 1969). Laying–hatching intervals were determined in 1967 in five nests, where both events were known to the nearest day (Table 8). Swartz (1966: 652) did not determine the exact incubation period of this species; however, in one nest it was "at least 38 days."

For the Common Puffin, Lockley (1953) gave incubation periods of 40, 42, and 43 days; Myrberget (1962) gave it as 40 to 45 days, and averaged 41.8 days; and Kartaschew (1960: 85) stated that this period was "usually 35–37 days" but "may be 40 to 42." The incubation period of the Rhinoceros Auklet is "slightly over 40 days" (Summers, 1970: 7) while that of the Tufted Puffin is unknown.

Brood Patches

During the breeding season, Horned and Tufted puffins develop a pair of lateral brood patches. These are present in adults of both sexes, are bare, and have loose and greatly vascularized skin. The average brood patch dimensions in four adult Horned Puffins were 55 by 27 mm.

Incubation Temperatures

I obtained spot measurements of the temperatures on the surface of the brood patches in adult Horned Puffins and body temperatures of incubating Horned and Tufted puffins in 1967 (Table 9). Comparative measurements from Common Puffins and Rhinoceros Auklets are included.

THE CHICK STAGE

A description of the egg tooth and hatching in Horned Puffin chicks has been presented elsewhere (Sealy, 1970). Horned Puffin chicks, like other puffins, are fed at the nest by both parents until they are fully developed (about 6 weeks old) and flutter out to sea to assume an apparently independent existence.

The Fledging Period

One observation of the fledging period in Horned Puffins in 1967 was 38 days; the chick departed for sea during the night or early morning and possessed complete juvenal plumage (Sealy, 1969). Swartz (1966) determined the fledging period in one nest at Cape Thompson as between 36 and 42 days.

In the Common Puffin, Lockley (1953) recorded fledging periods of 47, 49, and 51 days; Kartaschew (1960) gave it as 38 to 45 days; Myrberget (1962) reported an average of 47.7

TABLE 9

TEMPERATURES OF THE FULLY DEVELOPED BROOD PATCHES COMPARED TO BODY TEMPERATURES IN INCUBATING PUFFINS

SPECIES	BODY TEMPERATURE (°C)	BROOD PATCH TEMPERATURE (°C)
Horned Puffin‡	40.1 (3)*	38.0 (3)
Common Puffin§	42.3 (?)†	42.3 (?)
Rhinoceros Auklet‖	39.3 (2)†	–
Tufted Puffin‡	40.0 (1)*	38.2 (1)

NOTE: Sample sizes in parentheses.
* Esophageal temperature.
† Rectal temperature.
‡ Obtained on St. Lawrence Island, 1967.
§ From Lockley (1953).
‖ From Richardson (1961).

TABLE 10

BODY WEIGHTS AND MEASUREMENTS OF HORNED PUFFIN CHICKS AT HATCHING AND JUST PRIOR TO FLEDGING IN 1967 ON ST. LAWRENCE ISLAND

AGE IN DAYS	BODY WEIGHT (g)	CULMEN (mm)	TARSUS (mm)
1 (2)*	58.6	17.2	19.3
29 (2)	420.9	28.5	30.0
37 (1)	400.2	28.8	30.7

* Sample size in parentheses.

days; and Uspenski (1958) recorded two observations, 36 and 37 days. The mean fledging period in the Rhinoceros Auklet is 50 days (Summers, 1970) but it is unknown in Tufted Puffins.

Growth of Chicks

Growth of chicks was not studied on a daily basis; however, measurements were obtained at hatching and just prior to departure to sea (Table 10). One chick which was weighed the day before it departed to sea was 66.7 percent of the mean adult body weight of the Horned Puffin.

Thermoregulation

Rolnik (1948) and Kaftanowski (1951) were the first to investigate temperature control and its ontogeny in alcids. They placed newly hatched chicks in coolers at 10° C and recorded their body temperatures for several hours using thermocouples. Their observations demonstrated that essentially adult body temperatures were attained and maintained at about 3 days in Common Murres (*Uria aalge*), 3 to 4 days in Razorbills (*Alca torda*) and Black Guillemots (*Cepphus grylle*), and 6 to 7 days in Common Puffins. Richardson (1961) noted that body temperatures of young Rhinoceros Auklets were rather variable but indicated well-established temperature control on or shortly after hatching.

I conducted experiments on one newly hatched Horned Puffin chick in 1967 (Fig. 9). By the 6th day the chick was able to maintain its initial body temperature after being exposed to ambient temperatures of about 9° C for 50 minutes.

Departure of Adults and Chicks

I have only one departure date for Horned Puffin chicks, on 7 September 1967 (Fig. 8). Although most of the auklets had left the nesting slopes on Sevuokuk Mountain by the end

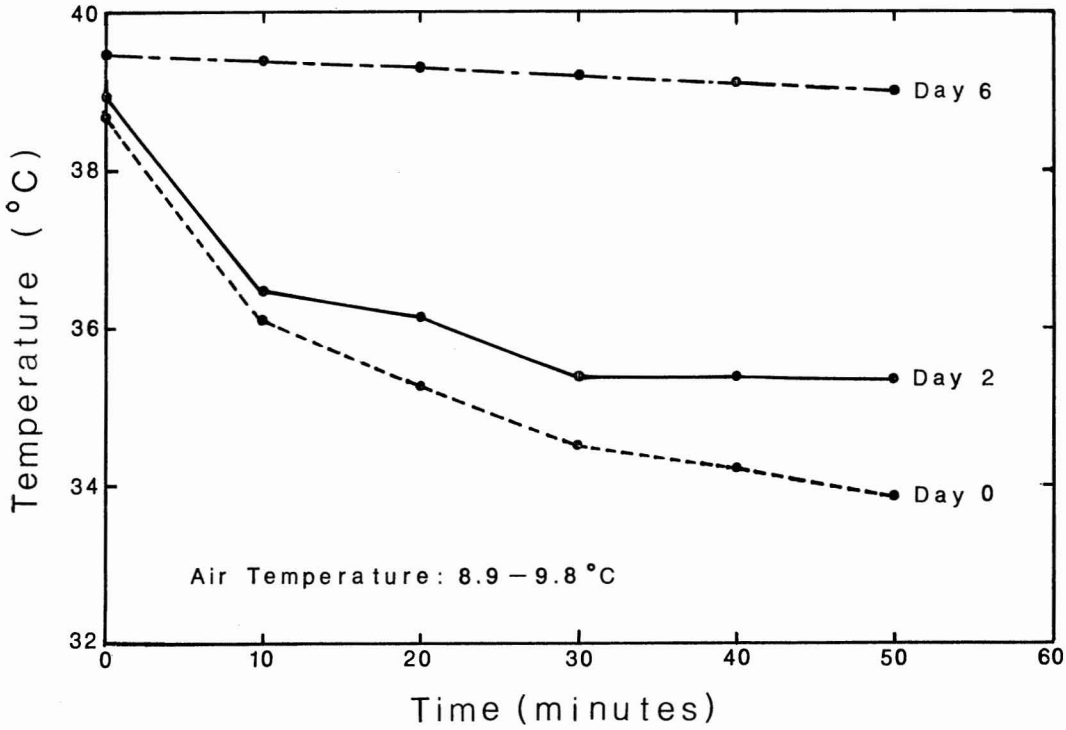

FIG. 9. Responses of a Horned Puffin chick of age 0 days to 6 days to ambient temperatures from 29 July to 3 August 1967 on St. Lawrence Island, Alaska. The same chick was used throughout the experiment.

of the 1st week in September (Sealy, 1968). Horned and Tufted puffins were still present on the cliffs when I left the island on 14 September 1966 and on 9 September 1967.

According to Swartz (1966), adult Horned Puffins at Cape Thompson appeared to occur in maximum numbers through 20 to 27 September 1960. During this period he saw many individuals sitting on deserted murre ledges or near crevice entrances and stated (p. 652) that "this observation suggests that less time was being spent in care of the young." Swartz last observed Horned Puffins there on 2 October 1960 and on 24 September 1961 and Tufted Puffins on 25 September 1960 and on 23 September 1961.

MOLT

Although Bent (1919: 101) stated that adult Horned Puffins have a "complete post-nuptial molt in August or September," observations by Kozlova (1957) and Dementiev (1968) showed that it occurs much later—in November and December. Late molting also occurs in Common Puffins (Salomonsen, 1944) and probably the Tufted Puffin (see Stresemann and Stresemann, 1966). My observations of individuals in early September on St. Lawrence Island indicate only that wing molt had not begun by that time.

DISCUSSION

From the foregoing examination of some events of the breeding biology of Horned Puffins with comparative observations on Tufted Puffins on St. Lawrence Island, it is evident that (1) Horned and Tufted puffins arrive about the same time in spring, toward the end of May, although the date may vary slightly between years, (2) the pre-egg stages in Horned and apparently Tufted puffins are about 3 weeks, (3) breeding Horned Puffins outnumber Tufted Puffins on Sevuokuk Mountain about 3:1, (4) Horned and Tufted puffins utilize natural crevices among boulders and cliffs as nesting sites on Sevuokuk Mountain, (5) molt

does not overlap the breeding effort, and (6) postbreeding dispersal of adult puffins appears to be complete by late September.

A striking feature of seabird distribution is the way that related forms tend to replace each other in different latitudinal zones (e.g. Murphy, 1936; Fleming, 1941; Storer, 1952; Ashmole, 1971). The Horned Puffin and more southern Tufted Puffin replace each other geographically in the Pacific Ocean (Table 1), although there is considerable overlap. Such geographical replacement is also exhibited by two other alcid species, the Thick-billed Murre (*Uria lomvia*) and Common Murre (Storer, 1952). That population numbers of both species of murres in areas of sympatry are not constant relative to one another from even one year to the next has been noted by Fay and Cade (1959); in fact, the population biology of these species is worth considerable study, a start of which has been made (e.g., Lack, 1934; Belopol'skii, 1957; Uspenski, 1958; Tuck, 1961; Southern, 1966).

Ashmole (1971: 270) has pointed out that such species replacement might be ascribed to competitive exclusion, but it "is equally probable that the critical factor is the low probability that two closely related forms can establish reproductively isolated populations at the same breeding stations." Ashmole also stated that probably the most important means by which two related forms can come to breed sympatrically while maintaining reproductive isolation is for an island to be colonized by members of a form with a breeding season different from the native population (Fleming, 1941). In high latitudes, significant differences in timing of breeding by various species of seabirds is generally precluded by the short summers there. However, sympatric species of seabirds do coexist there by selecting different nesting habitats (Bédard, 1969*b*), evolving morphological and behavioral isolating mechanisms (Smith, 1966) and/or feeding on different prey (Bédard, 1969*c*).

The varying sizes of the breeding populations of Horned and Tufted puffins throughout their area of sympatry strongly suggests that competition of some form is operating. In seabirds, the resources for which competition is most likely are food and nest sites (Ashmole, 1963; Lack, 1966; Carrick and Ingham, 1967).

As described earlier, the Horned Puffin generally utilizes natural crevices for nesting throughout its range which often overlaps that of the Tufted Puffin, usually a burrower; it is in the northern Bering Sea region where the Horned Puffin is the more abundant (Table 1).

Puffins which breed at northern latitudes possibly utilize natural crevices for nest sites for the following reasons: (1) digging is impossible where permafrost prevails, and (2) where the sod does thaw, there is probably not enough time in the short summers to dig burrows and rear young successfully. Frozen ground would pose several problems to the burrowing puffins. Depending on the exposure of a particular slope, melting of the upper layer of soil may not occur at all or may occur only slightly during the short summer (see Drew et al., 1958). Even in areas where the upper layers of soil do thaw, other problems can exist. Whereas some physical conditions of the soil (e.g., particle size) are constant, other physical conditions (e.g., water content, colloidity) may differ from one area to another. Although moist soil conditions would facilitate digging by hindering crumbling and consequent cave-ins, moisture would also increase the weight of the soil to be removed by the burrowing puffin. In areas of poor drainage, meltwater would possibly hinder severely the digging of a burrow and constantly threaten the stability of the completed burrow.

The "life expectancy" of a puffin burrow (which would be uninhabited for about 8 months each year) in Arctic soil would probably be short due to the effects of frost-heaving and other factors (see Drew and Tedrow, 1962). Since the Common Puffin (Nettleship, 1972) as well as the other alcids studied (see Sealy, 1972, for summary) exhibit a high degree of nest-site tenacity, it is probable that such is also the case with Horned and Tufted puffins. However, if each pair returns every year to find its burrow uninhabitable, valuable time and energy must be used to locate another suitable site and dig the burrow.

The pre-egg stages of Horned and Tufted puffins on St. Lawrence Island where only natural crevices are used for nest sites are 2 to 3 weeks. However, the pre-egg stage of the Common Puffin at Novaya Zemlya and in the Barents Sea regions, where it occasionally bur-

rows, is about 4 weeks (Uspenski, 1958; Belopol'skii, 1957), whereas at Pembrokeshire where it always burrows it is 5 weeks (Lockley, 1934). Thus, it is evident that, at least in the Common Puffin, the pre-egg stage is longer in areas where the birds dig their own nest sites than in the areas where natural crevices are used. Complicating the picture, however, is the fact that Tufted Puffins are able to dig burrows on Middle Punuk Island, near St. Lawrence Island, where the Horned Puffin does not breed (Thompson, 1967); also, Horned Puffins dig burrows on Chamisso Island where Tufteds are rare (Grinnell, 1900). Both of these islands are affected by permafrost, but the islands are small. It is also interesting to note that, on Kodiak Island, Bretherton (1896) emphasized that the rare Tufted Puffin did not burrow there, whereas the numerous Horned Puffin did. Therefore, the factors which influence the population numbers and distribution of these puffins are complex and only speculations can be made here.

"*Protofratercula*" probably dug its own burrows and possibly reused them in successive years. Although natural crevices were probably available, sociality possibly restricted the breeding populations to areas of sod. During the late Tertiary, *Fratercula* immigrated to the Atlantic Ocean (Johansen, 1958) where it became a boreal species (Udvardy, 1963). After spreading back to the Bering Strait *Fratercula* became sufficiently isolated into the high Arctic *corniculata* and *arctica*. Thus, *corniculata* was possibly faced with areas of frozen ground and was forced to seek natural crevices for nesting. It is possible that the presence of permafrost and the short summers provided the selective pressures necessary to remove the burrow-digging behavior from *corniculata*. As *corniculata* moved southward during periods of climatic amelioration, it came into contact with areas without permafrost but also populations of the burrowing *Lunda cirrhata*. Competition with *Lunda* for nest sites and/or food may have prevented *corniculata* from moving farther south and also forced the latter species to retain its habit of nesting in natural crevices; in most areas today where *cirrhata* and *corniculata* are sympatric, only *cirrhata* burrows. The presence of a third puffin, the exclusively burrowing *Cerorhinca monocerata*, which breeds in temperate areas of the Pacific Ocean coasts, also possibly influenced the southern limit of penetration by *corniculata*.

SUMMARY

Ancillary to a 2-year study of auklet breeding biology, observations on some aspects of the biology of Horned and Tufted puffins on Sevuokuk Mountain, St. Lawrence Island, Alaska, were obtained in 1966 and 1967. On this mountain, where breeding Horned Puffins outnumbered breeding Tufted Puffins about 3:1, these species utilize natural crevices among large boulders at the base of the slope and on cliffs along the rim of the mountain.

Horned Puffins, which are not sexually dimorphic in size or plumage, show a balanced sex ratio. Body weights of adults during the breeding season fluctuate less than 5 percent during this period. Although nonbreeders of both Horned and Tufted puffins were recognized and observed at the colony, no estimations of their numbers were obtained. Both species feed fish to their young in the nest but the adults apparently take both fish and invertebrates in their own diets.

Both Horned and Tufted puffins return to the nesting colonies about the same time in spring, toward the end of May on St. Lawrence Island; however, the arrival dates may vary slightly between years. The pre-egg stages in Horned and apparently in Tufted puffins are about 3 weeks. The eggs, which weigh 9.5 percent and 11.4 percent of the adult body weight in Horned and Tufted puffins, respectively, are laid during the last 2 weeks of June and the 1st week in July in the northern Bering Sea region. The incubation period of the Horned Puffin is about 41 days; two, bare, lateral brood patches develop in incubating males and females.

The fledging period in one Horned Puffin chick on St. Lawrence Island was 38 days; the chick weighed 66.7 percent of the mean adult body weight. By the 6th day young Horned Puffins are able to maintain essentially adult body temperatures after exposure to the low ambient temperatures.

The postnuptial molt, although not specifically studied, does not overlap the breeding effort in Horned and Tufted puffins.

The distributional history of puffins is dis-

cussed. Horned and Tufted puffins, although showing similar basic breeding habits and timing of breeding, exhibit varying population sizes in areas of sympatry. The Horned Puffin greatly outnumbers the Tufted Puffin in northern portions of their ranges. Whereas the Horned Puffin utilizes, almost exclusively, natural crevices for nesting, Tufteds are predominantly burrowers except in more northerly areas. The possible effects of permanently frozen ground on the nesting habits of burrowing puffins are discussed.

ACKNOWLEDGMENTS

The work on St. Lawrence Island in 1966 and 1967, conducted while I was undertaking graduate work at the University of British Columbia, was supported by National Research Council of Canada grants to Dr. M. D. F. Udvardy who also helped considerably with the preparation of this paper. Drs. Jean Bédard, Francis H. Fay, and L. Gerard Swartz provided unpublished observations and Dr. Bédard kindly read an earlier draft of the manuscript. Dr. Robert W. Storer provided access to the collections in the University of Michigan Museum of Zoology. Measurements from specimens contained in the University of Alberta Museum of Zoology and the University of British Columbia Museum of Zoology were provided by N. Panter and R. W. Campbell, respectively. My sincere thanks go out to these people.

LITERATURE CITED

ARNOLD, L. W. 1948. Observations on populations of North Pacific pelagic birds. Auk 65: 553–558.

ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103*b*: 458–473.

———. 1971. Sea bird ecology and the marine environment, p. 223–286. *In* D. S. Farner and J. R. King [ed.] Avian biology. Vol. 1. Academic Press, New York. 586 p.

AUSTIN, O. L., JR., and N. KURODA. 1953. The birds of Japan their status and distribution. Bull. Mus. Comp. Zool. 109: 280–637.

BÉDARD, J. 1967. Ecological segregation among plankton-feeding Alcidae (*Aethia* and *Cyclorrhynchus*). Ph.D. thesis, Univ. British Columbia. 177 p.

———. 1969*a*. Adaptive radiation in Alcidae. Ibis 111: 189–198.

———. 1969*b*. The nesting of the Crested, Least, and Parakeet auklets on St. Lawrence Island, Alaska. Condor 71: 386–398.

———. 1969*c*. Feeding of the Least, Crested, and Parakeet auklets around St. Lawrence Island, Alaska. Canad. J. Zool. 47: 1025–1050.

BELOPOL'SKII, L. O. 1957. Izdat'stvo Akademii Nauk SSSR, Moskva-Leningrad. [Ecology of sea colony birds of the Barents Sea.] Israel Prog. Sci. Transl., Jerusalem, 1961. 346 p.

BENT, A. C. 1919. Life histories of North American diving birds. Bull. U.S. Nat. Mus. 107. 245 p.

BRETHERTON, B. J. 1896. Kodiak Island. A contribution to the avifauna of Alaska. Ore. Nat. 3: 47–49.

BROOKS, A., and H. S. SWARTH. 1925. A distributional list of the birds of British Columbia. Pacif. Cst. Avif. 17: 1–158.

BROOKE, M. DE L. 1972. The puffin population of the Shiant Islands. Bird Study 19: 1–6.

BRUN, E. 1971. Census of Puffins (*Fratercula arctica*) on Nord-Fuglöy, Troms. Astarte 4: 41–45.

CARRICK, R., and S. E. INGHAM. 1967. Antarctic sea-birds as subjects for ecological research. Japan Antarctic Res. Exped., JARE Sci. Rep. 1 (special issue): 151–184.

DEMENTIEV, G. P. 1968. Birds of the Soviet Union. Israel Prog. Sci. Transl., Jerusalem. Vol. 2. 553 p.

DRENT, R. H. 1965. Breeding biology of the Pigeon Guillemot, *Cepphus columba*. Ardea 54: 100–160.

DRENT, R. H., and C. J. GUIGUET. 1961. A catalogue of British Columbia sea-bird colonies. Occ. Pap. B. C. Prov. Mus. 12: 1–173.

DREW, J. V., J. C. F. TEDROW, R. E. SHANKS, and J. J. KORANDA. 1958. Rate and depth of thaw in Arctic soils. Trans. Amer. Geophys. Un. 39: 687–701.

DREW, J. V., and J. C. F. TEDROW. 1962. Arctic soil classification and patterned ground. Arctic 15: 109–116.

FARNER, D. S., and D. L. SERVENTY. 1959. Body temperature and the ontogeny of thermoregulation in the Slender-billed Shearwater. Condor 61: 426–433.

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

FISHER, J., and R. M. LOCKLEY. 1954. Sea-birds. Houghton Mifflin, Boston. 320 p.

FLEMING, C. A. 1941. The phylogeny of the prions. Emu 41: 134–155.

FRIEDMANN, H. 1935. The birds of Kodiak Island, Alaska. Bull. Chicago Acad. Sci. 5: 13–54.

GABRIELSON, I. N., and F. C. LINCOLN. 1959. Birds of Alaska. Stackpole Co., Harrisburg, Penn. and Wildl. Mgmt. Inst., Wash., D. C. 922 p.

GABRIELSON, I. N., and S. G. JEWETT. 1970. Birds of the Pacific Northwest. Dover Publ., New York. 650 p.

GIZENKO, A. I. 1955. Ptitsy Sakhainskoi. [Birds of Sakhalin.] Publ. Acad. Sci. USSR Moscow. 328 p.

GRANT, P. R., and D. N. NETTLESHIP. 1971. Nesting habitat selection by puffins *Fratercula arctica* L. in Iceland. Ornis Scand. 2: 81–87.

GRINNELL, J. 1900. Birds of the Kotzebue Sound region, Alaska. Pacif. Cst. Avif. 1: 1–80.

GRINNELL, J., and A. H. MILLER. 1944. The distribution of the birds of California. Pacif. Cst. Avif. 27: 1–608.

HAMILTON, W. J., III. 1958. Pelagic birds observed on a North Pacific crossing. Condor 60: 159–164.

HEATH, H. 1915. Birds observed on Forrester Island, Alaska during the summer of 1913. Condor 17: 20–41.

JAQUES, F. L. 1930. Water birds observed on the Arctic Ocean and the Bering Sea, in 1928. Auk 47: 353–366.

JEWETT, S. G., W. P. TAYLOR, W. T. SHAW, and J. W. ALDRICH. 1953. Birds of Washington state. Univ. Wash. Press, Seattle. 767 p.

JOHANSEN, H. 1958. Revision und Entstehung der arcktischen Vogelfauna II. Acta arct., Kbh. 9: 50–131.

———. 1961. Revised list of the birds of the Commander Islands. Auk 78: 44–56.

JOHNSON, R. A. 1944. Weight records for some Atlantic Alcidae. Wilson Bull. 56: 161–168.

KAFTANOWSKI, Y. M. 1951. Chistikobye pstitsy vostochnoi Atlantiki. Materialy k poznaniyu fauny i flory SSSR. [Birds of the murre group of the eastern Atlantic. Studies of the fauna and flora of the USSR.] Published by the Moscow Society of Naturalists, new series, zoology section, vol. 28: 1–170.

KARTASCHEW, N. N. 1960. Die Alkenvögel des Nordatlantiks. Die neue Brehm-Bücherei 257. Wittenberg Lutherstadt (Ziemsen). 154 p.

KENYON, K. W., and J. W. BROOKS. 1960. Birds of Little Diomede Island, Alaska. Condor 62: 457–463.

KLEIN, D. R. 1959. Saint Matthew Island reindeer-range study. Spec. Rep. U.S. Fish Wildl. Serv. 43. 48 p.

KOSLOVA, E. V. 1957. Charadriiformes, suborder Alcae. Fauna of USSR: Birds 2(3): 1–140. [English translation by R. Ettinger, Israel Prog. Sci. Transl., Jerusalem, 1961.]

LACK, D. 1934. Habitat distribution in certain Icelandic birds. J. Anim. Ecol. 3: 81–90.

———. 1966. Population studies of birds. Oxford Univ. Press (Clarendon), London. 341 p.

LOCKLEY, R. M. 1934. On the breeding-habits of the puffin: with special reference to its incubation- and fledging-periods. Brit. Birds 27: 214–223.

———. 1953. Puffins. Dent, London. 186 p.

MARSHALL, A. J. 1952. Non-breeding among Arctic birds. Ibis 94: 310–333.

MURIE, O. J. 1959. Fauna of the Aleutian Islands and Alaska Peninsula. U.S. Fish Wildl. Serv. N. Amer. Fauna 61. 406 p.

MURPHY, R. C. 1936. Oceanic birds of South America. 2 vols. Amer. Mus. Nat. Hist., New York. 1245 p.

MYRBERGET, S. 1959. Lundeura på Lovunden, og lundebestanden der. Fauna 12: 143–156.

———. 1961. Reir og reibygging hos lundefuglen. Fauna 14: 24–28.

———. 1962. Undersøkelser over forplantnings-biologien til Lunde (*Fratercula arctica* [L.]). Meddr. St. Viltunders. 11: 1–51.

———. 1963. Systematic position of *Fratercula arctica* from a north Norwegian colony. Nytt Mag. Zool. 11: 74–84.

NETTLESHIP, D. N. 1972. Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. Ecol. Monogr. 42: 239–268.

PREBLE, E. A., and W. L. MCATEE. 1923. A biological survey of the Pribilof Islands, Alaska. U.S. Fish Wildl. Serv. N. Amer. Fauna 46. 255 p.

RAUSCH, R. 1958. The occurrence and distribution of birds on Middleton Island, Alaska. Condor 60: 227–242.

RICHARDSON, F. 1961. Breeding biology of the Rhinoceros Auklet on Protection Island, Washington. Condor 63: 456–473.

RIDGWAY, R. 1919. The birds of North and Middle America. Bull. U.S. Nat. Mus. 50, part 8.

ROLNIK, V. V. 1948. Razvitie termoregulyatsii u nekotorykh ptits Severa. [The development of thermoregulation in some birds of the north.] Zool. Zh. 27: 535–546.

SALOMONSEN, F. 1944. The Atlantic Alcidae. The seasonal and geographical variation of the auks inhabiting the Atlantic Ocean and adjacent waters. Göteborgs VetenskSamh. Handl. ser. B, Band 3, vol. 5: 1–138.

SCHÖNWETTER, M. 1963. Handbuch der oologie, p. 458–472. *In* W. Weise [ed.] Vol. 8. Akademie-Verlag, Berlin.

SEALY, S. G. 1968. A comparative study of breeding ecology and timing in plankton-feeding alcids (*Cyclorrhynchus* and *Aethia* spp.) on St. Lawrence Island, Alaska. M.Sc. thesis, Univ. British Columbia, Vancouver. 193 p.

———. 1969. Incubation and nestling periods of the Horned Puffin. Condor 71: 81.

———. 1970. Egg teeth and hatching methods in some alcids. Wilson Bull. 82: 289–293.

———. 1972. Adaptive differences in breeding biology in the marine bird family Alcidae. Ph.D. thesis, Univ. Michigan, Ann Arbor. 283 p.

SEALY, S. G., and R. W. NELSON. In press. The occurrences and status of the Horned Puffin in British Columbia. Syesis.

SHUNTOV, V. P. 1961. Migration and distribution of marine birds in southeastern Bering Sea during spring-summer season. [In Russian.] Zool. Zh. 40: 1058–1069.

SMITH, N. G. 1966. Evolution of some Arctic gulls (*Larus*): an experimental study of isolating mechanisms. Orn. Monogr. 4. 99 p.

SOUTHERN, H. N. 1966. Distribution of Bridled Guillemots in east Scotland over eight years. J. Anim. Ecol. 35: 1–11.

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

STORER, R. W. 1945. Structural modifications in the hind limb in the Alcidae. Ibis 87: 433–456.

———. 1952. A comparison of variation, behavior and evolution in the sea bird genera *Uria* and *Cepphus*. Univ. Calif. Publ. Zool. 52: 121–222.

STRESEMANN, E., and V. STRESEMANN. 1966. Die Mauser der Vogel. J. Orn., Lpz. 107: 3–445.

SUMMERS, K. 1970. Growth and survival of the Rhinoceros Auklet on Cleland Island. B.Sc. thesis, Univ. British Columbia, Vancouver. 34 p.

SWARTH, H. S. 1934. Birds of Nunivak Island, Alaska. Pacif. Cst. Avif. 22: 1–64.

SWARTZ, L. G. 1966. Sea-cliff birds, chap. 23, p. 611–678. *In* N. J. Wilimovsky and J. N. Wolfe [ed.] Environment of the Cape Thompson region, Alaska. U.S. Atomic Energy Comm. Oak Ridge, Tenn.

———. 1967. Distribution and movements of birds in the Bering and Chukchi seas. Pacif. Sci. 21: 332–347.

THOMPSON, C. F. 1967. Notes on the birds of the northeast cape of St. Lawrence Island and of the Punuk Islands, Alaska. Condor 69: 411–419.

TUCK, L. M. 1961. The murres. Canad. Wildl. Serv. ser. 1. 260 p.

UDVARDY, M. D. F. 1963. Zoogeographical study of the Pacific Alcidae, p. 85–111. *In* J. L. Gressitt [ed.] Pacific basin biogeography. 10th Pacif. Sci. Congr. Publ., Bishop Mus. Press, Honolulu. 564 p.

USPENSKI, S. M. 1958. The bird bazaars of Novaya Zemlya. Ottawa. [Translated from the Russian edition, Canadian Wildlife Service.] 159 p.

WILLETT, G. 1912. Report of George Willett, agent and warden stationed on St. Lazaria bird reservation, Alaska. Bird-lore 14: 419–426.

———. 1915. Summer birds of Forrester Island, Alaska. Auk 32: 295–305.