BIOLOGY OF NESTING ANCIENT MURRELETS

SPENCER G. SEALY

The breeding biology of the Ancient Murrelet (*Synthliboramphus antiquus*) previously has not been studied intensively. Contributions of C. Littlejohn (*in* Bendire 1895) from Alaska, Ishizawa (1933) from Korea, and Murata (1958) from Japan generally are incomplete and deal only with short periods. Observations made intermittently between 1946 and 1952 on Langara Island, British Columbia, by C. J. Guiguet (*in* Drent and Guiguet 1961, unpubl. observ.) provide important comparative data. In this paper I examine the breeding ecology of the Ancient Murrelet on Langara Island, Queen Charlotte Islands, British Columbia (fig. 1).

DISTRIBUTION

The breeding distributions of alcids, including the Ancient Murrelet, have been mapped and analyzed by Udvardy (1963). As with most alcids (see Sealy 1968), little is known of the post-breeding dispersal and winter distribution of the Ancient Murrelet. Adults and newly hatched young disperse rapidly from Langara Island during June, and intact family groups move apparently southward. Adults with downy young have been observed in May near Goose Island (Guiguet 1953a) east of the southern tip of the Queen Charlotte Islands, and adults with half-grown young have been seen along the west coast of Vancouver Island by mid-July (Martin and Myres 1969, Hatler et al. 1973). The Ancient Murrelet is not known to nest in these latter areas.

While some Ancient Murrelets move southward along the coast to California in winter (Grinnell and Miller 1944), many others apparently winter close to the breeding areas or well out to sea (Gabrielson and Lincoln 1959). The numerous records of inland wanderings, most of them in the fall, have been correlated with high westerly winds (Munyer 1965, Verbeek 1966).

STUDY AREA

My study was conducted on and in the vicinity of Langara Island, British Columbia, from 6 May to 10 July 1970 and 17 March to 12 August 1971. On the Island, studies were concentrated in three nesting colonies (fig. 1): Colony A on Iphigenia Point (54°12'N, 133°01'W), Colony B south of Egeria Bay (54°12'N, 132°58'W), and Colony C on McPherson Point (54°15'N, 132°59'W).

Langara Island (formerly North Island) is about 40 km² in area and lies at the northwest corner of the Queen Charlotte Islands chain. The chain is separated from the mainland coast of British Columbia by the Hecate Strait which is about 60 km wide. The physiography and geology of the Islands, including Langara, have been described by Holland (1964) and Brown (1968).

The Queen Charlotte Islands are characterized by very cool summers, but mild winters, with overcast skies, strong winds, and heavy rainfall in late fall and early winter. Summer days are long, but the duration of bright sunshine is among the lowest in Canada (Williams *in* Calder and Taylor 1968). Records from the Langara Lightstation (Williams *in* Calder and Taylor 1968:18–32) indicate an average annual precipitation of 167.6 cm and a frost-free period from late March to mid-November. Although maximum temperatures reach 21°C, the average monthly mean for the warmest part of the summer is only about 13°C. The average relative humidity on Langara Island is 94% in summer but slightly less during other seasons.

The physical oceanography of this region was described by Fleming (1955) and Crean (1967). Sealy (1975a) examined mainly biological aspects of the marine environment that may influence the feeding ecology of the Ancient Murrelet and Marbled Murrelet (*Brachyramphus marmoratus*).

The vascular flora and bryophytes of the Queen Charlotte Islands have been described extensively (Foster 1965, Calder and Taylor 1968, Schofield 1968). The plateau region of Langara Island is forested, and in well-drained spots, particularly along the periphery of the island, the forest consists of Sitka Spruce (*Picea sitchensis*), Western Red Cedar (*Thuja plicata*), and Western Hemlock (*Tsuga heterophylla*). The latter two are the most common trees in the Ancient Murrelet colonies studied (figs. 2, 3). Where stands are dense, underbrush is sparse, and a thick carpet of mosses covers the slopes.

METHODS

During 1970 and 1971, I collected a few Ancient Murrelets from the feeding areas each week for a total of 61 adults and 30 subadults (see Sealy 1972, 1974, 1975a for details of collecting trips). Also, 56 adults and 19 subadults were taken on the staging areas (see below). In both instances birds were obtained by non-selective shooting. Stomach contents were examined, and each specimen was weighed to the nearest 0.1 g on a triple beam balance, usually within 3–4 h after death. The culmen, bill height, flattened wing, and tarsus of each bird were measured in mm. The amount of subcutaneous fat was recorded using categories from 4 (extremely fat) to 0 (extremely lean). Each specimen was examined for body and wing molt.

Egg-laying dates were observed directly at nests visited daily until the first egg (A) and/or second egg (B) appeared in the burrow. These dates are accurate to about 4 h, as eggs are laid only during the four hours of darkness at that time. Each egg was labeled with the nest number and an A or B to denote laying order (when known). Estimated laying dates of A eggs were calculated from known laying dates of B
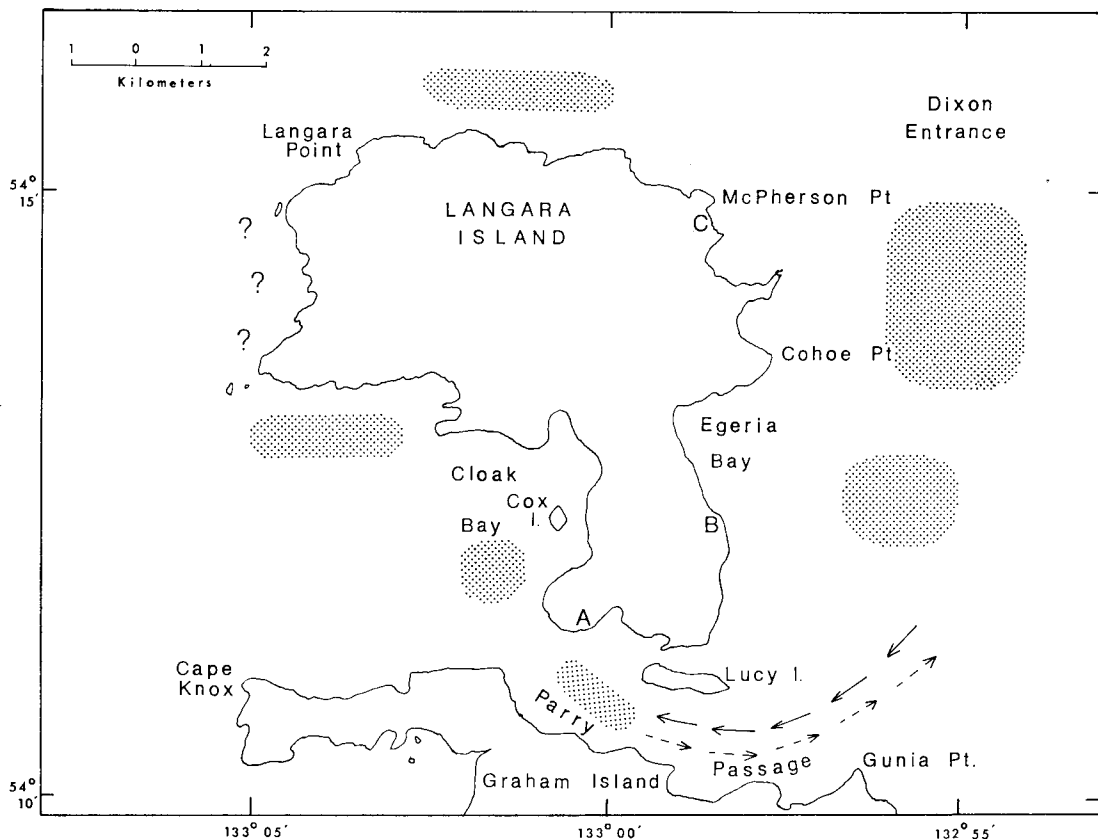
FIGURE 1. Map of Langara Island and vicinity, Queen Charlotte Islands, British Columbia, showing locations of Colonies A, B, and C where Ancient Murrelet nesting studies were conducted. Locations of staging areas adjacent to colonies are shaded. Solid arrows indicate direction taken by flocks arriving on the western Parry Passage staging area, and broken arrows indicate direction taken by departing flocks.

eggs. Dates obtained by dissection of adult females with fully shelled eggs in their oviducts are accurate to within 4–8 h. The birds were collected on the staging areas in early evening and presumably would have flown into the colony that night to lay. Post-ovulatory follicles were measured when present.

The greatest length and width of the eggs were measured to the nearest 0.1 mm using calipers. Unincubated and pipped eggs were weighed to the nearest 0.1 g.

At 15 nests one member of the pair was banded early in incubation. The incubation rhythm was determined by reaching into the burrow and feeling for the presence or absence of the band. As the birds cannot be sexed externally, I assumed that the banded and unbanded individuals were different sexes. Although Ancient Murrelets readily desert nests after being handled, none of these did so.

The developmental state of the brood patch of adult birds (subadults did not show brood patch development) was scored according to 6 classes: (0) no evidence of defeathering; (1) loss of down and some contour feathers; (2) almost complete loss of down and most contour feathers with vascularization beginning; (3) complete loss of feathers with heavy vascularization (maximum development); (4) regression beginning, down appearing, especially around the edges, and sheaths of new contour feathers appearing; (5) most of the area down-covered, contour feathers beginning to break out of sheaths; (6) complete

regression, appearance as in class 0. The length and width of the fully developed brood patch (class 3) were measured to the nearest mm with calipers.

Body temperatures of adult and young Ancient Murrelets were taken by gently inserting the vinyl-sheathed probe of a portable multichannel thermistor thermometer down the esophagus to the stomach, and reading after 1 min. Brood patch temperatures of incubating adults were measured with "banjo-tipped" thermistors pressed against the bare skin. Chicks were removed from the nest, and their temperatures were measured within 30 sec.

Canadian Wildlife Service standard aluminum bands (no. 3) were applied to 36 adults and 53 newly hatched Ancient Murrelets.

All times are Pacific Standard Time (PST).

RESULTS

SEXUAL DIMORPHISM AND SEX RATIOS

Sexual dimorphism in plumage (Bent 1919, Ridgway 1919, Kozlova 1957) is not pronounced, and the birds could not be sexed before dissection. Although males averaged larger (table 1) in most characters measured, differences were not significant ($P > 0.05$, t-tests). A balanced sex ratio was evident for all age classes (table 2).

FIGURE 2. Colony A on Iphigenia Point, Langara Island, 20 May 1971. The Ancient Murrelets nested on the slopes at the bases of the Western Hemlocks.

FIGURE 3. Ancient Murrelet nesting slope amid Western Hemlocks, Langara Island, 10 May 1971.

BODY WEIGHTS DURING THE BREEDING SEASON

Body weights in adult Ancient Murrelets change during the breeding season (fig. 4). The adults arrive on the breeding grounds at slightly below their maximum summer weight. A 5% increase in weight during egg-laying (late April to mid-May) is followed by a loss, with the result that they leave the breeding colonies in June at about the same weight or slightly below that on arrival. A slight increase in weight occurs later in those adults still incubating in late June; they also attain a weight comparable to that upon arrival before departing to sea with their chicks.

Adult males averaged 206.3 g (R = 184.8–242.9, N = 75), adult females 205.7 g (R = 176.7–248.6, N = 79). The mean weight of 18 subadult males was 200.1 g (R = 178.4–220.3) and of 31 subadult females, 194.3 g (R = 144.4–222.5).

AGE CLASSES

Ridgway (1919), Kozlova (1957), and Dement'ev and Gladkov (1951) have described the adult plumage in summer and winter, and Bent (1919) described the downy and juvenal plumages. Plumage characters which permit recognition of yearling, two-year-old, and adult birds have not been found. Subadults (i.e., nonbreeding yearlings and two-year-

olds) have smaller bills and shorter wings than adults (table 1), differ in molt progression and in gonadal development and histology, and lack brood patches (Sealy, unpubl. data). Ancient Murrelets of all ages have dark brown irides.

By mid-May subadults begin to accompany adults to the staging areas and nesting slopes at night. At this time subadults comprise about 20% of the total population on the nesting slopes on any given night. Increasing numbers visit the colonies until the end of the first week in July, or about one month after 90% of the adults and newly hatched young have departed to sea.

The subadults' circadian pattern appears to be identical to the adults' with whom they associate. However, whether each subadult returns to the slope on successive nights is unknown. They engage in aggressive acts and vocalize on the slope, but I do not know if any breed successfully.

MOLT

When they return to their colonies in late March, all adult Ancient Murrelets have com-

TABLE 1. Body measurements of adult and subadult Ancient Murrelets from Langara Island, British Columbia.

| Character		Adults				Subadults		
		x̄ ± 2 SE	(N)	Range		x̄ ± 2 SE	(N)	Range
Flattened wing (mm)	♂♂	141.4 ± 0.87	(41)	137–146	♂♂	139.0 ± 1.86	(15)	132–144
	♀♀	142.0 ± 1.02	(34)	137–149	♀♀	138.5 ± 1.56	(20)	135–147
Culmen (mm)	♂♂	13.9 ± 0.17	(58)	12.7–15.1	♂♂	13.6 ± 0.30	(19)	12.2–15.1
	♀♀	13.5 ± 0.17	(56)	12.6–15.1	♀♀	13.5 ± 0.24	(26)	12.4–14.8
Bill height (mm)	♂♂	7.7 ± 0.10	(46)	7.0–8.5	♂♂	7.5 ± 0.14	(19)	7.1–8.1
	♀♀	7.3 ± 0.11	(42)	6.8–8.4	♀♀	7.5 ± 0.22	(26)	6.4–8.0
Tarsus (mm)	♂♂	26.4 ± 0.19	(54)	25.1–27.9	♂♂	26.6 ± 0.32	(20)	25.3–27.9
	♀♀	26.2 ± 0.20	(62)	24.6–28.0	♀♀	26.2 ± 0.30	(26)	24.7–27.8
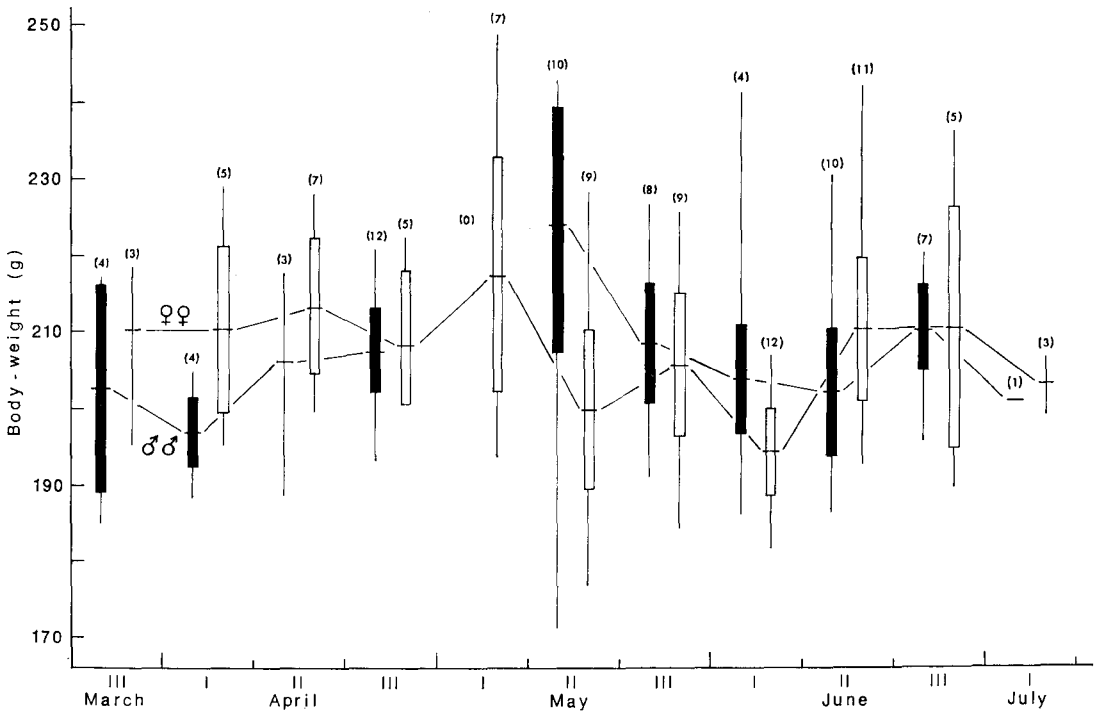
FIGURE 4. Body weights of adult male and female Ancient Murrelets taken near Langara Island, British Columbia, during the breeding seasons of 1970 and 1971. Mean weights for each 10-day period are represented by the horizontal lines; vertical lines indicate range; bars depict a distance twice the standard error on each side of the mean. Weights of egg-laying females are minus the fully shelled egg.

pleted their partial prealternate molt (Kozlova 1957). The prebasic molt has not begun in breeders when they depart to sea with their young in late May and early June.

Subadult Ancient Murrelets begin their body molt in the third week of June. Molt of the remiges has not begun when they leave the colonies in early July. One subadult female collected at sea on 8 August 1971 (the first one seen near Langara Island since 10 July) had not begun to molt its extremely worn remiges but showed active papillae on its neck, crown, and flanks.

ARRIVAL

Adult Ancient Murrelets were first observed at sea near Langara Island on 30 March and first seen on the nesting slopes on the night of 5/6 April 1971.

CIRCADIAN ACTIVITY

Ancient Murrelets are nocturnal, and all activities except incubation cease during the day. The circadian patterns exhibited in the various colonies on Langara Island are similar in aspect and timing (fig. 5).

The birds spend the day at sea feeding in flocks of 4–12 individuals and are seldom

encountered singly or in pairs (Sealy 1975a). About five hours before dark, individuals in the flocks that will return to the nesting slopes that night become "restless." The birds begin to make short flights in wide circles which gradually bring them closer to their respective staging areas. "Staging areas" are distinct areas of water near the breeding colonies where the birds assemble at predictable times in the evening before flying into the colonies and in the morning before going to sea to feed. Similar patterns of staging have been described for the Manx Shearwater (Puf-

TABLE 2. Sex ratios of Ancient Murrelets near Langara Island, British Columbia.

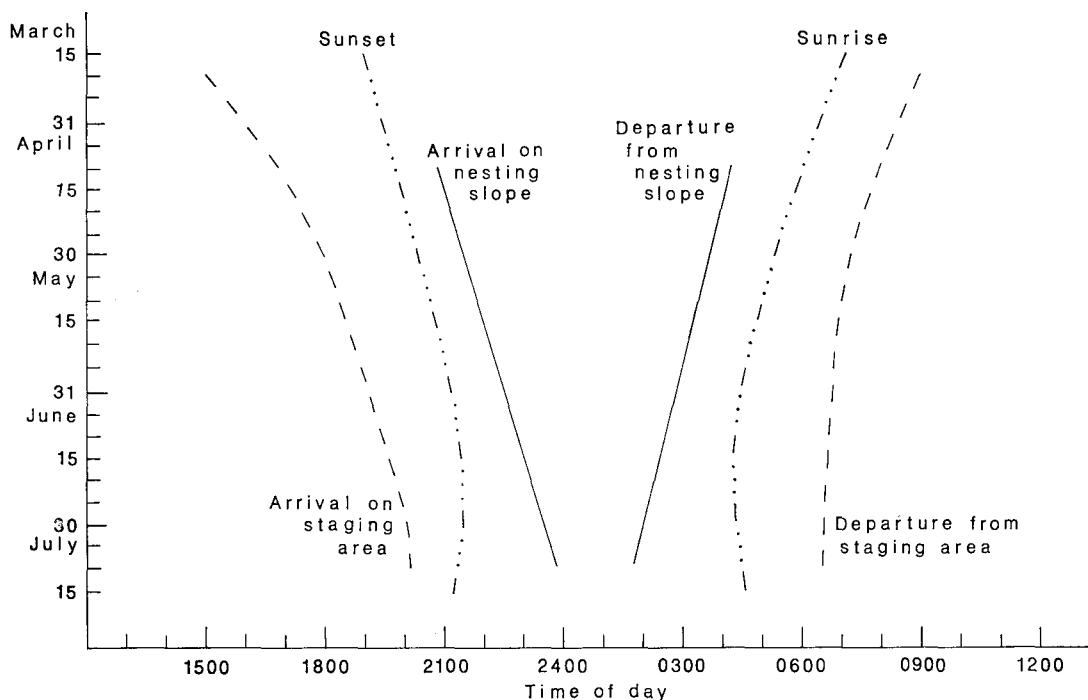|	Males	Females	Males/Females
Adults			
1970	20	22	0.91
1971	51	42	1.22
Total	71	64	1.11
Subadults			
1970	8	12	0.67
1971	17	24	0.71
Total	25	36	0.69
Juveniles			
1971	5	4	1.25

FIGURE 5. Schematic representation of seasonal changes in the time of arrival of the first Ancient Murrelets at night to and departure of the last individuals in the morning from the staging areas and nesting slopes. Sunset and sunrise times (PST) are from Royal Astronomical Society of Canada (1971).

finus puffinus; Lockley 1942), Slender-billed Shearwater (*P. tenuirostris*; Warham 1960), and Dark-rumped Petrel (*Pterodroma phaeo-pygia*; Harris 1970).

About three hours before dark, flocks of Ancient Murrelets begin to arrive on the staging areas (fig. 5). Flocks, particularly in Parry Passage adjacent to Colony A, follow remarkably precise routes. They arrive only from the east and fly westward at intervals of about 5 min along Parry Passage (fig. 1), landing on the water in the staging area. Individuals in flocks that arrive earliest spend 3–4 h on the staging area. At dark they gradually swim toward the nesting slopes and finally fly into the colony. In the morning, the flocks disperse to the feeding areas in Dixon Entrance.

Activities on the staging areas include comfort movements, apparent "play" among several individuals in the form of short flights, simultaneous diving, and chasing. Courtship apparently occurs only on the nesting slopes at night. Nocturnal observations with a flashlight and on moon-lit nights indicate that displays and vocalizations are common during the pre-laying and incubation stages. At least after incubation has begun, only one member of a given pair is on the staging area and then on only every third evening (see below). Birds do not feed on the staging areas (Sealy 1975a).

NESTING DISPERSION AND COLONY STRUCTURE

Drent (1965) pointed out that the apparently "disorderly mobs" in a seabird colony actually represent a well-organized system. Ancient Murrelets also nest in large colonies that appear to exhibit year-to-year stability. Three pairs of Ancient Murrelets banded and recaptured one year later in their same nest sites suggest that mate retention and nest site tenacity prevail. Single members of two pairs banded in 1970 used their same nests in 1971, but it was impossible to know whether their mates were the same.

TERRITORIALITY

Ancient Murrelets probably are territorial and defend the approach to their burrows. Much chasing occurred on moon-lit nights but the sex and position of the nest burrows of the initiators were not identified.

COPULATION

I did not see copulation during 300 h of observation of Ancient Murrelets on their staging areas or feeding grounds, nor do I know if copulation occurs at sea during the night. During the pre-laying stage, both members of the pair have been found in the burrows at
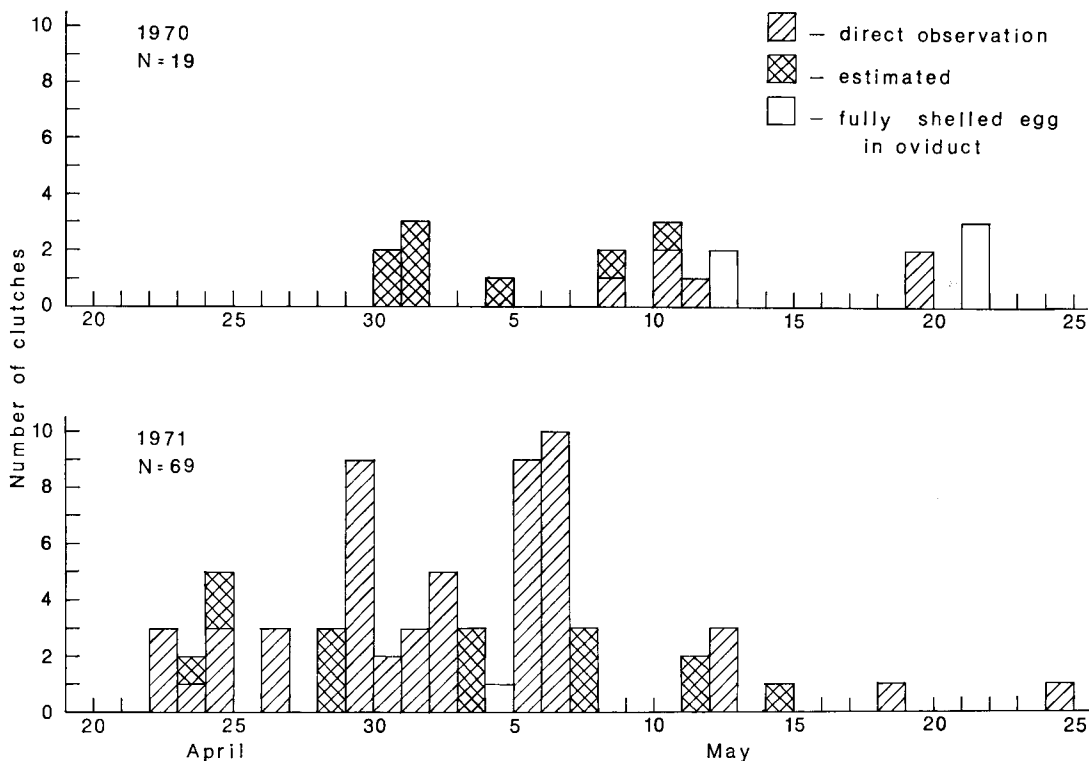
FIGURE 6.   Clutch commencement of the Ancient Murrelet on Langara Island, British Columbia, in 1970 and 1971.

night. Copulation probably occurs at this time.

Adult females producing their first egg do not visit the colony for about one week or until the egg is fully shelled in the oviduct and ready to be laid. They next appear on the slope about one week later when the second egg is laid. If copulation does occur in the burrow, then the period between insemination and egg-laying in this species is very long.

THE NEST

I examined 151 active Ancient Murrelet nests and believe that I found all existing types on Langara Island. Most of these nests were situated along the tops and slopes of bluffs, usually within 500 m of the shore. The burrows were located under fallen trees and amid roots of standing trees. Some nests were placed amid grass-covered talus slopes. In 134 nests there was an accumulation of salal leaves (*Gaultheria shallon*) and/or Western Hemlock needles in addition to a lining of grasses upon which the eggs were laid (Bendire 1895, Ishizawa 1933, Drent and Guiguet 1961). In 17 nests situated along eroded embankments, the eggs were laid on the moist earth and became stained during incubation. In 148 nests the birds incubated in total darkness.

EGG AND CLUTCH SIZE

The mean dimensions of 200 Ancient Murrelet eggs I examined were 59.4 × 37.4 mm with extremes of 65.7 × 35.3 mm, 61.3 × 39.9 mm, 54.0 × 37.8 mm, and 57.1 × 34.1 mm. These are comparable to the measurements of 51 eggs presented by Bent (1919:136).

The mean weight of 15 freshly laid eggs was 44.9 g (R = 40.4–46.2). At the time of pipping, this average for 7 eggs had dropped to 38.9 g (R = 36.1–41.4). The weight of Ancient Murrelet eggs is 21.9% of the adult body weight (Sealy 1975b).

Of 151 Ancient Murrelet nests examined, 147 had two eggs and four, one egg. An examination of reproductive tracts of 28 females taken during egg-laying revealed also that two eggs are normally laid. Sporadic observations by other workers also indicate that two-egg clutches prevail in Korea (Ishizawa 1933), Russia (Kozlova 1957), Alaska (Bendire 1895), and other colonies on the Queen Charlotte Islands (Drent and Guiguet 1961). Three additional nests found in 1971 contained more than two eggs and one in 1970, three chicks. In nest 70-36 three dead chicks and a dead adult female were found on 2 June 1970, all partly eaten by a Black Rat (*Rattus rattus*) (see Campbell 1968). It is possible that the

TABLE 3. Ancient Murrelet brood patch scores, Langara Island, British Columbia.

Period	Brood Patch Scores[a]							Mean Score
	0	1	2	3	4	5	6	
March 15–31	7	–	–	–	–	–	–	0.0
April 1–15	15	–	–	–	–	–	–	0.0
April 16–30	17	2	1	2	–	–	–	0.4
May 1–15	9	12	9	13	–	–	–	1.6
May 16–31	5	5	2	12	–	–	–	1.8
June 1–15	2	2	2	17	–	–	–	2.4
June 16–30	–	–	2	10	–	–	–	2.8
July 1–15	–	–	1	3	–	–	–	2.7

[a] Scores of adults of both sexes for 1970 and 1971 are combined; subadults are not included.

TABLE 5. Incubation periods of the Ancient Murrelet on Langara Island, British Columbia in 1970 and 1971.

Incubation Period[a]	No. Clutches
33 days	12
34 days	13
35 days	4
36 days	2
42 days	1
46 days	1
47 days	1
$\bar{x} = 34.9$ days	Total = 34

[a] Computations utilize data from the 19 completed clutches in table 7 and 15 clutches where the laying-hatching intervals were known only for egg B.

third chick inadvertantly entered this nest or was chased into the nest by the rat and killed there along with the resident adult and two chicks. Based on egg size and color pattern the three clutches of more than two eggs appeared to be the work of two females.

Clutch commencement dates for the Ancient Murrelet on Langara Island are presented in fig. 6. Early dates for 1970 are lacking. Few egg-laying dates for the species are available in the literature. Most reports are for eggs whose stage of incubation is unknown. Drent and Guiguet (1961:93–97) summarized the observations from the Queen Charlotte Islands, indicating that egg-laying occurs from about the end of April through May. However, Beebe (1960:169) stated that "were it not for a considerable spread in the time of egg laying, the birds would be ashore for a very brief time indeed. However, nesting is known to extend from May until mid-July, with downy young coming down to sea every night from about the first of June onward." My observations indicate an even shorter period of egg-laying. As pointed out earlier, observations in the three colonies showed that by mid-June 90% of the adults had departed to sea with their chicks. Those individuals which remained in the vicinity of Langara Island until mid-July and visited the nesting slopes at night were subadults. Beebe may have seen

subadults and concluded that they were incubating birds.

All Ancient Murrelet eggs on Langara Island were laid during darkness between 22:00 h and 02:00 h.

In 19 clutches an average of seven days elapsed between the laying of the two eggs (six days, 2; seven days, 11; eight days, 5; based on daily checks). This agrees with observations of Ancient Murrelets in Korea. Ishizawa (1933) found laying intervals of 2–12 days with an average of slightly less than six days. I have an additional 11 records of at least 6–9 days elapsing between the laying of the two eggs when the precise date of laying of egg A was unknown.

Examination of nine ovaries showed that when egg A is fully shelled in the oviduct, egg B has a mean diameter of 14.3 mm.

REPLACEMENT OF LOST EGGS

I have no evidence of re-laying in the Ancient Murrelet. Renesting did not occur, at least in the same burrows, in four nests where the clutches were destroyed early in incubation. Also, the abrupt departure of 90% of the breeding population by 15 June leaves mostly subadults in the colonies at night. If renesting occurred regularly, those adults who renested would be observed on the staging areas and colonies at night at later dates.

TABLE 4. Brood patch scores of adult Ancient Murrelets during the breeding cycle on Langara Island, British Columbia in 1970 and 1971.

Period of Breeding Cycle	Brood Patch Scores							Mean Score
	0	1	2	3	4	5	6	
♂ ♂ and ♀ ♀ at first arriving on nesting slopes	9	–	–	–	–	–	–	0.0
♀ ♀: egg A fully shelled in oviduct	–	4	–	–	–	–	–	1.0
♀ ♀: egg B fully shelled in oviduct	–	–	3	1	–	–	–	2.3
♂ ♂ and ♀ ♀ brooding young[a]	–	–	–	15	–	–	–	3.0

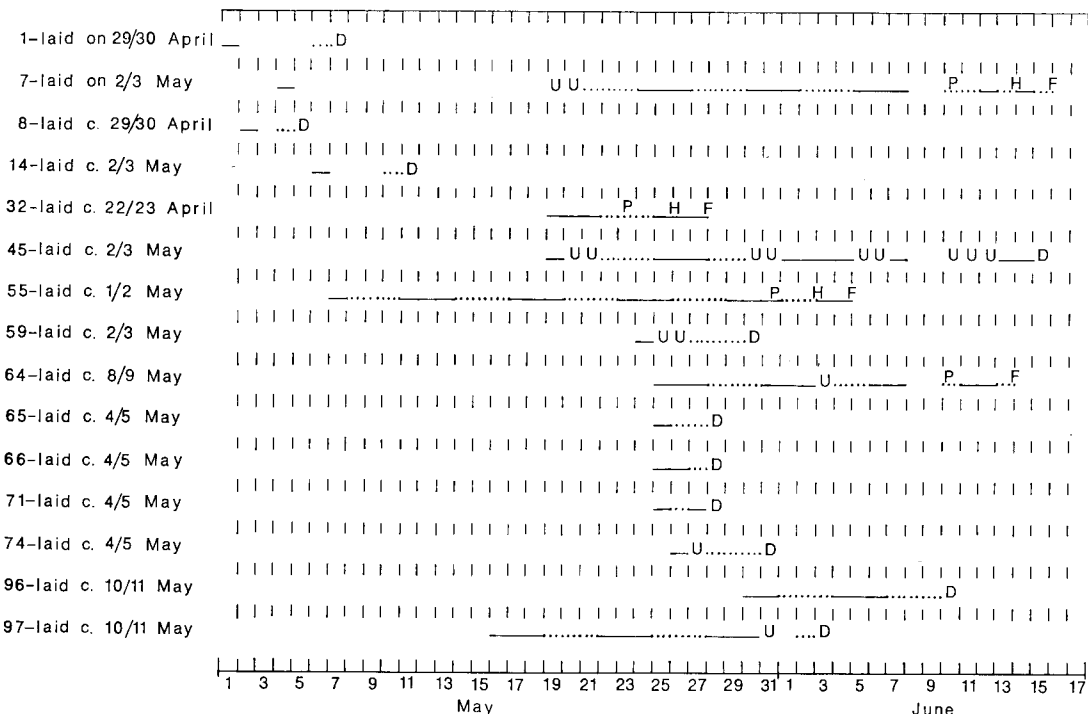[a] Birds removed from nest burrows and examined.

FIGURE 7. Incubation shifts at 15 Ancient Murrelet nests on Langara Island, British Columbia, in May and June, 1971. A solid line on the time axis represents an observation of the banded member of the pair, the dotted line the unbanded member. "U" = eggs unattended; blank space = nest not visited; "D" = nest deserted after being unattended for at least 5 days. The laying date for each nest is indicated on the left of the diagram. "P" = onset of pipping; "H" = hatching; "F" = fledging.

BROOD PATCHES

During the breeding season, adult male and female Ancient Murrelets develop a pair of lateral brood patches. These bare patches have loose and vascularized skin. The average dimensions of the fully developed patches (class 3) are 23.7 mm by 19.8 mm (N = 10). Stages in brood patch development are summarized in tables 3 and 4. Little or no re-feathering occurs during the late stages of incubation or up to the time the newly hatched chicks depart to sea.

INCUBATION

My observations indicate that egg A is not incubated before egg B is laid. The completed clutch is left unattended for an additional period of up to several days but most commonly one day. When one adult returns (it is not known which sex begins incubating), incubation persists until the eggs hatch about 35 days later (table 5).

Normally the eggs hatch within about one hour of each other (N = 61 nests). Only in nest no. 71-84 was there some disparity in hatching times. At 14:35 on 30 May, one chick had hatched just recently and was still wet; the second chick hatched about 6–8 hours later

and was dry by 22:00. Egg A hatches on the average 42.1 days after laying, egg B 34.9 days (table 6). Ishizawa (1933) found that the incubation periods averaged 32 days in Korea. Hatching is a prolonged procedure; typically, the first cracks appear one day, a definite hole two days later, and a freshly hatched chick the fourth day (29 of 34 cases in which the entire hatching procedure was observed daily).

TABLE 6. Laying-hatching intervals in 19 Ancient Murrelet clutches on Langara Island, British Columbia in 1970 and 1071.

Interval (days)	Number of Eggs	
	Egg A	Egg B
33		8
34		7
35		1
36		1
39	2	
40	5	
41	6	
42	3	1
44	1	
47		1
50	1	
55	1	
Mean	42.1 days	34.8 days

TABLE 7. Weight recession in young Ancient Murrelets in the nest.

Age (days)	No.	Weight (g) Mean	Weight (g) Range
0	26	30.7	26.2–37.5
1	14	27.7	23.2–32.7
2	3	26.1	24.2–28.7
3	1	22.2	—

Incubation is shared equally by both sexes in the Ancient Murrelet. The duration of each incubation shift is invariably 72 h, change-over taking place at night (fig. 7). From 28 May to 1 June 1952, C. J. Guiguet (1953b, pers. comm.) checked marked birds daily in 12 burrows on Langara Island. In one nest the birds alternated nightly, and in a second nest the same bird was present for three consecutive days. In the remaining nests the parents deserted at some stage, but the available data suggested to Guiguet that the usual shift was 48 h. I found that in some nests (nos. 7, 55, 64 in fig. 7) the incubation rhythm changed during hatching. As Guiguet's observations were made during the peak hatching period, he may have observed the nightly shifts in one nest where hatching was occurring. His one record of a 72-h shift agrees with my observations, but the desertions in the 10 other nests and the short period of his observations, although pointing to 48-h shifts, do not rule out the possibility of 72-h shifts in his nests. Once incubation had begun, I never found both parents together in the nest burrows during the day.

CHICK STAGE

Ancient Murrelet chicks are truly precocial; they are well developed and covered with down at hatching, and soon depart for sea. The age at departure has been estimated variously as the night after hatching (Beebe 1960, Guiguet in Drent and Guiguet 1961), one to two days (Heath 1915), two to three days (Storer in Thomson 1964), and four days
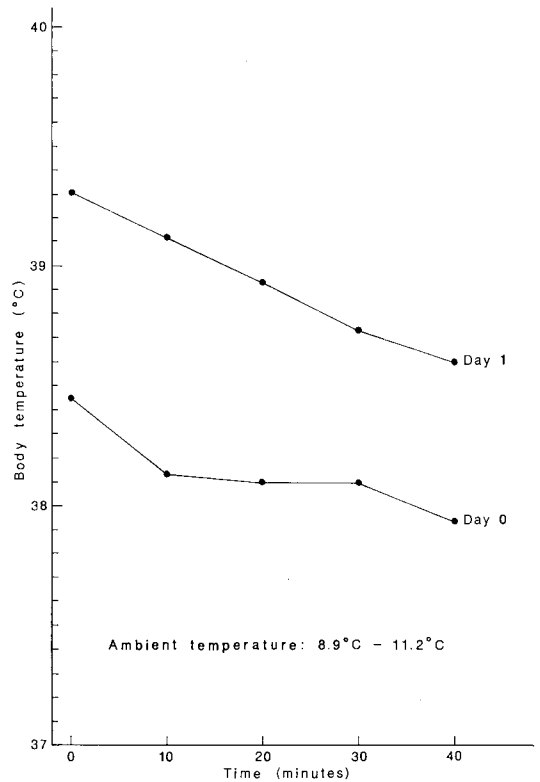

FIGURE 8. Responses of 11 newly hatched Ancient Murrelets at ages 0 and 1 day to ambient temperatures in May and June, 1971, on Langara Island, British Columbia.

after hatching (Willett 1915). Ishizawa (1933) stated that in Korea, the chicks are "warmed for one or two days, leave the islet by night."

Most chicks hatched during the night and spent an average of 2.2 days in the nest before departing to sea at night. Twenty-one chicks spent 2 days and two spent 2.5 days in the nest. The three chicks and one chick that, respectively, spent three- and four-day periods in the nest hatched simultaneously but around 12:00.

The chicks are brooded continuously while in the nest, usually by the same adult, but occasionally the parents alternate shifts (fig.

TABLE 8. Body weights and measurements of newly hatched (day 0) and juvenile Ancient Murrelets compared to those of adults.

Character[a]	Newly hatched $\bar{x} \pm 2$ SE	(N)	%[b] of adult	Juveniles[c] $\bar{x} \pm 2$ SE	(N)	%[b] of adult
Body weight (g)	30.7 ± 0.29	(26)	15.0	208.0 ± 7.73	(8)	101.5
Culmen (mm)	6.8 ± 0.10	(42)	49.7	11.9 ± 0.44	(8)	86.7
Bill height (mm)	—		—	6.4 ± 0.02	(8)	85.3
Tarsus (mm)	24.6 ± 0.20	(41)	93.5	26.4 ± 0.32	(8)	100.1
Flattened wing (mm)	—		—	127.0 ± 3.69	(8)	84.6

[a] Weights and measurements for 1970, 1971 combined.
[b] Data for adults from table 1 and body weight section.
[c] About six weeks old.

TABLE 9. Dates of departure of newly hatched Ancient Murrelets from Forrester Island, Alaska, and Langara and Lucy Islands, British Columbia.

Island	Date	Source
Forrester	29 May–1 July 1913	Heath (1915)
Forrester	23 May–2 July 1914	Willett (1915)
Lucy	5 July 1930	Cumming (1931)
Lucy	4 June 1960	Drent and Guiguet (1961)
Langara	6, 14 June 1946	Drent and Guiguet (1961)
Langara	26 May 1947	Drent and Guiguet (1961)
Langara	27 May 1952	Drent and Guiguet (1961)
Langara	5 June 1960	Drent and Guiguet (1961)
Langara	27/28 May–2/3 July 1970	This study
Langara	26/27 May–6/7 July 1971	This study

7). The chicks are not fed by the parents while in the nest. Stomachs of seven nestlings dissected were empty, and chicks exhibit significant weight-loss while in the nest (table 7). Adult Ancient Murrelets do not develop a neck pouch for carrying food during the chick-rearing season.

INCUBATION TEMPERATURES AND THERMOREGULATION

Brood patch and body temperatures of four incubating adult Ancient Murrelets were 34.9°C and 39.7°C, respectively.

Upon departing for sea at an age of two days, chicks have nearly attained the mean adult body temperature and essentially are able to maintain it when exposed to low ambient temperatures (fig. 8). However, chicks are brooded continuously in the nest and, therefore, are not exposed to the lower ambient temperatures until they actually leave the nest.

FLEDGING

Newly hatched young of Ancient Murrelets are adapted for their early departure to sea (table 8). Their tarsi are nearly the same size as the adults'. Such advanced development of the tarsi and feet enables the young to swim long distances with the adults to the feeding areas immediately after leaving the nesting slopes and to dive using their feet.

Although most observations of Ancient Murrelet Chicks leaving the nesting colonies (table 9) do not indicate the beginning or end of the departure period, it is interesting to note that in 1947, 1952, 1970 and 1971 on Langara Island

the first chicks were observed leaving the colonies on 26 or 27 May. The last chicks from two nests in 1970 and three in 1971 departed during the first few days in July. The observations from Forrester Island indicate a similar timing and span of breeding there. The chicks' departure to sea, which normally occurs at night, has been described by several authors (Heath 1915, Willett 1915, 1920, Guiguet 1953b, 1971, Beebe 1960).

On three nights during the chick stage in 1970 and six in 1971, downy young began to scramble to sea about 30–45 min before the first adults arrived on the slopes about 23:00 (fig. 5). The last chicks had left by about 01:00.

Although darkness made it impossible to observe young and adults on the water for long periods or to follow them out to sea by boat, on several occasions I saw unaccompanied chicks, alone or in groups of up to 10, and also adults with young at the base of the slope. Farther from shore (about 200 m) one adult with two young was encountered six times, and one adult with only one young once. As Willett (1915) noted, at dawn adults with young were not found within 10 km of shore.

That downy young Ancient Murrelets depart to sea accompanied by their presumed parents has been noted by several workers (Heath 1915, Willett 1915, Ishizawa 1933, Guiguet 1953a, 1971, Martin and Myres 1969). In Egeria Bay on the east side of Langara Island, I saw an adult with two flightless young on 18 July 1971, about one month after most of the adults and young left the nesting colonies. This adult (parent?) acted agitated when approached closely by the boat and frequently flew some 30 m repeatedly uttering a rasping call. The young dived at the approach of the boat, but when they surfaced, they soon were joined by the adult.

PREDATION

The major predator of the Ancient Murrelet on Langara Island is the Peregrine Falcon (*Falco peregrinus*). Studies on the Island (Beebe 1960, Nelson 1970) have shown that this raptor concentrates on adult Ancient Murrelets at least during the breeding season. Although other potential prey species with similar body-sizes occur in the area, for example, Leach's Petrel (*Oceanodroma leucorhoa*), Fork-tailed Petrel (*O. furcata*), Cassin's Auklet (*Ptychoramphus aleuticus*), and Marbled Murrelet (*Brachyramphus marmoratus*), they are seldom taken by Peregrines (Beebe 1960). Ancient Murrelets return to

the nesting slopes only at night; Peregrines apparently time their major hunting activities to correspond with these incoming flights at night and outgoing flights just before dawn (Beebe 1960, Nelson 1970).

The only mammalian predator of major importance to the Ancient Murrelet on Langara Island is the introduced Black Rat which is "in pure stock on Langara Island" (Cowan and Guiguet 1961). Campbell (1968) observed several instances of rat predation upon freshly laid but unattended Ancient Murrelet eggs. Out of 114 nests I examined in 1971, only two (both in Colony B) were destroyed by rats during incubation. No evidence indicating that newly hatched young were killed by rats was obtained in 1971; however, in 1970, one adult and three chicks (all partially eaten) were found in one burrow in Colony B, and three partially eaten chicks were found in different burrows in Colony A. During the egg-laying period in 1971, seven adults were found dead in Colonies A and C; three had been eaten only on the head and neck while only the skin and skeletons of the others remained. Only the Dusky Shrew (*Sorex vagrans*) and River Otter (*Lutra canadensis*) occur naturally on Langara Island, but there is no evidence that either preys on murrelets.

By leaving the nesting slopes at night, Ancient Murrelet chicks avoid potential predation by the largely diurnal gulls and Northwestern Crows (*Corvus caurinus*).

DISCUSSION

An aspect of obvious interest in the biology of the Ancient Murrelet is its precocial mode of post-hatching development. Murres (*Uria* spp.) and Razorbills (*Alca torda*) have been considered precocial alcids (Cody 1973, Scott 1973) because they leave their nests at only about 20% adult weight (Sealy 1973). However, it is only in the murrelet genera *Synthliboramphus* and *Endomychura* that we find precocity similar to that in waterfowl. Young Ancient Murrelets, Japanese Murrelets (*S. wumizusume*), Craveri's Murrelets (*Endomychura craveri*), and Xantus' Murrelets (*E. hypoleuca*) leave their nests a few days after hatching in their downy plumage and move out to sea (Deweese and Anderson, unpubl. data). Let us examine the adaptations of the truly precocial murrelets and compare them to other seabirds, none of which has evolved this breeding strategy.

Concomitant with the necessarily advanced state of development at hatching in precocial young (Kear 1965, Märcstrom 1966, Sealy 1975b), murrelets lay extremely large eggs. Each takes at least a week to form in the Ancient Murrelet.

I have suggested (Sealy 1975a) that the incubation shift of 72 h for the Ancient Murrelet, the longest known in the Alcidae, did not evolve to permit the "off-duty" adults to forage long distances from the colonies but rather to provide them with time to locate their patchily distributed planktonic prey. Ashmole and Ashmole (1967) pointed out that in some Procellariiformes long incubation shifts indicate that abundant food is not available close to the nest, as short flights are uneconomical if the time required to fly to and from the feeding areas is long. Therefore shifts lasting several days in many temperate zone petrels (Lack 1968) and the majority of tropical seabirds (Ashmole 1971) occur when the birds must travel great distances to feed. Moreover, selection for such long shifts will be strong, even if feeding grounds are nearby, if the food is patchy in distribution or sometimes even unavailable (e.g., during a storm).

However, it is interesting that in those seabirds with long incubation shifts, long periods also occur between each parent's successive feeding of the chick. In these species, rather than the young being precocious, the incubation and fledging periods in the nest are prolonged. Instead of taking their chicks to the food supply, individuals of these species fly up to several hundred kilometers to and from their feeding areas.

Lack (1968:266) suggested that the nests of precocial alcids, including *Uria* and *Alca*, are far from rich feeding areas, in part because feeding birds reduce food resources around the colonies. Hence it is energetically more efficient for the parents to take the young to the foraging areas than to commute between feeding areas and the colony. On the other hand, ecological segregation in feeding among various seabirds (including alcids) during the breeding season is achieved by the use of prey of different taxa or size (Swartz 1966, Bédard 1969, Sealy 1975a) at different distances from the colony (Ashmole and Ashmole 1967, Pearson 1968, Cody 1973, Sealy 1975a). However, Pearson (1968) found that most of the seabirds which breed on the Farne Islands disperse widely during winter. He suggested that competition between any of the species during that time would be minimal because the areas covered and their potential food resources are great in relation to the number of birds exploiting them. Thus, by dispersing away from the colonies with newly hatched young, Ancient Murrelets also probably reduce poten-

tial competition for food during the breeding season.

Scott (1973:83) discussed precocity in murres. He noted that (1) precocity makes practical, on an energetic balance basis, the procurement of smaller energy packages for the young and more frequent feedings, (2) the pair can go to areas beyond the effective foraging range of the adult when the chick is confined to the colony, (3) precocity permits the reduction of population density in a given area, and (4) the chick can learn to forage while still dependent upon the adult for food.

Cody (1973) presented a model of breeding strategies in alcids. He suggested that inshore feeders evolved precocial young to reduce energetic expenditures of foraging adults as well as intra- and interspecific competition for food near the colony. Cody's discussion is confusing in that, of the species discussed, only the Pigeon Guillemot (*Cepphus columba*), Marbled Murrelet, and to a lesser extent, the Common Murre (*Uria aalge*), are inshore feeders. Only the last-named has precocial young (Sealy 1973). Cody essentially ignored the truly precocial murrelets although he incorrectly included the Ancient Murrelet with the inshore-feeding alcids. Earlier, Cody (1971) explained the advantages of precocity in alcids on the basis of the relative safety of the nest sites, the murres leaving their exposed cliff ledges within 20 days after hatching. He again ignored the precocial murrelets which nest in concealed crevices or burrows.

SUMMARY

The breeding biology of Ancient Murrelets was studied on and near Langara Island, Queen Charlotte Islands, British Columbia.

Adults and subadults are not sexually dimorphic in size or plumage characters, sex ratios approach equality, and mate retention and nest site tenacity prevail. Two age categories, adult and subadult, were identifiable.

The partial prealternate molt and prebasic molt do not overlap breeding. Adults return to the vicinity of Langara Island in mid-March and begin to visit the colonies in early April. The birds are nocturnal on the nesting slopes. Two-egg clutches are usual, with each egg weighing about 22% of the adult weight. The eggs are laid about 7 days apart. Incubation shifts are 72 h over the 35-day incubation period. The young are truly precocial and leave the nest burrows 2 days after hatching.

The major predator on adult Ancient Murrelets on Langara Island is the Peregrine Falcon. Predation on adults, eggs, and young by the introduced Black Rat is considered to be negligible in the colonies where and when observations were made.

The adaptive significance of precocity in alcids is discussed.

LITERATURE CITED

ASHMOLE, N. P. 1971. Sea bird ecology and the marine environment. pp. 223–286. *In* D. S. Farner, J. R. King, and K. C. Parkes, (eds.) Avian Biology, Vol. 1. Academic Press, New York.

ASHMOLE, N. P., AND M. J. ASHMOLE. 1967. Comparative feeding ecology of sea birds of a tropical oceanic island. Peabody Mus. Nat. Hist. Yale Univ. Bull. 24:1–131.

BÉDARD, J. 1969. Feeding of the least, crested, and parakeet auklets around St. Lawrence Island, Alaska. Can. J. Zool. 47:1025–1050.

BEEBE, F. L. 1960. The marine peregrines of the northwest Pacific coast. Condor 62:145–189.

BENDIRE, C. 1895. Notes on the ancient murrelet (*Synthliboramphus antiquus*), by Chase Littlejohn. With annotations. Auk 12:270–278.

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

BROWN, A. S. 1968. Geology of the Queen Charlotte Islands, British Columbia. B. C. Dep. Mines Petrol. Res. Bull. 54.

CALDER, J. A., AND R. L. TAYLOR. 1968. Flora of the Queen Charlotte Islands, Part I. Systematics of the vascular plants. Can. Dep. Agric. Mongr. 4.

CAMPBELL, R. W. 1968. Alexandrian rat predation on ancient murrelet eggs. Murrelet 49:38.

CODY, M. L. 1971. Ecological aspects of reproduction. pp. 461–512. *In* D. S. Farner, J. R. King, and K. C. Parkes, (eds.) Avian Biology, Vol. 1. Academic Press, New York.

CODY, M. L. 1973. Coexistence, coevolution, and convergent evolution in seabird communities. Ecology 54:31–44.

COWAN, I. McT., AND C. J. GUIGUET. 1961. The mammals of British Columbia. B. C. Prov. Mus. Nat. Hist. Anthropol. Handb. 11.

CREAN, P. B. 1967. Physical oceanography of Dixon Entrance, British Columbia. Fish. Res. Board Can. Bull. 156.

CUMMING, R. A. 1931. Some birds observed in the Queen Charlotte Islands. Murrelet 12:15–17.

DEMENT'EV, G. P., AND N. A. GLADKOV. 1951. Birds of the Soviet Union, Vol. 2. (Transl. by IPST, Jerusalem, 1968.)

DRENT, R. H. 1965. Breeding biology of the pigeon guillemot, Cepphus columba. Ardea 53:99–160.

DRENT, R. H., AND C. J. GUIGUET. 1961. A catalogue of British Columbia sea-bird colonies. Occas. Pap. B. C. Prov. Mus. 12.

FLEMING, R. H. 1955. Review of the oceanography of the northern Pacific. Int. N. Pac. Fish. Comm. Bull. 2.

FOSTER, J. B. 1965. The evolution of the mammals of the Queen Charlotte Islands, British Columbia. Occas. Pap. B. C. Prov. Mus. 14.

GABRIELSON, I. N., AND F. C. LINCOLN. 1959. Birds of Alaska. Stackpole Co., Harrisburg, Pennsylvania, and Wildl. Manage. Inst., Washington, D. C.

GRINNELL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. Pacific Coast Avifauna 27:1–608.

GUIGUET, C. J. 1953a. An ecological study of Goose Island, British Columbia, with special reference to mammals and birds. Occas. Pap. B. C. Prov. Mus. 10.

GUIGUET, C. J. 1953b. The ancient murrelet. Victoria Nat. 10:68–70.

GUIGUET, C. J. 1971. The birds of British Columbia. 9) Diving birds and tube-nosed swimmers. B. C. Prov. Mus. Nat. Hist. Anthropol. Handb. 29.

HARRIS, M. P. 1970. The biology of an endangered species, the dark-rumped petrel (Pterodroma phaeopygia), in the Galapagos Islands. Condor 72:76–84.

HATLER, D. F., R. W. CAMPBELL, AND A. DORST. 1973. Birds of the Pacific Rim National Park, British Columbia. Can. Wildl. Service.

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

HOLLAND, S. S. 1964. Landforms of British Columbia: a physiographic outline. B. C. Dep. Mines Petrol. Res. Bull. 48.

ISHIZAWA, T. 1933. Life history of Synthliboramphus antiquus. Plants and Animals, Tokyo 1:279–280.

KEAR, J. 1965. The internal food reserves of hatching mallard ducklings. J. Wildl. Manag. 29:523–528.

KOZLOVA, E. V. 1957 Charadriiformes, suborder Alcae. Fauna of USSR: Birds 2:1–140. (Transl. by IPST, Jerusalem, 1961.)

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

LOCKLEY, R. M. 1942. Shearwaters. J. M. Dent and Sons, London.

MÄRCSTROM, V. 1966. Mallard ducklings (Anas platyrhynchos L.) during the first days after hatching. Viltrevy 4:343–370.

MARTIN, P. W., AND M. T. MYRES. 1969. Observations on the distribution and migration of some seabirds off the outer coasts of British Columbia and Washington State, 1946–1949. Syesis 2:241–256.

MUNYER, E. A. 1965. Inland wanderings of the ancient murrelet. Wilson Bull. 77:235–242.

MURATA, E. 1958. The breeding of the ancient auk, Synthliboramphus antiquus (Gmelin) on the Island of Teuri, Hokkaido. Tori Bull. Ornithol. Soc. Jpn. 14:22–26.

NELSON, R. W. 1970. Some aspects of the breeding behaviour of peregrine falcons on Langara Island, B. C. M.Sc. Thesis, Univ. Calgary.

PEARSON, T. H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521–552.

RIDGWAY, R. 1919. The birds of North and Middle America. Part VIII. U. S. Natl. Mus. Bull. 50.

ROYAL ASTRONOMICAL SOCIETY OF CANADA. 1971. The observer's handbook. Toronto.

SCHOFIELD, W. B. 1968. A selectively annotated checklist of British Columbia mosses. Syesis 1:163–175.

SCOTT, J. M. 1973. Resource allocation in four syntopic species of marine diving birds. Ph.D. Diss. Oregon State Univ., Corvallis.

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.

SEALY, S. G. 1972. Adaptive differences in breeding biology in the marine bird family Alcidae. Ph.D. Diss. Univ. Michigan, Ann Arbor.

SEALY, S. G. 1973. Adaptive significance of post-hatching developmental patterns in the Alcidae. Ornis Scand. 4:113–121.

SEALY, S. G. 1974. Breeding phenology and clutch size in the marbled murrelet. Auk 91:10–23.

SEALY, S. G. 1975a. Feeding ecology of the ancient and marbled murrelets near Langara Island, British Columbia. Can. J. Zool. 53:418–433.

SEALY, S. G. 1975b. Egg size of murrelets. Condor 77:500–501.

SWARTZ, L. G. 1966. Sea-cliff birds. pp. 611–678. In N. J. Wilimovsky, and J. N. Wolfe (eds.) Environment of the Cape Thompson region, Alaska. U.S.A.E.C., Div. Tech. Inf., Washington, D. C.

THOMSON, A. L. (ed.) 1964. A new dictionary of birds. McGraw-Hill, New York.

UDVARDY, M. D. F. 1963. Zoogeographical study of the Pacific Alcidae. pp. 85–111. In J. L. Gressitt (ed.) Pacific basin biogeography. Bishop Museum Press, Honolulu.

VERBEEK, N. A. M. 1966. Wanderings of the ancient murrelet: some additional comments. Condor 68:510–511.

WARHAM, J. 1960. Some aspects of breeding behaviour in the short-tailed shearwater. Emu 60:75–87.

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

WILLETT, G. 1920. Additional notes on the avifauna of Forrester Island, Alaska. Condor 22:138–139.

Department of Zoology, University of Manitoba, Winnipeg, Manitoba R3T 2N2. Accepted for publication 27 May 1975.