ASPECTS OF THE BREEDING BIOLOGY OF THE MARBLED MURRELET IN BRITISH COLUMBIA

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INTRODUCTION

Although the Marbled Murrelet (Brachyramphus marmoratus) is an abundant marine bird along the Pacific Coast of North America from northern California to the Aleutian Islands (Guiguet, 1956; Gabrielson and Lincoln, 1959; Drent and Guiguet, 1961), its nest has only recently been found on this continent (L. C. Binford, pers. comm.). However, the population of Marbled Murrelets in the vicinity of Langara Island, Queen Charlotte Islands, British Columbia (Fig. 1), has received considerable attention, albeit superficial, since the 1920's by workers who have searched for its nest there (Drent and Guiguet, 1961). During 1970 and 1971, I collected Marbled Murrelets near Langara Island for food habits analysis (Sealy, 1972, 1975a) and from an examination of reproductive tracts, particularly of females, and observations of birds at sea, ascertained its clutch size and breeding phenology (Sealy, 1974).

In the present paper, additional aspects of its biology are examined and, where pertinent, are compared to the biology of other alcid species. The terrestrial and marine environments of the Langara Island area have been described elsewhere (Sealy, 1972, 1974, 1975a, Ms). Details of collecting trips, handling of specimens, and observations at sea have been summarized by Sealy (1974, 1975a). Field work on Langara Island was conducted from 6 May to 10 July 1970 and 17 March to 12 August 1971.

DISTRIBUTION

The Marbled Murrelet has a disjunct breeding distribution which shows a gap bracing the Aleutian chain with subspecific differences on the two sides of this gap—B. m. marmoratus of the Northeastern Pacific coast, the race studied here, and B. m. perdix of the Northwestern Pacific coast (Dement'ev and Gladkov, 1951; Udvardy, 1963). The form perdix apparently breeds along the coast of the Kamchatka Peninsula (Kozlova, 1957) where one nest was recently found (Kuzyakin, 1963). Recent observations of Marbled Murrelets during the summer along the Aleutian chain (Bartonek and Gibson, 1972; Byrd, Gibson, and Johnson, 1974) reveal the need for close scrutiny for possible interbreeding between races.

The Marbled Murrelet is a regular and abundant summer resident along the northeast Pacific coast from northern California (Grinnell and Miller, 1944), Oregon (Gabrielson and Jewett, 1940), Washington State (Jewett et al., 1953), British Columbia (Drent and Guiguet, 1961) and southeastern Alaska (Gabrielson and Lincoln, 1959). Evidence for its breeding in these areas comes primarily from adults collected during the breeding season, the discovery of flightless young, and observations of young recently

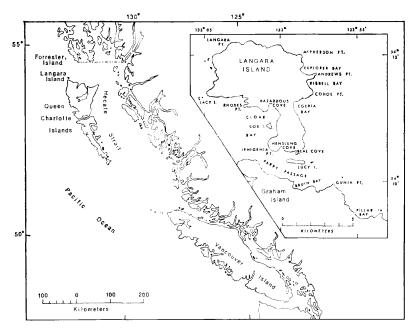


Figure 1. Map of the British Columbia coast. Inset shows Langara Island and portion of the northern shore of Graham Island where observations of Marbled Murrelets were made.

arrived at sea (Drent and Guiguet, 1961; Harris, 1971; Sealy, 1974). This species has been taken as a straggler in the Bering Sea near St. Paul and St. Lawrence islands (Hanna, 1920; Bédard, 1966). In the Glacier Bay region, Alaska, the Marbled Murrelet is sympatric with the congeneric Kittlitz's Murrelet (B. brevirostris) (Gabrielson and Lincoln, 1959).

Little evidence exists for any migratory movements of the Marbled Murrelet, "the birds being permanent residents of the territory occupied" (Gabrielson and Lincoln, 1959: 489). However, Marbled Murrelets in winter plumage have been observed and taken in southern California, south of the usual breeding season distribution (Grinnell and Miller, 1944). In the present study, Marbled Murrelets were absent from the vicinity of Langara Island during late winter and early spring but returned in late April.

SEX RATIOS AND SEXUAL DIMORPHISM

Sex ratios of the Marbled Murrelet are presented in Table 1; a balanced sex ratio in all age classes is evident.

In 1970, Marbled Murrelets were collected non-selectively; however, in 1971, pairs were taken at sea where possible and, therefore, there probably is a slight bias toward a balanced sex ratio. Subadults, on the other hand, were collected either as single individuals or from mixed flocks of adults and subadults.

Table 1
Sex ratios of the Marbled Murrelet near Langura Island, British Columbia.

	Males	Females	Males/Females
Adults			
1970	9	12	0.75
1971	28	24	1.16
Both years	37	36	1.03
Subadults			
1970	4	4	1.00
1971	3	4	0.75
Both years	7	8	0.88
Juveniles			
1971	4	5	0.80

Sexual dimorphism in plumage (Bent, 1919; Ridgway, 1919; Kozlova, 1957) is not pronounced in the Marbled Murrelet and birds could not be sexed before dissection. Although the males have slightly larger mean dimensions (Table 2) for all characters measured, these differences are not significant (P > 0.05 in all cases). However, measurements of individuals taken as pairs show the females being slightly larger in about 50% of the cases (Table 3).

BODY WEIGHTS DURING THE BREEDING SEASON

The mean weight of 37 adult males was 217.0 g (range 196.2 — 252.5 g), that of 37 adult females 222.7 g (range 188.1 — 269.1 g), and a combined weight (including egg-laying females) 222.6 g. The mean weight of 5 subadult males was 222.9 g (range 207.1 — 237.1 g) and of 8 subadult females 218.6 g (range 199.6 — 242.9 g).

Changes in adult body weights during the breeding season are illustrated in Figure 2. Adult male and female Marbled Murrelets undergo a rapid increase in body weight soon after their return to the vicinity of Langara Island in late April. This increase is followed by a gradual weight-loss throughout the breeding season to that weight shown upon their return. The Marbled Murrelet is similar to the Ancient Murrelet (Synthliboramphus antiquus) in that neither species arrives at its breeding area in spring at maximum body weight (see also Sealy, 1972, Ms). This is in contrast to the seasonal patterns of body weight of particularly the Arctic-nesting alcids. Bédard (1967) demonstrated that plankton-feeding auklets return to their breeding grounds in the Bering Sea at maximum weight, but in the case of the Least Auklet (Aethia pusilla) and Crested Auklet (A. cristatella) have lost 10-15% of this weight by the end of their breeding season. The Parakeet Auklet (Cyclorrhynchus psittacula), on the other hand, loses only

TABLE 2.

Measurements o	f adult	and subadult Ma	rbled Murrelets	Measurements of adult and subadult Marbled Murrelets collected near Langara Island, British Columbia in 1970 and 1971.	gara Islan	d, British Columb	ia in 1970 and	1971.
			Adults			Sub	Subadults	
Character		$\bar{\mathbf{x}} \pm 2 \text{ SE (n)}$		Range		х ± 2 SE (n)		Range
Flattened wing (mm)	Б О Ф	134.2 ± 1.2 132.6 ± 1.8	(25) (23)	128 - 140 122 - 139	₽	$\vec{\sigma} \vec{\sigma}$ 127.8 ± 5.1 (5) $\varphi \varphi$ 123.2 ± 3.4 (5)		121 - 135 120 - 129
Exposed culmen (mm)	<i>р</i> о+	15.5 ± 0.3 15.3 ± 0.4	(36) (32)	13.2 - 17.4 13.7 - 17.6	6 0 ↔	$15.4 \pm 0.4 (6)$ $15.0 \pm 0.7 (8)$		14.8 - 16.3 13.6 - 15.9
Bill height (mm)	F O O+	6.0 ± 0.1 (2 5.8 ± 0.1 (2	(26) (23)	5.4 - 6.6 5.3 - 6.8	F O O+	6.2 ± 0.4 (6) 6.0 ± 0.4 (8)		5.8 - 7.0
Tarsus (mm)	φ'ς φ φ	$16.2 \pm 0.2 15.9 \pm 0.3$	(37) (39)	15.1 - 17.6 13.9 - 17.3	₽	$15.9 \pm 4.7 (6)$ $15.7 \pm 0.6 (8)$		15.1 - 16.8 14.9 - 16.8

Table 3.

Weights and measurements of Marbled Murrelet males and females taken in pairs near Langara Island, British Columbia, 1971.

	Body weight	Culmen	Flattened wing	Date collected
♂ ♀	200.5g 211.8	15.7mm 16.4	133mm 137	30 April
o ⁷¹ ♀	$247.5 \\ 253.8$	$?\\15.0$	130 139	5 May
් ♀1	$232.3 \\ 255.2$	$\begin{array}{c} 14.8 \\ 15.8 \end{array}$	$\begin{array}{c} 135 \\ 138 \end{array}$	9 May
♂ ♀	$\begin{array}{c} 196.2 \\ 188.1 \end{array}$	$14.6 \\ 14.1$	$\frac{135}{134}$	13 May
♂ ♀1	$\begin{array}{c} 228.6 \\ 240.9 \end{array}$	$14.6 \\ 16.2$	$\begin{array}{c} 140 \\ 130 \end{array}$	14 May
♂ ♀1	$216.1 \\ 272.9$	$\begin{array}{c} 15.3 \\ 16.2 \end{array}$	136 133	22 May
o ⁷ ♀²	$\begin{array}{c} 227.3 \\ 230.7 \end{array}$	$14.6 \\ 14.4$	$\begin{array}{c} 134 \\ 128 \end{array}$	29 May
් ♀	$\begin{array}{c} 226.2 \\ 203.3 \end{array}$	$14.6 \\ 15.4$	136 130	26 June
♂ ♀	$\begin{array}{c} 216.2 \\ 243.1 \end{array}$	15.5?	$\frac{135}{126}$	7 July
♂ ♀	$210.0 \\ 173.6$	$16.5 \\ 14.3$	$\begin{array}{c} 132 \\ 122 \end{array}$	13 July
♂ ♀	$232.2 \\ 240.0$	$\begin{array}{c} 16.7 \\ 15.8 \end{array}$	$\frac{138}{132}$	31 July

¹Producing egg.

²Recently laid egg, postovulatory follicle present.

about 5% of its maximum body weight over its breeding season. Swartz (1966) found that Murres (*Uria* spp.) showed a similar seasonal pattern of body weight to that of *Aethia* species but in the Horned Puffin (*Fratercula corniculata*), body weights are remarkably free from annual variation (Sealy, 1973a).

AGE CATEGORIES AND MOLT

Ridgway (1919) and Kozlova (1957) have described adult plumages of the Marbled Murrelet in summer and winter and Drent and Guiguet (1961) figured these plumages along with the juvenal plumage. No differences in plumage patterns in summer between subadults (yearlings and two-year-olds) and adults were found. The subadults, which comprise about 15% of the population in the Langara Island area during the breeding season (late April to late August), differ from breeders only in their slightly smaller average dimensions of the bill and wing (Table 2) and on the basis of molt condition, the lack of brood patches, and by their gonadal development and histology (Sealy, unpublished data).

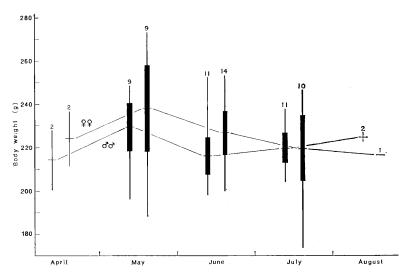


Figure 2. Body weights of adult male and female Marbled Murrelets from the vicinity of Langara Island, B. C. Mean monthly weights are represented by horizontal lines, the vertical lines denote range, and the solid bars, a distance of twice the standard error on each side of the mean.

Iris coloration differs in different age classes of auklets (Cyclor-rhynchus and Aethia, Sealy, unpublished data; Ptychoramphus, Manuwal, 1972). In fact, Manuwal (1972) has used these differences as valid age indicators in the Cassin's Auklet (Ptychoramphus aleuticus). The irides of juveniles, subadults, and adult Marbled Murrelets were all dark brown.

Subadult Marbled Murrelets returned to the Langura Island vicinity in late April with the adults. At this time the subadults are particularly recognizable as they are in their winter plumage although actively molting on their capital and spinal tracts, whereas the adults have nearly completed their partial prealternate molt. The subadults were usually encountered at sea as single individuals but after late June mixed flocks of subadults and adults were common (borne out by collecting).

Upon their return to the vicinity of Langara Island in late April, Marbled Murrelet adults were essentially in their summer plumage; however, up to 14 May 1971 adults (n = 12) were still actively molting on their capital and spinal tracts. Body molt in these tracts had begun again in some adults examined 20 July but the remiges and rectrices had not begun to molt when observations ceased on 12 August.

Kozlova (1957) stated that complete molt of adult Marbled Murrelets occurs in September and October, and may extend into November. The partial spring molt begins in April and is completed by late May. She found that this molt may be delayed until June, especially in immature birds. Stresemann and Stresemann (1966) also noted that molt of the flight feathers occurs

during September and October and is so rapid that the birds are temporarily flightless.

On 9 July 1971, an adult female Marbled Murrelet was collected in Egeria Bay. It had a fully developed brood patch (stage 3, Sealy, 1974) but with some feathering at its periphery, and a flaccid ovary. Also, it had undergone a nearly complete body molt and was white on the underparts except for some mottling on the upper breast. The rufous feathers on its back had been replaced by the grayish ones characteristic of the winter plumage. It is probable that this individual failed at breeding and underwent a rapid and premature body molt when its breeding effort was unsuccessful. Bédard (1969) described a similar situation in auklets (Aethia spp.) on St. Lawrence Island, Alaska.

The information obtained on molt in the present study indicates that molt of the remiges does not overlap the breeding effort in the Marbled Murrelet. The simultaneous wing molt of the congeneric Kittlitz's Murrelet begins in early September and also does not overlap its breeding effort (Sealy, unpublished data).

BEHAVIOR

Although the Marbled Murrelet is usually considered resident throughout its range (Brooks and Swarth, 1925; Munro and Cowan, 1947; Gabrielson and Lincoln, 1959), it was not present in the vicinity of Langara Island and northwestern Graham Island until 25 April 1971 (see Sealy, 1974). The adults returned in pairs, probably mated because 11 of 13 such "pairs" that were collected (Table 3) were composed of an adult male and female ($\chi^2 = 9.0$, P < 0.01). A "pair" taken on 22 May consisted of two females; a "pair" taken on 3 July consisted of two males. The individual pairs are maintained, usually aloof from other pairs, from their return to the area in spring until the eggs are laid, when single "off-duty" birds are usually encountered at sea. The subadults returned also in late April but were encountered only as single individuals until late June and early July when mixed groups ("off-duty" adults and subadults), of 4-11 individuals (mean = 7, n = 75 flocks) were often observed. During late July newly fledged young were frequently seen in these groups. During the chick rearing period beginning in late June, pairs of Marbled Murrelets once again were in evidence, indicating that both adults remain together during the day until night (see also Guiguet, 1956) when they return to feed the chick at the nest site.

The occurrence of Marbled Murrelets in pairs at sea has been noted during summer and winter by Laing, 1925; Willett, 1926; Guiguet, 1971; Hatler et al., 1973; and Byrd, Gibson, and Johnson, 1974). These observations are not supported by examinations of collected birds, but it is probable that such "pairs" represent a mated male and female, particularly in view of evidence presented above. Laing stated (1925:8) that "Birds of this genus [Brachyramphus] work in winter and summer, in pairs, but not as a defensive measure, for they dive almost together. It is suggested that they hunt double for mutual advantage just as two dogs do

in a chase." I believe that the occurrence of these pairs can be adequately explained on the basis of pair bond maintenance and that an advantage to feeding need not be invoked.

A phenomenon observed in the Marbled Murrelet apparently immediately prior to the appearance of the first young at sea deserves attention, although an adequate explanation is still lacking. Guiguet (1950:39) noted that when young Marbled Murrelets "... are ready to come off the nest large concentrations of adults have been observed in certain areas along the coast. These masses of birds often numbering four to five hundred individuals which keep up a continual din throughout the day. As evening approached the calling activities and fighting intensify, then gradually the pairs disappear." Such concentrations, according to Guiguet, do not occur in the same location in successive years. I observed only one such aggregation when a group of 55 individuals was seen in the western end of Pillar Bay on 22 June 1970 but the first young was not seen at sea that year until 6 July. No such aggregation was seen in the area in 1971.

It is interesting to note that the aggregation in 1970 occurred about two weeks prior to the first young observed at sea out of its nest. Also, such an aggregation was never encountered in the Langara Island vicinity up to or after that date, although total numbers of adult and subadult Marbled Murrelets almost doubled there after mid-July in both years.

"Off-duty" Marbled Murrelets spend the daylight period on their feeding areas (Sealy, 1975a). At the onset of darkness they begin to fly inland to the nest site and by dawn the "off-duty" birds have returned to sea (Guiguet, 1956). Copulation has never been observed at sea despite about 200 hours of observations. Presumably it occurs on the water at night or on the nest site.

Copulating at sea is generally uncommon in alcids but has been most frequently observed in Common Puffins (Lockley, 1953; Myrberget, 1962) and only rarely on water in murres (Tuck, 1961). Copulation in auklets (Cyclorrhynchus and Aethia) occurs in the nest crevice (Sealy, 1968) but in other plankton-feeding alcids, Cassin's Auklet (Thoresen, 1964; Manuwal, 1972) and Dovekie (Alle alle) (Ferdinand, 1969), it occurs on the rocks of the colony at night and on the snow or rocks in the daytime, respectively.

THE EGG

Two indisputable Marbled Murrelet eggs removed from the oviducts of adult females have been described (Cantwell, 1898; Sutton and Semple, 1941). Cantwell's egg, which was too broken to be measured accurately, was described by Bent (1919:142) as "cylindrical ovate" in shape. The ground color is "pale chalcedony yellow," it is uniform but not thickly spotted with small spots of very dark "blackish brown" or nearly black. An egg taken by Sutton and Semple (1941:580) is "pale glass green spotted with lavender gray (light), deep madder blue, sepia, bone brown, and black." Their egg measured 58.5 by 39.5 mm. An egg taken from

a nest of the Asiatic race perdix by Kuzyakin (1963) measured 63.6 by 39.3 mm. The clutch size of the Marbled Murrelet is one (Sealy, 1974), and the egg weighs 36 g or 16.2% adult weight

(Sealy, 1975b).

The egg of the Kittlitz's Murrelet was initially described as being pure white and numbering one or two; however, more recent authentic reports (Ford, 1936; Murie, 1959; Thompson et al., 1966; Bailey, 1973) indicate that only one, cryptically colored and patterned egg is its usual clutch.

Several alleged Marbled Murrelet eggs collected on Cox Island by Darcus (1927) have been considered to be probably of the Ancient Murrelet (Drent and Guiguet, 1961; Sealy, 1974).

THE CHICK

The downy young of the Marbled Murrelet has never been described and only recently was it described in the Kittlitz's Murrelet (Thompson et al., 1966; Bailey, 1973). Probably newly hatched Marbled Murrelet chicks are semiprecocial like those of the Kittlitz's Murrelet, that is, they possess a downy plumage at hatching and are fed at the nest by both parents for about 21 days (Sealy, 1974). The newly fledged Marbled Murrelets arrive on the sea with a complete juvenal plumage (but some individuals still show some down in the neck and crown regions) and at about 70% of the adult weight (Table 4).

Although direct observations are lacking, probably young Marbled Murrelets depart for sea only at night. How the young reach the sea is speculative (e.g. Guiguet, 1956; Kuzyakin, 1963); if they fledged during daylight hours, they would surely have been observed doing so. Kuzyakin (1963) considered that the young, before attaining the power of flight, probably walk overland to the nearest stream and follow it to the sea. However, as Guiguet (1956) has noted, such young would also inevitably have been seen and collected in the many streams and rivers of the Pacific Northwest.

To date such young have not been observed.

My observations in 1971 indicate that young Marbled Murrelets probably fly out to sea. Of the first 12 young seen at sea near Langara Island (beginning on 7 July 1971), 11 flew when approached by the boat and one dived in an effort to escape (which does not mean that it could not fly). Six of these young flew distances of at least one km before landing on the water but one individual flew only about 300 m. In three instances where a young and two adults were observed leaving the water together, the young lagged behind and alighted about one minute later.

The newly fledged young have measurements comparable to those of the adults with the wing being 86% adult size but with a body weight of only 70% adult weight (Table 4). Their egg tooth is still intact at fledging (Sealy, 1970).

The first young Marbled Murrelet (plumage illustrated by Drent and Guiguet, 1961:80) was observed near Langara Island on 6 July 1970 and on 7 July 1971. Young were then seen daily in 1971 along the northern shore of Graham Island to east of

Table 4.

Measurements of nine newly fledged Marbled Murrelets of both sexes taken near Langara Island, British Columbia, in mid-July, 1971.

Character	$ar{ ext{X}} \pm 2 ext{SE}$	Relative to Adults ¹ (percent)
Body weight (g)	157.0 ± 19.0	70.5
Flattened wing (mm)	114.8 ± 2.3	86.1
Culmen (mm)	12.9 ± 0.4	83.8
Bill depth (mm)	5.7 ± 0.3	96.6
Tarsus (mm)	16.1 ± 0.4	100.6

¹Data from Table 2.

Pillar Bay and near Langara Island from 7 July to 12 August. Young Marbled Murrelets apparently assume an independent existence once they have arrived on the sea. Although single young were often seen in company with one or more adults (parents?), young were more frequently seen alone or in groups of two (Guiguet, 1971; Sealy, 1974).

About 50 hours were spent from 7 July to 10 August 1971 observing adults and young Marbled Murrelets, much of this time on their feeding areas. I did not observe young being fed by adults; in fact, on 17 and 24 July single young were seen diving among kelp beds (Nereocystis leutkeana) along the northern shore of Graham Island and surfacing with single sand lances (Ammodytes hexapterus), the principal prey species taken by adults and young there at that time (Sealy, 1975a). Each fish was swallowed head first by the young murrelets.

Daily counts of young Marbled Murrelets were made in Cloak Bay and the western portion of Parry Passage between 8 July and 2 August 1971. The numbers of young varied from 3 on 8 July to a peak of 45 on 21 July. On 21 July about 400 adults and subadults were observed there indicating that some movement of adults and young probably occurs because an average adult and subadult count on 27 June in the same area was only about 50 individuals.

PREDATION

Predation on Marbled Murrelets has seldom been observed. Beebe (1960:168) stated that it "may at times be taken [by Peregrine Falcons (Falco peregrinus) near Langara Island] . . . but it cannot be very important, being neither as numerous nor, by its habits, as exposed to attack by the falcons. It is, however, within the size range of the species regularly taken." R.W. Nelson (pers. comm.) found the wings of two juvenile Marbled Murrelets in July, 1971 near a Peregrine eyrie on Langara Island.

DISCUSSION

Despite the fact that observations at Marbled Murrelet nest

sites are lacking, comments regarding its breeding strategy can be made. First, as in other alcids (Sealy, 1972), sexual dimorphism in size or plumage characteristics is lacking, sex ratios are equal, and a monogamous mating system apparently prevails. Second, it seems certain that the Marbled Murrelet lays one-egg clutches (Sealy, 1974) in nests that may be considerably dispersed, sometimes several km inland (Booth, 1927; Jewett, 1930; Barber, 1941). The congeneric Kittlitz's Murrelet also lays single-egg clutches in widely dispersed, solitary nests (Murie, 1959; Thompson

et al., 1966; Bailey, 1973).

Young Marbled Murrelets, which hatch from eggs about 16% of the adult weight (Sealy, 1975b), are semiprecocial, that is, they possess a downy plumage at hatching (L. C. Binford, pers. comm.) and are fed at the nest probably by both parents until they have attained the juvenal plumage and about 70% adult weight when they fledge. I estimated the period of development in the nest to be only about 21 days based on my observations on the interval when adults were first seen holding fish in their bills at dusk (indicating the first young had hatched) and the first appearance at sea of newly fledged young (Sealy, 1972, 1974). Cody (1973), on the other hand, guessed that after spending 42 days in the nest, young Marbled Murrelets depart for sea still unable to fly at 75% adult weight. Cody did not provide observations on which these figures were based.

Both sexes incubate and both develop single brood patches (Sealy, 1974). Both sexes have been taken at sea during the incubation period; presumably their mates were at the nest sites at the time. The length of the incubation shift in the Marbled Murrelet is questionable but is certainly some multiple of 24 hours because adults visit the nest site only at night. I have argued elsewhere (Sealy, 1972, 1975a, Ms) that the 72-hour incubation shifts in the nocturnal Ancient Murrelet (long for an alcid) evolved to provide "off-duty" adults with enough time to locate food (largely plankton) which, although within a few km of shore, is patchy in The Marbled Murrelet, on the other hand, feeds within 500 m of shore on an apparently stable food source (mostly Ammodytes) (Sealy, 1975a). I believe, therefore, that despite the fact that some Marbled Murrelet nests may be up to 30 km inland—the majority are closer to sea (Drent and Guiguet, 1961) and because excessive time is not required to locate food, that the birds are able to exchange incubation duties every 24 hours. The other truly inshore feeding alcids, the guillemots (Cepphus spp.) are diurnal and have incubation shifts of only a few hours (Drent, 1965; Preston, 1968).

The number of visits to the nest site with food for the growing young can also be discussed. In some of the other nocturnal alcids, Cassin's Auklet and Rhinoceros Auklet (Cerorhinea monocerata), actually a puffin (Storer, 1945), the nest is visited once per night by each parent with food for the young (Sealy, 1973b). Each Marbled Murrelet parent probably makes only one trip each night, carrying 1-4 fish to feed the young (Guiguet, 1956; Cody,

1973; Hatler et al., 1973; Sealy, pers. observations).

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