

Chapter 4

Nesting Chronology Of The Marbled Murrelet

Thomas E. Hamer¹

S. Kim Nelson²

Abstract: We compiled 86 breeding records of eggs, downy young, and fledgling Marbled Murrelets (*Brachyramphus marmoratus*) for which the fledging date could be estimated. Records were collected from California ($n = 25$), Oregon ($n = 13$), Washington ($n = 13$), British Columbia ($n = 23$), and Alaska ($n = 12$). The number of young fledging increased rapidly from 6 June to 19 July and peaked by the 10-day period beginning 19 July. A second peak in the number of young fledged was observed for the 10-day period beginning 18 August, with a rapid decrease in late August and early September. From these results, a gradual accumulation of fledglings on the ocean would be observed from 30 May until 16 September. By 27 August, only 84 percent of the juveniles in a given year would be expected to be counted at sea. In California and Oregon, it is likely that two distinct periods of breeding activity result from some proportion attempting to lay a second clutch, or pairs renesting after nesting failure. The breeding season appears to be much longer and less synchronous than that of many other members of the alcid family. We conclude that egg-laying and incubation spanned a long period, beginning 24 March and ending 25 August, with the nestling period beginning 23 April and ending with a fledging record on 21 September, a breeding period of 182 days.

Detailed information on the breeding chronology of the Marbled Murrelet (*Brachyramphus marmoratus*) has been limited. More recently, a large amount of unpublished information has been collected from research projects being conducted throughout the range of the Marbled Murrelet. In this paper we review the nesting chronology of the Marbled Murrelet using data from four published studies that specifically addressed the topic ($n = 26$ records), additional published breeding records ($n = 26$), and unpublished breeding accounts ($n = 35$) of the Marbled Murrelet from Alaska, British Columbia, Washington, Oregon, and California. This information was used to estimate the fledging dates for each record collected. We then summarized these fledging dates and used them to construct the timing of egg laying, incubation, and nestling period for each state and province to more accurately document the breeding chronology of the Marbled Murrelet.

An understanding of the breeding chronology of the Marbled Murrelet is important for several reasons. To learn more about the nesting ecology of this species, it is important to understand the timing and lengths of breeding activities and what factors affect this timing. To avoid disturbance to nesting colonies from land management activities, land

managers will need to know the timing of the incubation and nestling periods for each geographic area. Biologists conducting nest searches and gathering information on nesting biology will want to know the optimum period to conduct these activities. In addition, biologists conducting marine surveys to collect information on the numbers of juveniles observed at sea, as an indication of reproductive success, will need nesting chronology data to determine the appropriate timing of these surveys.

Several studies have addressed the breeding chronology of the Marbled Murrelet. In British Columbia, Sealy (1974) collected female specimens at sea and examined the maturation of the ovarian follicles, the size of the brood patch, and the date juveniles were first observed on the ocean. Carter and Sealy (1987b) used 41 records of downy young and grounded fledglings to estimate the timing of breeding. Carter and Erickson (1992) used additional records of grounded chicks and fledglings to estimate the timing of egg laying, incubation, and chick rearing for murrelets in California. In addition, the breeding phenology of the murrelet in British Columbia was reviewed by Rodway and others (1992), adding some records to the previous work of Sealy (1974) and Carter and Sealy (1987b).

Methods

We compiled unpublished breeding records from intensive field work conducted on murrelets over the last five years, and from published observations of breeding records, downy young and fledgling Marbled Murrelets (table 1). Fledging dates were estimated using a 30-day incubation period and a 28-day nestling period (Sealy 1974, Simons 1980, Hirsch and others 1981). For example, if a grounded chick was found and, from the description, was estimated to be 10 days old, we added 18 days to determine the approximate fledging date. Similarly, if an egg-laying date was available, but the egg was destroyed before hatching, we added 30 days for incubation and a 28-day nestling period to estimate the fledging date. The initiation of egg laying, incubation, and hatching were estimated for each record in the same manner. In some cases, where the size and plumage of a chick were not described completely, a subjective estimate of the age of the chick was made. These records were given a higher error estimate. Fledging dates were used for the analysis only if the date could be estimated with an error of <8 days so that the results would accurately describe the nesting chronology. Records were not used when a description of the plumage or size of the chick was not available. Records derived from juveniles first observed at sea were used only if the researcher was conducting weekly boat surveys within

¹ Research Biologist, Hamer Environmental, 2001 Highway 9, Mt. Vernon, WA 98273

² Research Wildlife Biologist, Oregon Cooperative Wildlife Research Unit, Oregon State University, Nash 104, Corvallis, OR 97331-3803

Table 1—Inland and at-sea records of eggs, downy young, and fledglings of Marbled Murrelets in North America (n = 86) where the fledging date could be estimated. The term “grounded” under “Record type” refers to chicks or fledglings that were found on the ground

Location	Sources	Record type	Estimated fledge date
California			
Big Basin State Park	Singer (pers. comm)	Grounded chick	5/20/89
Big Basin State Park	Binford and others (1975)	Grounded chick	8/20/74
Big Basin State Park	Carter and Erickson (1992)	Grounded fledgling	6/12/76
Big Basin State Park	Carter and Erickson (1992)	Grounded fledgling	6/14/79
Portola State Park	Anderson (1972)	Grounded fledgling	6/15/57
Big Basin State Park	Carter and Erickson (1992)	Grounded fledgling	6/17/73
Portola State Park	Desante and LeValley (1971)	Grounded fledgling	6/27/71
Gasquet Ranger District	Craig (pers. comm.)	Grounded fledgling	6/30/92
Big Basin State Park	Carter and Erickson (1992)	Grounded fledgling	7/04/76
Sequoia Park	Carter and Erickson (1992)	Grounded fledgling	7/04/24
Memorial County Park	Singer (pers. comm.)	Grounded fledgling	7/19/88
Big Basin State Park	Carter and Erickson (1992)	Grounded fledgling	8/11/82
Prairie Creek State Park	Carter and Erickson (1992)	Grounded fledgling	8/13/84
Big Basin State Park	Singer (pers. comm.)	Grounded fledgling	8/15/90
Big Basin State Park	Singer and Verado (1975)	Grounded fledgling	8/18/60
Big Basin State Park	Singer (pers. comm.)	Grounded fledgling	8/25/92
Big Basin State Park	Erickson and Morlan (1978)	Grounded fledgling	8/31/77
Loma Mar	Carter and Erickson (1992)	Grounded fledgling	8/31/85
Big Basin State Park	Singer (pers. comm.)	Grounded fledgling	9/03/88
Big Basin State Park	Singer (pers. comm.)	Grounded fledgling	9/05/93
Big Basin State Park	Singer and Verado (1975)	Grounded fledgling	9/09/74
Big Basin State Park	Singer (pers. comm.)	Grounded unknown	5/18/84
Big Basin State Park	Singer (pers. comm.)	Nest observed	6/07/92
Big Basin State Park	Singer (pers. comm.)	Nest observed	7/03/91
Elkhead Springs	Chinnici (pers. comm.)	Nest observed	8/23/92
Waddell Creek	Naslund (1993a)	Nest observed	8/26/89
Oregon			
Five Rivers	Nelson and Peck (in press)	Grounded chick	7/07/90
God's Valley	Nelson and Peck (in press)	Grounded fledgling	9/13/90
Powers Ranger District	Nelson and Peck (in press)	Grounded fledgling	7/26/92
North Fork Siuslaw River	Jewett (1930)	Grounded fledgling	9/08/18
Siletz	Heinl (1988)	Grounded fledgling	9/21/87
Five Rivers	Nelson and Peck (in press)	Nest observed	6/22/91
Boulder and Warnicke Creeks	Nelson and Peck (in press)	Nest observed	7/08/92
Iron Mountain	Nelson and Peck (in press)	Nest observed	7/09/92
Cape Creek	Nelson and Peck (in press)	Nest observed	7/20/91
Siuslaw River	Nelson and Peck (in press)	Nest observed	8/29/91
Valley of The Giants	Nelson and Peck (in press)	Nest observed	8/30/90
Valley of The Giants	Nelson and Peck (in press)	Nest observed	7/09/91
Siuslaw River	Nelson and Peck (in press)	Nest observed	9/09/91
Washington			
Rugged Ridge	Leschner and Cummins (1992a)	Grounded chick	7/09/82
Helena Creek	Reed and Wood(1991)	Grounded chick	7/22/89
Baker Lake	Hamer (pers. obs.)	Grounded chick	7/24/90
Heart of the Hills Trail	Hamer (pers. obs.)	Grounded chick	8/07/91

continues

Table 1—continued

Location	Sources	Record type	Estimated fledge date
Aberdeen	Leschner and Cummins (1992a)	Grounded chick	8/09/83
Matheny Creek	Leschner and Cummins (1992a)	Grounded fledgling	7/17/81
North Fork Quinalt	Leschner and Cummins (1992a)	Grounded fledgling	7/23/86
Sedro Woolley	Hamer (pers. obs.)	Grounded fledgling	7/24/90
North Rosedale	Leschner and Cummins (1992a)	Grounded fledgling	7/24/71
Federal Way	Leschner and Cummins (1992a)	Grounded fledgling	8/07/74
Long Beach	Ritchie (pers. comm.)	Nest observed	6/22/93
Lake 22	Hamer (pers. obs.)	Nest observed	7/18/90
Lake 22	Hamer (pers. obs.)	Nest observed	8/27/90
British Columbia			
Langara Island	Sealy (1974)	Egg development	7/20/71
Langara Island	Sealy (1974)	Egg development	7/26/71
Langara Island	Sealy (1974)	Egg development	7/30/71
Langara Island	Sealy (1974)	Egg development	8/02/70
Langara Island	Sealy (1974)	Egg development	8/02/70
Langara Island	Sealy (1974)	Egg development	8/04/71
Langara Island	Sealy (1974)	Egg development	8/06/71
Langara Island	Sealy (1974)	Egg development	8/08/70
Langara Island	Sealy (1974)	Egg development	8/19/70
Langara Island	Sealy (1974)	Egg development	8/30/71
Vancouver Island	Harris (1971)	Grounded chick	8/30/67
Chilliwack	Rodway and others (1992)	Grounded fledgling	7/07/87
Hope Village	Rodway and others (1992)	Grounded fledgling	7/12/47
Queen Charlotte Island	Sealy (1974)	Grounded fledgling	7/15/47
Sayward	Rodway and others (1992)	Grounded fledgling	7/15/86
Karen Range	Paul Jones (pers. comm.)	Nest observed	8/20/93
Frederick Island	Drent and Guiguet (1961)	Sea observation	6/28/61
Frederick Island	Drent and Guiguet (1961)	Sea observation	6/28/61
Barclay Sound	Carter (1984)	Sea observation	6/28/80
Barclay Sound	Carter (1984)	Sea observation	7/04/79
Langara Island	Sealy (1975a)	Sea observation	7/06/70
Langara Island	Sealy (1975a)	Sea observation	7/07/71
Cox Island	Brooks (1926b)	Sea observation	7/22/20
Alaska			
Montague Island	Mendenhall (1992)	Egg development	8/10/77
Skagway	Mendenhall (1992)	Grounded fledgling	7/18/87
Afognak Island	Carter and Sealy (1987b)	Grounded fledgling	8/18/76
Cordova Airport	Carter and Sealy (1987b)	Grounded fledgling	8/20/78
Port Chatham	Johnston and Carter (1985)	Nest observed	Unknown
Naked Island	Naslund and others (in press)	Nest observed	7/23/92
Kodiak Island	Naslund and others (in press)	Nest observed	7/24/92
Kodiak Island	Naslund and others (in press)	Nest observed	8/03/92
Naked Island	Naslund and others (in press)	Nest observed	8/13/91
East Amatuli Island	Hirsch and others (1981)	Nest observed	8/16/79
East Amatuli Island	Simons (1980)	Nest observed	8/27/78
Auke Bay	Speckman (pers. comm.)	Sea observation	7/10/93
Auke Bay	Speckman (pers. comm.)	Sea observation	7/29/92

the same geographic area and surveys commenced before the fledging period of the breeding season. Therefore, only one datum was used for each boat survey in each year, indicating the first fledging date for that season. These observations made up a small portion of the records used.

Birds were assumed to be juveniles when a grounded juvenile was reported, and a plumage description was not provided. Fortunately, the use of the word “juvenile” to describe a young bird that had lost its downy plumage was consistent throughout the literature. We assumed that grounded juveniles were recently fledged individuals. The majority of records of grounded juveniles included descriptions of remaining down on the back and head and the presence of an egg tooth, confirming recent fledging.

Records of eggs collected or found and of incubating adults were not used because the development period of the embryo was unknown. But the presence of a postovulatory follicle, unshelled egg in the oviduct, or mature follicles from collected females indicated that egg laying would occur in 1-3 days (Sealy 1974). Therefore, egg-laying dates were estimated for these records by adding 2 days to the collection date and then estimating the fledging date by adding 58 days.

Sealy (1974) obtained 12 breeding records in British Columbia. He collected murrelet specimens in weekly intervals during the breeding season between 30 April and 10 August. He examined the size of the brood patch in male and females and the size and maturation of the largest follicle in each ovary of females to estimate the timing of egg laying, incubation, and chick rearing. Observations of adults carrying fish in their bills at dusk were used to estimate the hatching dates of eggs. The first fledglings observed on the water were used as an indication of the earliest fledging dates. For our summary, we used only records from Sealy in which the size and maturation of the ovarian follicles of females enabled an accurate estimate of the egg-laying date, and two cases in which juveniles were first observed at sea. Observations of brood patch development and fish-carrying behavior were not used because the accuracy of these methods in estimating the nesting stage of the Marbled Murrelet is unknown.

Carter and Erickson (1992) reviewed the breeding chronology of the murrelet in California by examining inland records of downy young and grounded juveniles, molt conditions of museum specimens, and records of juveniles observed at sea from 1892 to 1987. Carter and Erickson used 28 days for a nestling period and 30 days for an incubation period to estimate breeding chronology. In addition, 41 inland records of downy young and fledgling murrelets from 1918 to 1986 were summarized in North America by Carter and Sealy (1987b). Records of grounded nestlings and juveniles from these studies, in which an accurate fledging date could be estimated, were used in this analysis.

Fledgling dates were estimated using 86 breeding records from California ($n = 25$), Oregon ($n = 13$), Washington ($n = 13$), British Columbia ($n = 23$), and Alaska ($n = 12$) (table

1). Records used for this analysis included observations of the presence of a postovulatory follicle ($n = 9$) or unshelled egg in the oviduct of collected females ($n = 2$), known egg-laying dates ($n = 2$), known egg-hatching dates ($n = 5$), observations of young on nests ($n = 4$), grounded chicks ($n = 9$), grounded fledglings ($n = 35$), juveniles observed to fledge ($n = 10$), and dates that juveniles were first observed at sea from marine census studies ($n = 9$). Fledging dates for a large proportion of the records (67 percent) could be estimated accurately because the egg-laying date or the hatching date was known, the young were accurately aged on the nest, a grounded fledgling was recorded, or a nestling was actually observed to fledge ($n = 56$).

Results

Records of the earliest and latest breeding records of the Marbled Murrelet were all collected from California and Oregon. The earliest fledging record in North America was of a grounded downy chick discovered in Big Basin State Park in central California on 20 May 1989. The chick was estimated to be at least 2 weeks old (S.W. Singer, pers. comm.). The next fledging was a nestling observed to fledge on 7 June 1992 from a nest also in Big Basin State Park (S.W. Singer, pers. comm.) (fig. 1). A record also exists of a grounded murrelet in Big Basin State Park on 18 May 1984, but it was not clear whether the bird was an adult or juvenile (S.W. Singer, pers. comm.). The next four earliest fledging dates, from 12 June to 17 June, were all from Big Basin and Portola State Parks in central California (Anderson 1972; Carter and Erickson 1992; S.W. Singer, pers. comm.).

The latest fledging date was a record of a fledgling found on 21 September 1987 in a parking lot in the town of Siletz, Oregon (Heinl 1988, Nelson and Peck, in press). The next four latest fledging dates, from 30 August to 9 September, were all recorded from California and Oregon (Carter and Erickson 1992, Erickson and Morlan 1978, Jewett 1930, Nelson and others 1992, Singer and Verardo 1975).

The number of young observed or estimated to have fledged for all North American records was summarized for each 10-day period during the breeding season. Fledging rates increased rapidly from 6 June to 19 July, and peaked by the 10-day period beginning 19 July (fig. 1). A possible second peak in the number of young fledged was evident for the 10-day period beginning 18 August, with a rapid decrease in the number of young leaving nests in late August and early September. Egg laying and incubation began 24 March and ended 25 August, with the nestling period beginning 23 April and ending with a fledging record on 21 September, a breeding period of 182 days.

An analysis of the cumulative number of young fledged in North America for each 10-day period was used to predict the percentage of total juveniles that would be observed in the marine environment during different periods of the breeding season. This analysis also demonstrated the broad nesting chronology of the Marbled Murrelet (fig. 2). The

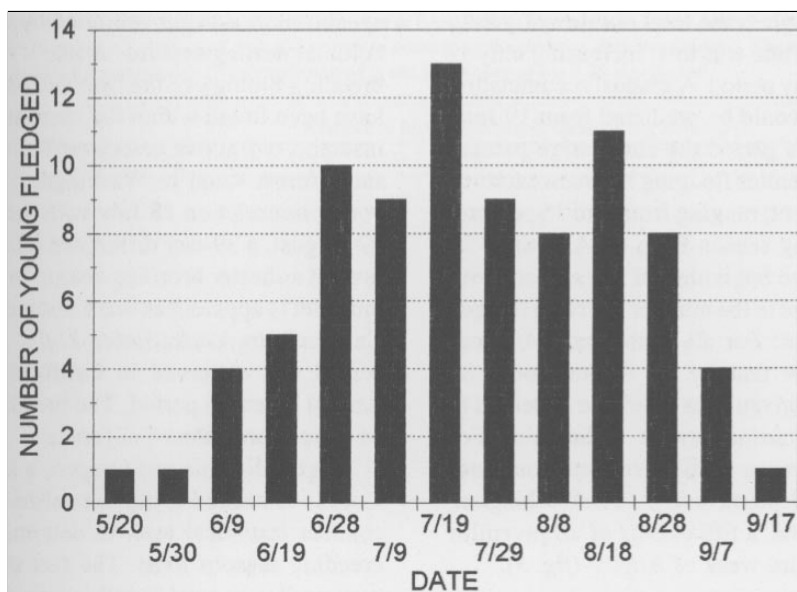


Figure 1—Fledging dates of Marbled Murrelet young from nests in North America ($n = 86$) in 10-day intervals. The date displayed for each histogram is the beginning of a 10-day period. Records were used only if the error in estimating the fledging date was <8 days.

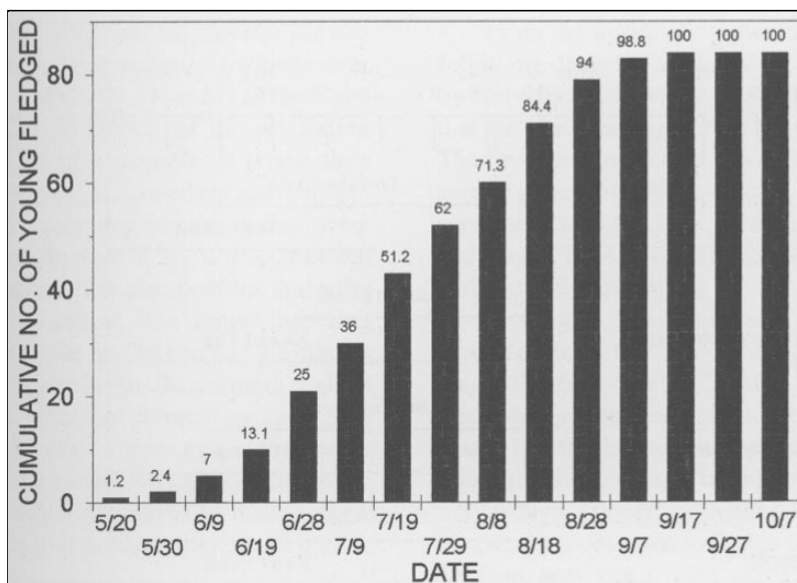


Figure 2—The cumulative number of Marbled Murrelet young fledged from nests in North America ($n = 86$) in 10-day intervals. The cumulative percentage of total young fledged in each 10-day interval is shown at the top of each histogram. The date displayed for each histogram is the beginning of a 10-day period.

cumulative percentage change in the total number of young fledged from 20 May to 18 June was low, increasing only 1-6 percent between each 10-day period. A gradual accumulation of fledglings on the ocean would be predicted from 19 June until 27 August. During this period the cumulative percent change in the number of juveniles fledging between each 10-day period was very consistent, ranging from 9 to 15 percent. The latter part of the nesting season from 28 August to 26 September was similar to the beginning of the season, with the cumulative percent change in the number of young fledged ranging from 1 to 5 percent. For all states and provinces combined, the results show that by 27 August, only 84 percent of the juveniles in a given year would be expected to be counted at sea using marine census techniques. For California and Oregon, a census of all juveniles would not occur until the third week of September (*fig. 3*). In Washington, British Columbia, and Alaska, a full census of all juveniles would not occur until the third week of August (*fig. 3*).

Discussion

The breeding season of the Marbled Murrelet appears to be much longer than that of many other members of the alcid family. The long breeding period indicates that the

synchronous nesting exhibited by many colonial and semi-colonial nesting seabirds is likely not a characteristic of the breeding biology of the Marbled Murrelet. Few active nests have been found within the same stand to verify this. In one instance, two active nests were found only 100 m apart in the same forest stand in Washington. The first nest fledged a young murrelet on 18 July with the second nest fledging on 27 August, a 39-day difference (Hamer, pers. obs.). A trend toward a shorter breeding season in the northern range of the murrelet is apparent as one examines the fledging dates from California to Alaska (*table 2, fig. 3*). The longest breeding period was observed in California. Oregon had the next longest breeding period. The breeding season in Alaska was 64 days shorter than California.

For California and Oregon, a larger sample of breeding records is needed to further refine the breeding period and conduct statistical tests to determine whether two distinct breeding seasons exist. The fact that each breeding period was similar in total length supports the idea that there are two periods. When examined separately, the second breeding period was only 12 and 16 days shorter than the first breeding period for Oregon and California, respectively. The first breeding period in California (103 days) was similar to the total breeding season in Alaska (106 days).

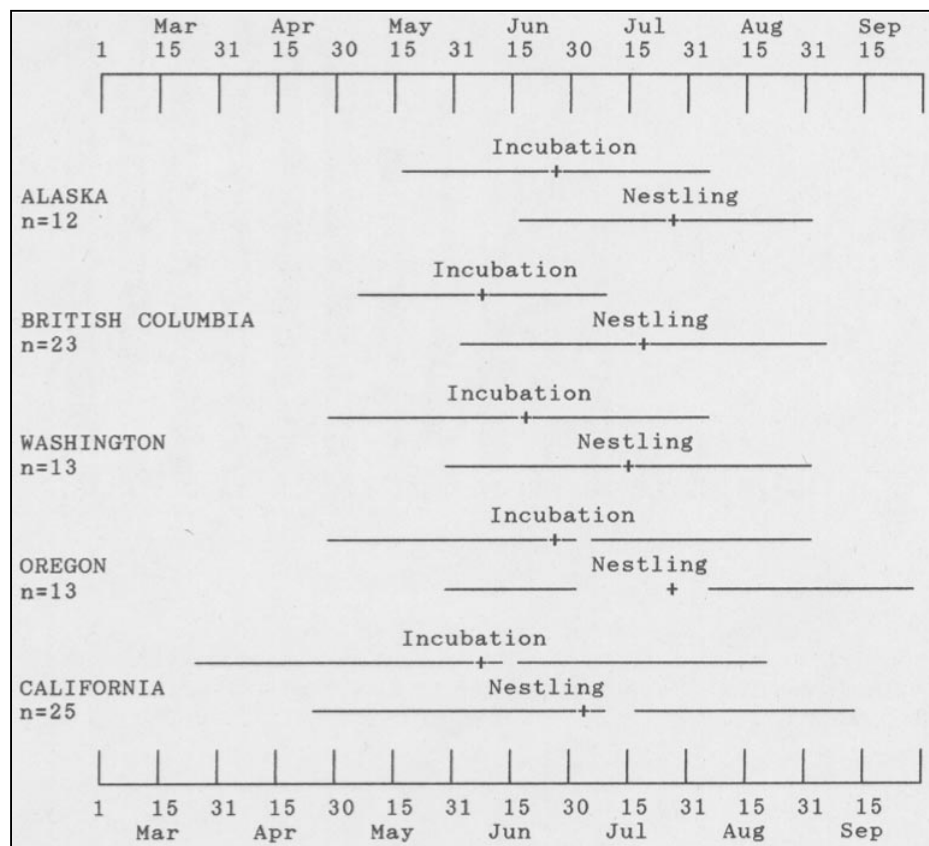


Figure 3—Breeding phenology of the Marbled Murrelet in North America organized by state and province. The median for each incubation and nestling period is shown.

Table 2—Number of Marbled Murrelet young observed and estimated to have fledged from nests in North America in 10-day intervals and listed by state and province. Records (n = 86) were used only if the error in estimating the fledging date was <8 days. The total length of the breeding period is listed under each state or province. The date displayed is the beginning of each 10-day period

State or province	Number of birds observed in each 10-day interval													
	5/2	5/30	6/9	6/19	6/29	7/9	7/19	7/29	8/8	8/18	8/28	9/7	9/17	9/27
Alaska 106 days						2	2	2	3	3				
British Columbia 118 days				3	4	3	3	5	1	2	2			
Washington 124 days				1		3	5	2	1	1				
Oregon 149 days				1	3	1	2				2	3	1	
California 170 days	1	1	4	1	4		1		3	5	4	1		

Explanations for the presence of two distinct breeding periods include: (1) small sample sizes, (2) variations in the timing of breeding of murrelets between years (as suggested by Carter and Erickson 1992), or (3) variation in oceanic and environmental conditions that promote breeding within these two distinct periods. Small sample sizes may not adequately explain this phenomenon, because it occurs only in the southern portions of the murrelet range, with sample sizes very similar to regions to the north. If the between-year variation in the timing of breeding was responsible for this trend, some young would have been expected to fledge over a period of years within the 1- to 2-week gap between breeding periods. A distinct proportion of the population nesting during each period is also possible. It is not clear what environmental or biological agents might cause this to occur. However, the most likely explanation is that some proportion of murrelets may attempt to lay a second clutch within the same breeding period. It is also possible that pairs with failed nests attempt to renest. The longer breeding season available for the murrelet in Oregon and California may make renesting more likely than in the northern regions of the range. The gap in breeding chronology may give females enough time to develop a new egg and select a different nest site. The shorter incubation and nestling period in the Marbled Murrelet, when compared to that of other species, such as the puffins and auklets, may make double brooding more feasible.

Egg replacement is a regular occurrence in ledge-nesting Alcids (Johnsgard 1987). Tuck (1960) estimated that 44 percent of Thick-billed Murres (*Uria lomvia*) pairs lost at least one egg during a 32-day period, with 30 percent of pairs laying one replacement egg; 11 percent laid two replacements, and the remaining 3 percent deserted or did not lay again. For higher arctic forms there are probably no opportunities to renest because of a short breeding season (Johnsgard 1987). The Xantus' Murrelet (*Synthliboramphus hypoleucus*) may lay two broods because egg laying has been observed until July, and Murray and others (1983)

found evidence of occasional egg replacement in this species. Both Sealy (1975a) and Gaston (1992) found no evidence of replacement clutches in the Ancient Murrelet (*S. antiquus*). If renesting and egg replacement does occur in the Marbled Murrelet, it will affect the interpretation of inland survey data and at-sea census results and population modeling for this species.

Breeding Phenology Dates

From the information presented above, we propose the following dates for the breeding phenology of the murrelet by state and province (fig. 3). In California, we estimated that the total breeding season lasted approximately 170 days. The first breeding period was 103 days long while a possible second period was 87 days long. The breeding periods were separated by 8-11 days. Incubation commenced 24 March and ended 13 August. The nestling period began 23 April and ended 9 September.

In Oregon, incubation was estimated to begin on 26 April and last until 25 August (fig. 3). The nestling period was estimated to begin 26 May and end on 21 September. The total breeding season length was 21 days shorter than that in California and was approximately 149 days long. The two possible periods of breeding activity were separated by only 6 days. The earliest recorded fledging date in Oregon is of a nestling observed to fledge from a nest on 22 June 1993 (Nelson, pers. obs.).

North of California and Oregon, the length of the breeding season was more restricted (fig. 3) (table 2). In Washington, the breeding season might appear shorter because of the smaller sample of breeding records used to predict fledging dates. However, it is probably similar to that found in British Columbia. Incubation was estimated to begin 26 April and end 30 July. The nestling period began 26 May and ended on 27 August. The total length of the breeding season was 124 days long, 25 days less than Oregon. The earliest fledging record is a nestling observed to fledge on 22 June 1993 (Ritchie, pers. comm.). The latest record is that of a nestling

recorded on video tape fledging from a nest on 27 August 1990 (Hamer, pers. obs.).

In British Columbia, incubation was estimated to commence on 2 May and ended by 4 July (*fig. 3*). The nestling period began 1 June and ended by 30 August. The total breeding season was approximately 118 days. The earliest fledging date recorded was for a juvenile collected by Drent and Guiguet (1961) on 28 June 1961. The next five earliest records are of all juveniles observed or collected at sea. The first grounded fledging was not recorded until 7 July 1987 (Rodway and others 1992). The latest two fledging dates occurred on 30 August. One was of a chick that was discovered after a tree was felled (Harris 1971), and the second was a description of the follicle development of a female (Sealy 1974).

The length of the Alaska nesting season was greatly restricted and was estimated to be only 106 days. Incubation was estimated to begin on 14 May and end by 30 July. The nestling period ranged from 13 June to 27 August. The earliest fledging record was a juvenile observed at sea on 10 July 1993. The next earliest was a grounded fledging observed on 18 July 1987 (Mendenhall 1992). The latest estimated fledging date of 27 August 1978 was from an active ground-nest observed by Simons (1980).

Sealy (1974) discovered that murrelets laid eggs in British Columbia over a 6- to 7-week period beginning 15 May and ending in late June or early July. Adults with fish in their bills were first observed on 16 June. Young birds were first observed on the water on 6 July 1970 and on 7 July 1971. Sealy concluded that the period of egg laying and incubation began around 15 May and lasted until 31 July. He estimated that the period of hatching and chick rearing started 15 June and ended around 15 August. Fledging began in the first week of July and continued to some time after 15 August (Sealy 1974). Sealy's study took place in the most northern portion of coastal British Columbia and thus may be more representative of Alaska than British Columbia. His breeding dates closely resemble the breeding chronology we report for Alaska (*fig. 3*). Rodway and others (1992) reached similar conclusions.

For North America, Carter and Sealy (1987b) calculated that egg-laying dates began between 15 and 22 April. The latest fledging dates reported were 8 and 9 September. Additional breeding records that we collected extend these dates by several weeks in California and Oregon. However, observations by Carter and Sealy of adults holding fish at sea as late as 17 September and records of several young still in downy plumage on 4 and 13 September led them to believe that the nestling period of the murrelet may extend into late September. Carter and Sealy concluded that murrelets may nest earlier and have a longer breeding season south of British Columbia. Carter (1984) speculated that the breeding season was protracted in southern British Columbia as compared to northern British Columbia.

Carter and Erickson (1992) estimated that egg-laying dates ranged from 15 April to 12 July in California, and hatching from 15 May to 10 August. New records that we examined extend these dates (*fig. 3*). Carter and Erickson

found that fledging dates fell into two periods, 12 June to 4 July, and 11 August to 9 September. They believed the two different fledging periods in California were due either to low sample size, unknown factors affecting the grounding of fledglings, or variation between years in the timing of breeding. They concluded that egg laying begins earlier in California than farther north. An earlier breeding chronology was further supported by an examination of 45 museum specimens which showed an earlier timing of prealternate body molt for birds in California.

Juvenile/Adult Ratios

Adults molting into winter plumage can make it difficult to discriminate between adults and juveniles after 15 August (Carter and Stein, this volume). Because of this, for all provinces and states combined, 29 percent of the juvenile population produced in a given year may go uncounted if surveys after 15 August cannot accurately census young birds (*fig. 2*). It is impossible, at this time, with the small sample sizes to calculate the percent of young expected to be counted at sea during the breeding season for each state or province. When collected, this information would be valuable to researchers attempting to calculate juvenile/adult ratios or model population trends. A full census of juveniles would not be possible until after 16 September for California and Oregon, and after late August in Washington, British Columbia, and California. Sealy (1974) collected an adult female in British Columbia on 9 July 1971 that had already undergone a nearly complete body molt and was nearly in winter plumage. He suggested that this female may have undergone a premature body molt after an unsuccessful breeding effort. A complete census of juveniles may not be necessary for year-to-year comparisons of reproductive success. But, if complete censusing is not done, researchers should be careful of variations in the timing of breeding between years when conducting any annual comparisons. In addition, ratios of juveniles to adults observed at sea can be adjusted for birds that have not yet fledged (Beissinger, this volume) which may aid population modelling efforts and annual comparisons of reproductive success.

Acknowledgments

We are grateful for the unpublished accounts of nest observations, grounded chicks, and grounded fledglings provided to us by Nancy Naslund of the U.S. Fish and Wildlife Service, U.S. Department of Interior, Steve Singer of the Santa Cruz Mountains Murrelet Group, Bill Ritchie of the Washington Department of Wildlife, Paul Jones, Phyllis Reed, and Brenda Craig of the USDA Forest Service. Ray Miller and Sal Chinnici of the Pacific Lumber Company provided information from a nest in northern California. We thank Craig Strong, C.J. Ralph, Kathy Kuletz, and Susan Speckman for providing records of juveniles first observed at sea during marine survey efforts. Joanna Burger, Anthony Gaston, and Frank Pitelka provided helpful comments on early drafts of this manuscript.