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TECHNIQUES FOR INVESTIGATING BREEDING CHRONOLOGY IN MARBLED MURRELETS, DESOLATION SOUND, BRITISH COLUMBIA

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Abstract. We used several methods to study the chronology and synchrony of breeding events of the Marbled Murrelet (*Brachyramphus marmoratus*) population at Desolation Sound, British Columbia, from 1996 to 1998. The timing of breeding events varied among years; on average the breeding season lasted from 21 April to 5 September. We assessed the biases of each method used by comparing the results to the estimate of the integrated breeding chronology. Counts of hatch-year birds at sea were biased toward earlier breeders, missing an estimated 24% of the fledglings. Two other methods, physiological analysis of the yolk precursor vitellogenin from blood samples and monitoring by radio-telemetry could produce a complete distribution of breeding events if sampling were done throughout laying. Observations in the forest, date of first observation of a fledgling at sea during the breeding season, and fish-holding behavior produced insufficient data to be used as sole indicators of breeding chronology of this species. In general, breeding synchrony in alcids, assessed using data from a literature review, was unrelated to feeding habits but increased with latitude (41% of the variation was explained by latitude). Marbled Murrelets, however, bred less synchronously than predicted for an alcid at this latitude (50°N).

Key words: *Alcidae*, *Brachyramphus marmoratus*, *breeding chronology*, *British Columbia*, *chronology*, *Marbled Murrelet*, *radio-telemetry*, *seabird*.

Técnicas para Investigar la Cronología Reproductiva de *Brachyramphus marmoratus* en Caleta Desolación, Columbia Británica

Resumen. Utilizamos varios métodos para investigar la cronología reproductiva de la población de *Brachyramphus marmoratus* en la Caleta Desolación de la Columbia Británica desde 1996 a 1998. Encontramos variaciones temporales en la época reproductiva entre años. En promedio, la estación reproductiva se extendió del 21 de abril al 5 de septiembre. Evaluamos el sesgo de los métodos utilizados comparando los resultados individuales con los resultados de la cronología obtenida al integrar todos los métodos. Los conteos de juveniles en el mar estuvieron sesgados hacia aquellas aves que anidan temprano, no detectando aproximadamente 24% de los juveniles producidos en la estación reproductiva. Los otros dos métodos, análisis fisiológico de muestras de sangre para detectar el precursor de vitelogenina en la yema y monitoreo por telemetría, podrían producir una distribución completa de las etapas reproductivas siempre que el muestreo se lleve a cabo a lo largo de todo el período de puesta. Las observaciones directas en los sitios de anidación, la fecha de la primera observación de juveniles en el mar y las observaciones de aves con pescado en el pico produjeron datos insuficientes para ser considerados indicadores únicos de la cronología reproductiva para esta especie. Con base en una revisión bibliográfica se investigó la sincronía reproductiva en álcidos, encontrándose que ésta no está relacionada con hábitos alimenticios pero que aumenta con la latitud (41% de la variación fue explicada por cambios latitudinales). Sin embargo, *B. marmoratus* se reprodujo menos sincrónico que lo predicho para un álcido a esta latitud (50°N).

INTRODUCTION

Details of breeding chronology and its variability are crucial to understanding life-history strat-

egies and environmental influences on reproduction (Birkhead and Harris 1985, Perrins et al. 1991). Most research on the timing of breeding in seabirds has been conducted on land at breeding colonies where large samples can be obtained year after year (Gaston and Jones 1998). Unlike most seabirds and nearly unique among members of their family (Alcidae), Marbled Murrelets (*Brachyramphus marmoratus*) are

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known for nesting solitarily on the mossy branches of large-diameter trees, and for their elusive breeding habits (Nelson 1997).

Its cryptic nesting behavior makes the Marbled Murrelet a difficult species to study, constraining the amount and type of information collected; therefore, chronology estimates have been largely based on incidental or fortuitous observations pooled over several locations and years (Carter and Sealy 1987, Hamer and Nelson 1995, Nelson and Hamer 1995, Ralph et al. 1995, Nelson 1997). Consequently, the details of Marbled Murrelet breeding chronology and breeding biology have remained as significant gaps in our knowledge of the life history of this threatened species. We studied the breeding chronology of the Marbled Murrelet population at Desolation Sound, British Columbia, Canada, during three breeding seasons. Each year, we pooled data from several methods. We examined potential biases of these methods and their effects on the interpretation of the results. We also examined the interannual variability in timing of breeding.

Marbled Murrelets are thought to be more asynchronous in breeding than other alcids, perhaps because of their solitary nesting habits (Hamer and Nelson 1995) or as a strategy to reduce the risk of nest predation. We tested the hypothesis that Marbled Murrelets are less synchronous breeders than other alcids. We also examined the relationship between latitude, feeding habits, and breeding synchrony by looking at laying dates reported for alcids in other studies. In addition we tested for differences in the lengths of the breeding season among Marbled Murrelets breeding at different latitudes.

METHODS

Fieldwork was conducted in Desolation Sound from 1996–1998. Data on egg laying, hatching, and fledging were collected using at-sea surveys, physiological analysis, radio-telemetry, and observations in the forest.

The survey area included the southern portion of Desolation Sound (between 50°04'N, 124°50'W and 50°07'N, 124°44'W) and the adjacent glacial fjords of Malaspina, Lancelot, Okeover, and Theodosia Inlets (for a map of the study area see Loughheed et al. 2002). At-sea surveys were conducted from a 4.5-m hard-shell inflatable boat in 1996 and 1997, and from a comparable 5.2-m fiberglass boat in 1998 fol-

lowing a standardized strip transect protocol with one driver and two observers, one on each side of the vessel (Resources Inventory Committee 1995). The transect was 92 km long and 600 m wide, covering 50.2 km² of water. Surveys were conducted from early in the morning to early in the afternoon, but when ocean conditions were not favorable in the morning surveys were conducted in the afternoon. A global positioning system ensured that all surveys followed the same route. At-sea surveys were conducted between May and mid-August each year, after which time hatch-year (HY) birds cannot be accurately differentiated at a distance from after-hatch-year (AHY) birds in basic plumage (Carter and Stein 1995); we confirmed this by studying the characteristics of captured HY and AHY birds in the study area (LWL, unpubl. data). We ended the survey period when we observed AHY birds entering advanced body molt and starting wing molt. Surveys were canceled during rain or rough seas (beyond 2 on the Beaufort scale). Totals of 24, 23, and 17 surveys were completed during the 1996, 1997, and 1998 breeding seasons, with an average time between surveys of 4, 4, and 6 days, respectively (range 1–12 days).

Observers recorded the presence of murrelets holding fish. Following Sealy (1974), we used the initiation of fish-holding behavior, which implies that adults are feeding nestlings, as direct evidence of the beginning of hatching. Observers also recorded plumage of murrelets: juvenile or alternate plumage, and evidence of body or wing molt. We present the total number of HY birds recorded during the surveys each year and the average number of HY birds recorded per survey. The lack of information of fledgling emigration rates at sea has previously limited the use of HY bird sightings to determining only the beginning of fledging (Hamer and Nelson 1995), and not its extent. For this study, we used a correction to estimate the number of birds that were likely to stay in the area, which allowed us to estimate the frequency of fledging throughout the breeding season. This correction takes into account the number of juveniles counted in the previous survey that did not emigrate; therefore only “new” (not previously counted) HY birds are included in the sample. In Desolation Sound, we estimated that 17% of HY birds dispersed from the survey area daily (Loughheed et al. 2002).

Egg-laying dates for captured female Marbled Murrelets were estimated by measuring the levels of vitellogenic zinc (VTG-Zn) in the plasma, an index of vitellogenin (VTG). VTG is an important egg-yolk precursor of oviparous vertebrates, which is synthesized and secreted by the liver in response to oestradiol (E2), and is greatly elevated in the blood during egg production (Griffin and Hermier 1988, Mitchell and Carlisle 1991). Vanderkist (1999) used Cassin's Auklets (*Ptychoramphus aleuticus*) to validate the technique of using the level of VTG-Zn as an indicator of fecund Marbled Murrelets because they are similarly sized alcids, they lay one egg, and both breeding chronology and the process of egg formation (Astheimer 1986) are known. Marbled Murrelets with levels of VTG-Zn $\geq 0.61 \mu\text{g mL}^{-1}$ VTG-Zn are thought to be producing eggs (Vanderkist 1999). VTG-Zn levels were measured for Marbled Murrelets captured between 6 June and 13 August in 1996 and between 14 May and 11 August in 1997 at Theodosia Inlet by mist netting (Kaiser et al. 1995). The levels of VTG-Zn were also analyzed for murrelets captured in Desolation Sound from 14 May–19 June and from 3 July–7 August in 1997 by nightlighting (Whitworth et al. 1997). We assumed that the process of egg formation in Marbled Murrelets is similar to that of Cassin's Auklets and takes about 14 days (Astheimer 1986). Assuming a random sample, captured female murrelets with elevated VTG-Zn would have been, on average, halfway through egg formation; therefore, we estimated laying date by adding 7 days to the capture date of birds showing elevated levels of VTG-Zn.

Radio-transmitters were used on 40 Marbled Murrelets to locate nests and study activity patterns of nesting birds in 1998. Murrelets were captured by nightlighting from 4 May–18 May. Transmitters were attached using a subdermal anchor modified from the technique of Newman et al. (1999), but we used epoxy glue instead of a suture to secure the device. Radio-transmitters were manufactured by ATS (Model 394, Advanced Telemetry Systems, Isanti, Minnesota), weighed 2.0 g, and had a battery life of 45 days. We radio-tracked the birds every day, weather permitting, by boat, helicopter, or both. We tracked the daily patterns of presence or absence of radio-marked birds on the water to detect changes in nest status. Marbled Murrelets have 24-hr incubation shifts, with one adult brooding

while the other forages at sea (Simons 1980, Hirsch et al. 1981, Nelson and Peck 1995). We defined egg-laying date as the date when a breeding bird equipped with a radio-transmitter started to show a daily "on-off" pattern at sea.

Observations of seven active nests, four from 1996 (Manley 1999) and three from 1998, located using a combination of dawn activity surveys and tree climbing in old-growth forest adjacent to Desolation Sound, were also incorporated into the estimates of breeding chronology. Because these nests were found at different stages of the breeding cycle, and the nests were only visited a few times during the breeding season, we were not able to determine exact start and end dates of the breeding periods. For all nests we were only able to estimate intervals in which hatching, fledging, incubation, or chick rearing occurred, except for one nest for which we determined fledging date.

BREEDING CHRONOLOGY

We estimated the breeding chronology for each year of the study by pooling data from all the methods used that year, and the overall breeding chronology by averaging results from the three years. Incubation was defined as the interval from the first detection of laying to the last detection of hatching, and chick rearing as the interval from the first detection of hatching to the last detection of fledging. Because Marbled Murrelet breeding was asynchronous (see Results), with incubation and chick rearing spread over a long period, we also estimated core incubation and core chick-rearing periods for each year. The core periods were estimated as the middle 50% of the frequency distribution for incubation or chick rearing. Each of the methods described above produced information on laying, hatching, or fledging dates, except for some of the forest observations. The unknown events for each known event were extrapolated assuming a 30-day incubation period and a 28-day nestling period, following Carter and Sealy (1987) and Hamer and Nelson (1995), to allow comparisons with other studies.

COMPARING METHODS

We compared laying, hatching, and fledging periods separately by method and by year to detect potential biases in each method. For methods that produced frequency distribution data, we compared the fledging dates with one-way

ANOVA on log-transformed data of (1) corrected juvenile counts from at-sea surveys vs. physiological analysis of VTG-Zn for 1997, and (2) corrected juvenile counts from at-sea surveys vs. radio-telemetry for 1998.

We calculated the proportion of fledging events that were likely missed during the at-sea surveys in 1997 at the end of the season. Two methods that produced frequency distribution data were available, at-sea surveys and VTG-Zn analysis. We combined the data from these two methods to obtain a complete distribution of fledging events. We then compared the date of the last at-sea survey to the estimated distribution of fledging, and calculated the proportion of fledging events for the missed period.

INTERANNUAL VARIABILITY

Interannual variability among 1996, 1997, and 1998 was evaluated in two ways: (1) by comparing the midpoints of the range of breeding-season dates, and (2) by comparing the timing of fledging of juveniles from at-sea survey counts. Although at-sea surveys did not sample the end of the fledging season, they were conducted at equivalent periods each year of the study, from the appearance of the first HY bird until the adults began to molt. Differences in the timing of fledging were tested with one-way ANOVA on log-transformed data of HY bird counts corrected for juvenile dispersal. Pairwise comparisons were done with a post-hoc Student Newman-Keuls test.

BREEDING SYNCHRONY

We tested for relationships between latitude, the primary type of food fed to chicks (fish or plankton) and breeding synchrony among 22 members of the family Alcidae, using information published in the literature (see Appendix), first with ANCOVA (food type vs. breeding synchrony, covariate latitude) and then with univariate least-squares linear regression models using the range of laying dates (from the date that the first egg was detected to the date that the last egg was detected). We chose to use the range of laying dates because it is the most commonly reported statistic of breeding synchrony. Details of the data selection are explained in the Appendix. To determine if breeding synchrony of Marbled Murrelets is different from that of other Alcidae, we compared our estimate of the length of the laying period to the 95% confidence in-

tervals around the predicted value from the regression of range of laying dates of other alcids on latitude (Sokal and Rohlf 1981). We looked for an effect of taxonomic position on breeding synchrony by comparing the mean laying period length within subfamilies of alcids (following Strauch 1985) with one-way ANOVA. In addition, we used least-squares regression to test the hypothesis that the differences in the duration of the breeding season are related to latitude using information from this study and information reported for Marbled Murrelets in the literature (Nelson and Hamer 1995).

We used SAS (SAS Institute 1996) for all statistical analyses. Dependent variables were first tested for normality using Shapiro-Wilk tests and were log-transformed prior to analyses if necessary (Sokal and Rohlf 1981). Values are reported as mean \pm SE unless otherwise indicated. Statistical significance was accepted at $P \leq 0.05$.

RESULTS

SURVEYS AT SEA

Surveys at sea were done from 14 May–14 August in 1996, 11 May–5 August in 1997, and 6 May–12 August in 1998. Fish-holding behavior was first detected on 1 June in 1996, 24 May in 1997, and 7 June in 1998 (Table 1). HY birds were observed from 25 June–14 August in 1996, 27 June–5 August in 1997, and 11 June–12 August in 1998. The last dates of observations of HY birds reflect the end of the surveying period (Table 1). Totals of 159, 38, and 29 HY Marbled Murrelets were counted during surveys in 1996, 1997, and 1998. The average number of HY birds per survey was 9.3 in 1996, 2.7 in 1997 and 2.4 in 1998. Totals of 67, 21, and 20 “new” HY birds were estimated after correcting the number of observed HY birds for the daily rate of emigration (see Lougheed et al. 2002). The proportion of the fledging season missed by at-sea surveys was obtained by comparing the date of the last at-sea survey to the estimated distribution of fledging. Approximately 24% of the fledging period, as derived from VTG-Zn indicators, was missed by surveys.

PHYSIOLOGICAL ANALYSIS: 1996–1997

No egg-producing females were detected from the 1996 mist-net samples (mean VTG-Zn = $0.18 \pm 0.15 \mu\text{g mL}^{-1}$, $n = 24$), and only two egg-producing females were detected from the

TABLE 1. Laying, hatching and fledging dates of Marbled Murrelets in Desolation Sound, British Columbia, estimated by several methods for 1996, 1997 and 1998. Each method provided an estimate of a known event (boldface) that was used to calculate the events that the method did not detect. Data from forest surveys for 1996 and 1998 represent the range estimated from all nest observations.

Year	Method	Laying		Hatching		Fledging		<i>n</i>
		Start	End	Start	End	Start	End	
1996	Fish-holding ^a	2 May	—	1 Jun	—	29 Jun	—	1
	HY counts at sea	28 Apr	17 Jun	28 May	17 Jul	25 Jun	14 Aug	67 ^b
	Forest ^c	12 May	19 Jul	11 Jun	18 Aug	16 Jul	15 Sep	4
1997	Fish-holding ^a	24 Apr	—	24 May	—	21 Jun	—	1
	HY counts at sea	30 Apr	8 Jun	30 May	8 Jul	27 Jun	5 Aug	21 ^b
	VTG-Zn	21 May	10 Jul	20 Jun	9 Aug	18 Jul	6 Sep	23
1998	Fish-holding ^a	8 May	—	7 Jun	—	5 Jul	—	1
	HY counts at sea	14 Apr	15 Jun	14 May	15 Jul	11 Jun	12 Aug	20 ^b
	Telemetry	11 May	19 Jun	10 Jun	19 Jul	8 Jul	16 Aug	24
	Forest	1 Jun	30 Jun	1 Jul	30 Jul	29 Jul	27 Aug	3

^a The first observation of fish-holding behavior each year, used to estimate the beginning of laying and fledging only.

^b Number of hatch-year birds, corrected for local survival.

^c Manley (1999).

1997 mist-net samples (mean VTG-Zn = $0.18 \pm 0.29 \mu\text{g mL}^{-1}$, $n = 52$, Fig. 1). In 1997, 21 egg-producing females were captured by night-lighting (mean VTG-Zn = $1.93 \pm 2.66 \mu\text{g mL}^{-1}$, $n = 55$, Fig. 1); 20 in the first capture period (14 May–19 June) and one on 3 July in the second capture period (3 July–7 August). Unfortunately, no samples were available from 20 June–2 July 1997 due to decreased night-

lighting effort. The laying period estimated from analysis of VTG-Zn during 1997 was 21 May–10 July (Table 1).

RADIO-TELEMETRY: 1998

Twenty-three active nests were located from birds with radio-transmitters. At one of these nests both members of the pair had been radio-tagged (24 of 40 breeding birds). All birds started incubation between 11 May and 19 June (Table 1). On average, birds started incubation 12.6 ± 9.6 days ($n = 24$) after capture, except for one bird that may have already been incubating when captured.

FOREST OBSERVATIONS

Of the seven active nests found by dawn activity surveys and tree climbing, one (in 1998) was monitored around fledging, three were monitored before and after hatching or fledging, and three were monitored only during incubation or chick rearing (Table 1).

BREEDING CHRONOLOGY

Chronology estimates varied by method (summarized in Table 1). This variability could have been due to chance variation or bias. The beginning of laying, hatching, and fledging periods predicted from the initiation of fish-holding behavior each season were similar to the estimates from HY survey counts for 1996 and 1997 but

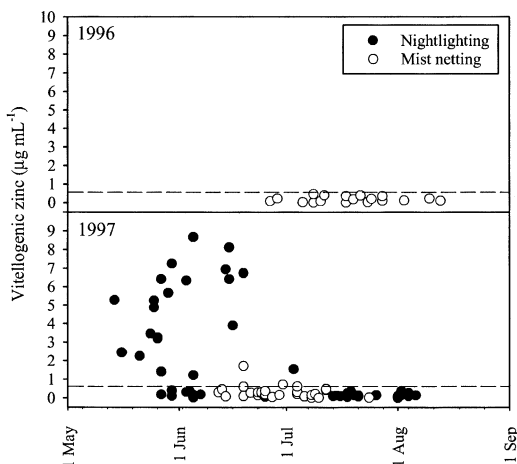


FIGURE 1. Levels of vitellogenin zinc (VTG-Zn) for Marbled Murrelets captured during the breeding seasons of 1996 (top) and 1997 (bottom) at Desolation Sound. Birds captured by mist netting are represented by unfilled circles, and birds captured by nightlighting by solid circles. Values below the dashed line indicate birds that were not producing eggs (Vanderkist 1999).

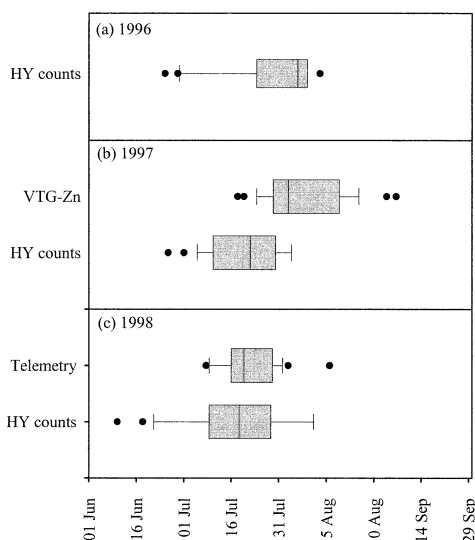


FIGURE 2. Fledging dates derived from (a) HY counts at sea ($n = 67$) from 1996, (b) HY counts at sea ($n = 21$) and egg-producing females from VTG-Zn analysis ($n = 23$) for 1997, and (c) HY counts at sea ($n = 20$) and radio-telemetry ($n = 24$) for 1998. Date of fledging was significantly different between HY counts and VTG-Zn analysis, but not significantly different between HY counts and radio-telemetry methods. Date of fledging from HY counts differed among years. Plots show the median, 10th, 25th, 75th, 90th percentiles, and outliers.

not for 1998, when initiation of fish-holding occurred later.

Chronology estimates derived from HY counts at sea and VTG-Zn analysis for 1997 were significantly different ($F_{1,42} = 25.4$, $P < 0.01$). Data from HY counts suggested an earlier breeding period than that derived from VTG-Zn data (Fig. 2b). The median fledging date was 22 July for HY bird counts and 3 August for VTG-

Zn, with a 17-day overlap between the two. Pooling both methods, the median fledging date was 30 July.

There were no significant differences between chronologies derived from HY counts at sea and radio-telemetry data from 1998 ($F_{1,42} = 1.9$, $P = 0.17$, Fig. 2c). The median fledging date was 19 July for HY counts at sea and 20 July for radio-telemetry; however, the breeding period derived from radio-telemetry started and ended later than the breeding period derived from HY bird counts. Breeding intervals calculated from observations of active nests in 1996 and 1998 both suggested later breeding compared to the other methods (Table 1).

The murrelet breeding season in Desolation Sound, derived from pooling results from all the methods, ranged from 28 April to 15 September in 1996 (140 days), from 24 April to 6 September in 1997 (135 days), and from 14 April to 27 August in 1998 (135 days), with a three-year average of 137 days. Among methods, there was an overlap of 79 days on average between incubation and chick rearing, but the overlap was only 20 days for the core periods (Table 2).

INTERANNUAL VARIABILITY

The comparison of the midpoints of the breeding seasons showed a trend for increasingly early breeding, from 7 July in 1996 to 30 June in 1997 and 20 June in 1998. Timing of fledging varied significantly among years ($F_{2,105} = 9.4$, $P < 0.01$). Fledging was latest in 1996, followed in order by 1997 and 1998 (Fig. 2a). Pairwise comparisons were significant between 1996 and 1997 and between 1996 and 1998, but not between 1997 and 1998.

TABLE 2. Ranges and core periods of incubation and chick rearing for Marbled Murrelets in Desolation Sound during the 1996, 1997, and 1998 breeding seasons, determined by pooling results of four methods.

Year		Incubation	Duration (days)	Chick rearing	Duration (days)
1996	Range	28 Apr–18 Aug	112	28 May–15 Sep	110
	Core ^a	24 May–12 Jul	49	23 Jun–9 Aug	47
1997	Range	24 Apr–9 Aug	107	24 May–6 Sep	105
	Core ^a	22 May–9 Jul	48	21 Jun–6 Aug	46
1998	Range	14 Apr–30 Jul	107	14 May–27 Aug	105
	Core ^a	13 May–3 Jul	51	12 Jun–29 Jul	47
Average	Range	22 Apr–8 Aug	109	22 May–5 Sep	107
	Core ^a	19 May–8 Jul	49	18 Jun–4 Aug	47

^a Core period calculated by taking the middle 50% of observations.

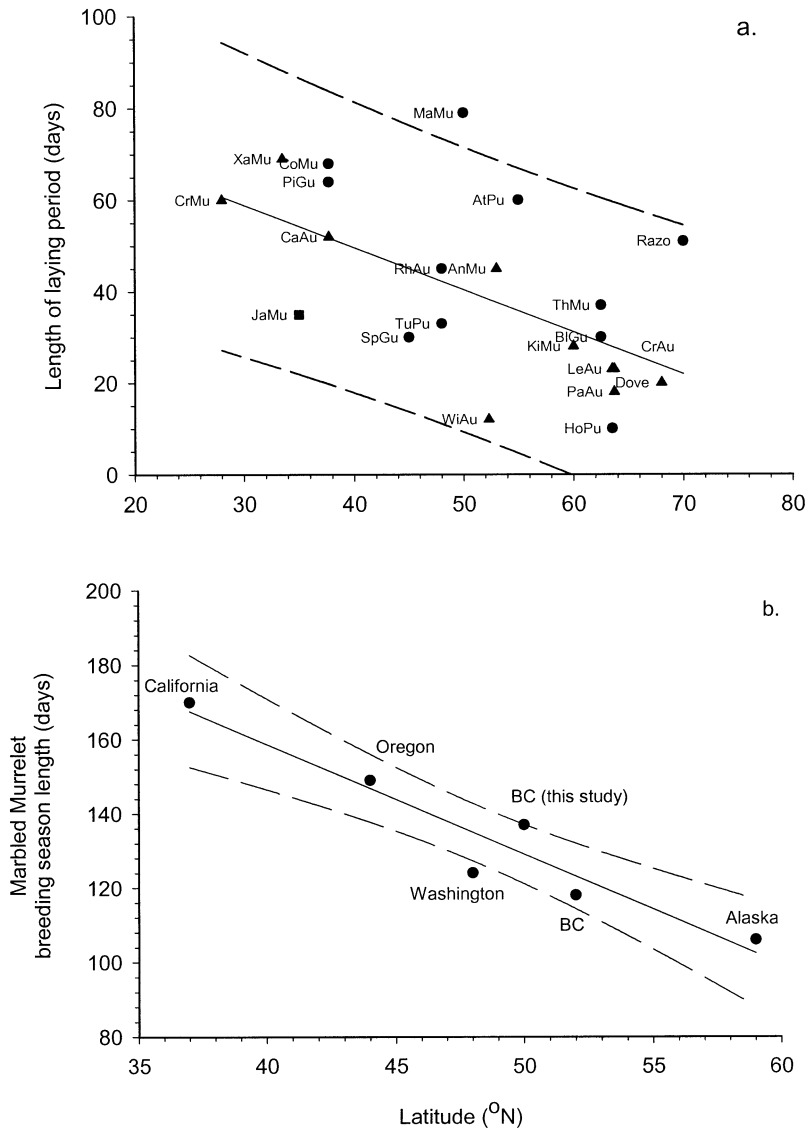


FIGURE 3. (a) Range of laying (days) vs. latitude for the 22 members of the Alcidae, showing the regression line (solid line) with 95% CI (broken lines). Marbled Murrelet laying range falls outside the 95% CI. See Appendix for species codes. (b) Relationship between length of breeding season and latitude, from this study and other studies (Nelson and Hamer 1995), showing regression line (solid line) with 95% CI (broken lines).

BREEDING SYNCHRONY

There was no significant difference in latitude-adjusted breeding synchrony between the groups of alcids that feed their chicks either fish or plankton (ANCOVA $F_{1,18} = 3.4$, $P = 0.08$). Latitude was strongly associated with breeding synchrony (ANCOVA $F_{1,18} = 15.9$, $P < 0.001$). Using a univariate least-squares model, about 41% of the variation in range of laying dates was ex-

plained by latitude ($y = -0.93x + 86.7$, $r^2 = 0.41$, $P < 0.05$; Fig. 3a). Marbled Murrelet laying range was 79 days based on the three-year average, which was greater than the predicted value for an alcid at this latitude (50°N), and fell outside the 95% confidence intervals. Laying dates did not differ significantly among subfamilies ($F_{4,17} = 1.2$, $P = 0.33$). The length of the Marbled Murrelet breeding season was negative-

ly related to latitude ($y = 2.96x + 277.3$, $r^2 = 0.89$, $P < 0.01$; Fig. 3b).

DISCUSSION

BREEDING CHRONOLOGY

The breeding season of Marbled Murrelets in Desolation Sound lasted on average from 21 April to 5 September. The duration of the breeding season was longer and with a greater overlap between incubation and chick rearing than previously reported for British Columbia: 118 days (Hamer and Nelson 1995) compared to our 137-day average. The differences could reflect the differences in latitude between Hamer and Nelson's study (52°N) and ours (50°N); murrelet breeding season shortens with increasing latitude. The core incubation and core chick-rearing periods had a smaller overlap than the whole range, with core incubation occurring mostly in June and core chick rearing occurring mostly in July.

INTERANNUAL VARIABILITY

The duration of the breeding season was broadly consistent among years, but there was a trend toward increasingly early breeding from 1996 to 1998. In addition, mean fledging, as measured by HY counts at sea, occurred significantly later in 1996 than in 1997 and 1998, with no differences between 1997 and 1998. Changes in the marine environment affect breeding cycles of seabird communities (Nelson 1997, Gaston and Jones 1998). This trend of earlier breeding for the murrelet population in Desolation Sound coincides with significant interannual increases of sea-surface temperature during the breeding season in the study area. Mean sea-surface temperature was lower in 1996 (15.8°C) than in 1997 (16.5°C) and 1998 (16.6°C; Lougheed 1999).

COMPARING METHODS

The estimation of breeding chronology by method and by year using data collected from within one population permitted the assessment of biases and limitations in each method. Some estimates of breeding chronology, calculated using two different methods for the same year, produced different results in terms of length and timing of breeding; however, the biases in some instances were methodological and could be overcome in future studies. Methods that produce large sample sizes and frequency distributions of the breeding events such as physiolog-

ical analysis (VTG-Zn), telemetry monitoring of breeding activities, and HY counts at sea, conducted throughout the breeding season, are preferable to methods that produce a few scattered data points. Other methods such as the first fish-holding event, the first sighting of a juvenile at sea, and various types of forest observations are less desirable because they are limited by small sample sizes, and only permit researchers to estimate ranges of breeding dates. However, these methods are still of value because in many cases they are the only information available for a basic understanding of the breeding chronology in an area (e.g., Hamer and Nelson 1995, Nelson and Peck 1995, Manley 1999).

Estimates of initiation of the breeding periods were similar for fish-holding behavior and HY count data, except for 1998 when fish-holding estimates were 25 days later than those from HY counts. In Theodosia Inlet, the number of birds holding fish increased at dusk (P. Dehoux, unpubl. data), and other studies have found that murrelets feed chicks mostly at dawn and dusk (Carter and Sealy 1990, Nelson 1997). In 1998, surveys were carried out only during the morning to early afternoon, so we may have missed fish-holding behavior. The use of fish-holding behavior as an indicator of hatching relies on the assumption that birds are using the monitored area as their primary feeding area during that stage of the breeding season. It also has the disadvantage that fish-holding behavior could be missed during surveys for two reasons: (1) because most birds are seen holding fish toward dusk, while most surveys are carried out during the day, and (2) fish-holding behavior is difficult to observe and could go undetected easily. If fish holding is to be used as an indicator of hatching, we recommend that surveys for this purpose be carried out at dusk.

The chronologies estimated from HY counts and from VTG-Zn analysis were biased in opposite directions. The breeding season estimated from survey counts started and ended earlier than that estimated from VTG-Zn analysis. The bias from the VTG-Zn analysis was methodological: evidence of egg production might have been detected earlier had the captures by night-lighting started earlier. This bias could be avoided if capture and blood sampling were conducted throughout the laying period. The bias of HY counts stemmed from the difficulty in distinguishing HY birds from AHY birds that had

started their prebasic molt. This difficulty caused us to truncate the data set, and miss an estimated 24% of the fledglings. This could explain the apparent earlier ending of the breeding season when estimated from surveys of HY birds. The comparison of HY birds from at-sea surveys is, however, useful due to the consistency of the method (the same survey route is used every year), which allows for interannual comparisons.

Because HY counts were biased toward the early part of the breeding season, and there were no significant differences between telemetry and HY count estimates, we suggest that radio-telemetry in 1998 was similarly biased. The fact that radio-transmitters were deployed on birds only early in the season and not throughout the laying period may have biased the sampling toward earlier breeders.

The breeding estimates from forest observations in 1996 and 1998 were the latest, overall 9 days later than the latest breeding date estimated from VTG-Zn levels. Manley (1999) speculated that the 1996 bird might have re-nested based on earlier evidence of breeding at the same site.

Individual variation in the length of incubation and nestling periods may have affected our estimates of breeding chronology. In other alcids, the length of incubation and nestling periods varied among years and within seasons (Ainley and Boekelheide 1990). Marbled Murrelet nests monitored in Desolation Sound from 1998–2000 showed that the average incubation and nestling periods were both 30 days, and that incubation ranged from 28–34 days ($n = 15$; Bradley 2002) and the nestling period also ranged from 28–34 days ($n = 48$; R. W. Bradley, unpubl. data). For Marbled Murrelet nests monitored elsewhere ($n = 4$), incubation varied from 28–30 days and the nestling period from 27–40 days (Simons 1980, Hirsch et al. 1981, Nelson and Peck 1995). To allow comparisons with other studies, we assumed a 30-day incubation period and a 28-day nestling period (Carter and Sealy 1987, Hamer and Nelson 1995).

BREEDING SYNCHRONY AND DURATION

Our analyses indicate that Marbled Murrelets breed significantly more asynchronously than predicted at this latitude, based on the measured synchrony of other Alcidae. The decision to breed is generally thought to be state dependent (McNamara and Houston 1996). Marbled

Murrelet breeding asynchrony might be a response to the seasonal (temporal) availability of prey. The relationship between Marbled Murrelet prey availability and reproductive success is unknown (Burkett 1995). It is also possible that breeding asynchrony in Marbled Murrelets is related to their solitary nesting behavior. Seabird colonies are generally viewed as information centers where seabirds receive clues from neighbors regarding the locations of foraging areas (Kaiser 1994), so synchrony with neighbors during the breeding season is important. Being non-colonial, murrelets do not have the opportunity to exchange information at the nest site and so would gain no advantage from synchrony. Kaiser (1994) suggested that the Marbled Murrelet's inland nesting habits allow them to take advantage of high prey concentrations in the coastal fjords during the summer and related these to the evolution of solitary nesting in this species.

A strong relationship exists between latitude and the duration of the breeding season among Marbled Murrelets breeding at different latitudes. Marbled Murrelets have the longest and earliest breeding seasons in California, and the shortest and latest in Alaska (Carter and Sealy 1987, Hamer and Nelson 1995). The latter may explain the difference between our estimates of the duration of the breeding season and the estimate for British Columbia reported by Hamer and Nelson (1995), which was based mostly on data collected at higher latitudes.

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APPENDIX. Length of the laying period for 22 species of Alcidae reported in the literature and used to evaluate the effect of latitude on breeding synchrony. When more than one year was reported, the mean range of all years was used. In some cases, such as the Common Murre, several years of data were available for several colonies at different latitudes. We used data from the study that reported the most years of complete ranges of laying dates. When laying and hatching were reported as ranges of dates, we used the midpoints of each of these ranges to estimate the extent of the laying period. In other cases, data were sparse, so we used estimates from Gaston and Jones (1998). Dates that were indicated as renests were excluded, to make all data comparable. Subfamily and species names are as in Table 2 of Gaston and Jones (1998), based on Strauch (1985).

Subfamily	Common name	Scientific name	Code	Latitude (°N)	Length of laying period (days)	Primary chick diet	Source
Aethini	Cassin's Auklet	<i>Ptychoramphus aleuticus</i>	CaAu	37.7	52 ^a	Plankton	Ainley et al. 1990a; Vermeer 1987
	Parakeet Auklet	<i>Aethia psittacula</i>	PaAu	63.7	18	Plankton	Sealy 1975; Vermeer 1987
	Least Auklet	<i>Aethia pusilla</i>	LeAu	63.7	23	Plankton	Bedard 1969; Vermeer 1987
	Whiskered Auklet	<i>Aethia pygmaea</i>	WiAu	52.3	12	Plankton	Knudson and Byrd 1982; Vermeer 1987
Alcini	Crested Auklet	<i>Aethia cristatella</i>	CrAu	63.5	23	Plankton	Platt et al. 1990; Vermeer 1987
	Dovekie	<i>Alle alle</i>	Dove	68	20 ^b	Plankton	Gaston and Jones 1998; Bradstreet and Brown 1985
	Razorbill	<i>Alca torda</i>	Razo	70	51	Fish	Gaston and Jones 1998; Bradstreet and Brown 1985
Brachyramphini	Common Murre	<i>Uria aalge</i>	CoMu	37.7	68 ^c	Fish	Boekelheide et al. 1990; Vermeer 1987
	Thick-billed Murre	<i>Uria lomvia</i>	ThMu	62.5	37	Fish	Gaston and Jones 1998; Bradstreet and Brown 1985
	Kitlitz's Murrelet	<i>Brachyramphus brevirostris</i>	KiMu	60	28	Plankton	Day 1996; Day et al. 1999
Cepphini	Marbled Murrelet	<i>Brachyramphus marmoratus</i>	MaMu	50	79	Fish	This study; Nelson 1997
	Black Guillemot	<i>Cepphus grylle</i>	BlGu	62.5	30	Fish	Gaston et al. 1985; Bradstreet and Brown 1985
	Pigeon Guillemot	<i>Cepphus columba</i>	PiGu	37.7	64 ^d	Fish	Ainley et al. 1990b; Vermeer 1987
	Spectacled Guillemot	<i>Cepphus carbo</i>	SpGu	45	30 ^b	Fish	Gaston and Jones 1998; Vermeer 1987
	Xantus' Murrelet	<i>Synthliboramphus hypoleucus</i>	XaMu	33.5	69	Plankton	Murray et al. 1983; Drost 1995
	Craveri's Murrelet	<i>Synthliboramphus craveri</i>	CrMu	28	60 ^b	Plankton	Gaston and Jones 1998
Fratrerculini	Ancient Murrelet	<i>Synthliboramphus antiquus</i>	AnMu	53	45	Plankton	Gaston and Jones 1998; Gaston 1994
	Japanese Murrelet	<i>Synthliboramphus wumizusume</i>	JaMu	35	35 ^b	?	Gaston and Jones 1998
	Rhinoceros Auklet	<i>Cerorhinca monocerata</i>	RhAu	48	45	Fish	Gaston and Jones 1998; Vermeer 1987
	Tufted Puffin	<i>Fratrercula cirrhata</i>	TuPu	48	33	Fish	Burrell 1980; Vermeer 1987
	Atlantic Puffin	<i>Fratrercula arctica</i>	AtPu	55	60	Fish	Harris 1984; Bradstreet and Brown 1985
	Horned Puffin	<i>Fratrercula corniculata</i>	HoPu	63.7	10 ^e	Fish	Sealy 1973; Vermeer 1987

^a 1970–1983.

^b Approximate data.

^c 1972–1983.

^d 1971–1982.

^e Small sample.