The Condor 95:831–848

ACTIVITY PATTERNS OF MARBLED MURRELETS IN OLD-GROWTH FOREST IN THE QUEEN CHARLOTTE ISLANDS, BRITISH COLUMBIA[1]

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Abstract. Activity patterns of Marbled Murrelets (*Brachyramphus marmoratus*) in old-growth forest were compared at two sites in the Queen Charlotte Islands, British Columbia. Number of detections peaked in late July at both sites. More activity was recorded on cloudy mornings than on clear mornings and the duration of activity was greater on cloudy days than on clear days. Number of detections, number of calls and duration of the activity period per survey were highly variable and were correlated on a coarse scale (seasonally) but not always on a fine scale (weekly). Activity levels at the two stations were correlated over the entire season but not on a monthly or weekly basis. Detections were always more numerous in the morning than in the evening. Most detections were auditory only, but birds were seen in 20 and 26% of detections at the two sites. Approximately half of visual detections were of silent birds. Most birds sighted were either singles or in pairs and the majority of single birds were silent and tended to fly at lower altitudes than grouped birds. Knowledge of the behavior of Marbled Murrelets at inland locations is essential for the design of survey methodology and interpretation of survey results.

Key words: Marbled Murrelet; Brachyramphus marmoratus; *old-growth forest; activity patterns; British Columbia.*

INTRODUCTION

Concern for Marbled Murrelets (*Brachyramphus marmoratus*) has heightened in recent years due to mounting evidence that the species depends on unique characteristics of old-growth forest for nesting in the southern portion of their range in North America (Binford et al. 1975, Sealy and Carter 1984, Marshall 1988, Quinlan and Hughes 1990, Rodway 1990, Singer et al. 1991). The continuing harvest of old-growth forest habitat has prompted intensive efforts to identify forest stands used by Marbled Murrelets, especially in California, Oregon and Washington (Carter and Erickson 1988; Paton and Ralph 1988; Nelson 1989; Varoujean et al. 1989; Paton and Ralph 1990; Hamer and Cummins 1990, 1991; Paton et al. 1992) and more recently in British Columbia (Eisenhawer and Reimchen 1990, Rodway et al. 1991, Manley et al. 1992). Marbled Murrelet nests are difficult to find, and survey methodology has depended on visual and auditory detections (Paton et al. 1988) of birds flying to and from inland locations. Numbers of detections are used as coarse indicators of habitat use, but interpretations are limited because of the variability in the number of detections at particular sites (Paton et al. 1988, 1990; Nelson 1989; Ralph et al. 1989) and because the behavior of breeding birds in the vicinity of nests is poorly known (Singer et al. 1991). To interpret counts of detections made in different areas and at different times of the breeding season, it is important to know what factors affect the variability of detection counts and how activity levels vary daily, seasonally and geographically. As a detection is broadly defined as "the sighting and/or hearing of a single bird or a flock of birds acting in a similar manner" (Paton et al. 1990), changes

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in flock size or behavior will affect the interpretation of numbers of detections. This becomes important when attempting to compare Marbled Murrelet activity levels among sites and set priorities for habitat protection.

This paper is a portion of a larger study of Marbled Murrelets in the Queen Charlotte Islands, British Columbia (Rodway et al. 1991). Our objectives were to: (1) monitor seasonal changes in Marbled Murrelet activity at two inland sites in old-growth forest habitat where breeding was suspected, (2) determine the effects of weather on inland activity, (3) determine whether numbers of detections per survey, numbers of calls per survey, and duration of activity per survey provide similar measures of activity and show similar trends, (3) compare the variability of those measures between stations and at different temporal scales from daily to seasonally, (5) monitor changes in flock size and behavior over the breeding season, (6) compare evening and morning activity levels, and (7) consider the implications that observed activity patterns have for survey methodology and interpretation of survey results. This study extends our knowledge of the inland behavior of Marbled Murrelets in a poorly studied part of their range (Rodway 1990).

STUDY SITES

The two study sites were located in old-growth (325+ year-old) forest in the Lagins Creek (53°14′14″N, 132°22′33″W) and Phantom Creek (53°20′44″N, 132°20′49″W) valleys on Graham Island in the Queen Charlotte Islands, British Columbia. Stations were 3.6 and 4.8 km inland at elevations of 90 and 250 m respectively. Forest habitat was a Western Redcedar (*Thuja plicata*)/Sitka Spruce (*Picea sitchensis*)—foamflower (*Tiarella unifoliata*) site association within the Wet Hypermaritime Coastal Western Hemlock biogeoclimatic subzone (Banner et al. 1990). Dominant tree species in the vicinity of the stations were Western Hemlock (*Tsuga heterophyla*) and Sitka Spruce. The Lagins Creek survey station was located in the bottom of an east-facing valley in the middle of an alluvial flat about 1 km wide. The station was under an opening in the canopy providing clear visibility of about 20% of the sky. About 80% of the sky was visible at the Phantom Creek station, situated on a road running along the side of a 'V-shaped' valley and overlooking the canopy in the valley bottom. The station was located near the divide between west and east flowing drainage systems. Access to the ocean was to the west. The Lagins Creek valley was encircled by mountains and was probably not used as a fly-way to other areas, whereas the Phantom Creek valley provided access to interior areas of Graham Island and may have been used as a corridor by birds travelling further inland to other sites where Marbled Murrelet activity had been recorded (Rodway et al. 1991).

METHODS

Intensive inventory methods were used at the two fixed stations (Paton et al. 1988, 1990). Morning surveys were conducted in 1990 between 7 May and 23 August at Phantom Creek (n = 49), and between 22 May and 28 July at Lagins Creek (n = 33). Surveys were done in sets of four to six consecutive days repeated at one to two week intervals, except for the week of 21 August when only two surveys were performed (Table 1). Concurrent morning surveys were conducted at the two stations during the weeks of 22 May, 29 May, 12 June, 11 July and 24 July (n = 24). Observations were initially conducted from 45 min before to 75 min after sunrise, but times were changed to 75 min before to 45 min after sunrise on 15 May when it became apparent that Marbled Murrelets were active earlier in the Queen Charlotte Islands than further south, probably due to longer twilight periods. If murrelets were still active at the end of the standard survey period, observations were continued until there was a 15 min interval since the last detection. Evening surveys followed by morning surveys were conducted on 26 nights (19 at Lagins Creek and 7 at Phantom Creek) between 22 May and 27 July from 45 min before to 75 min after sunset. We used sunrise and sunset times for Sandspit, provided by Atmospheric Environment Service, Environment Canada. All times are Pacific Standard Time.

We distinguished primary "keer" calls from other calls and attempted to count all keer calls heard for each detection. When activity was intense, making counting difficult, numbers of keer calls >10 were recorded as "multiple." To analyze total keer calls, we replaced "multiple" with the mean number of calls >10 that were actually counted. The duration of the activity period was defined as the time between the first and the last detection recorded during a survey.

We retained the same observers as long as possible at each station in order to maintain observer consistency. The availability of personnel required that we change observers twice over the season at each station. We assessed inter-observer reliability by having replacement personnel conduct concurrent, independent surveys for two days at the station with the person being replaced. This was not possible for one change in August at Phantom Creek.

Coefficients of variation (CV = 100 × standard deviation/mean) were calculated to assess and compare variability in number of detections, number of calls and duration of activity period per survey. Daily and seasonal activity patterns at each site were compared. Analysis of covariance (ANCOVA) was used to separate effects of weather and date. Weather conditions were divided into two categories: fog or ≥80% cloud (cloudy) and <80% cloud (clear). These categories were used to distinguish overcast, low-light conditions from brighter, high-light conditions. Only birds seen were used to analyze behavior and group size. Tolerance for Type I error was set at 5% for all tests. Residuals were checked for acceptability.

RESULTS

INTER-OBSERVER RELIABILITY

Numbers of detections recorded on the same day at the same site by paired observers were closely correlated ($r = 0.97$, $P = 0.002$, $n = 6$), as were estimates of the duration of activity ($r = 0.96$, $P = 0.003$). Numbers of keer calls estimated by different observers showed more variation, but were still highly correlated ($r = 0.88$, $P = 0.021$). Differences between observers were inconsistent and we concluded that there was no bias through time due to change of observers.

There were significant differences between observers in the proportion of visual detections recorded. One observer stationed at Lagins Creek from 22 May to 20 June recorded very few visual detections and was found to see a consistently lower proportion of birds than the observer replacing her ($\chi^2_1 = 20.96$, $P < 0.0001$). This did not affect the total number of detections she recorded which were similar or higher than those counted by her replacement, but did compromise the analysis of visual detections at Lagins Creek in May and June (see below). The bias in proportion of visual detections recorded was confined to the one observer as other observers recorded proportions similar to the person that replaced her ($\chi^2_1 = 0.53$, $P = 0.465$).

EFFECTS OF WEATHER AND DATE ON ACTIVITY LEVELS

Cloudy weather tended to be more frequent at the Phantom Creek station (62% of survey days) than at Lagins Creek (55% of survey days), but overall weather patterns at the two stations were significantly correlated ($r = 0.70$, $P < 0.001$). The highest proportion of cloudy days occurred in May at Phantom Creek and in June at Lagins Creek. Clear days were more frequent in July at both stations (Table 1). There were no significant differences among months in the proportions of cloudy and clear weather at either station (Phantom Creek: $\chi^2_3 = 0.87$, $P = 0.833$; Lagins Creek: $\chi^2_2 = 3.45$, $P = 0.178$).

Number of detections. Numbers of detections per survey increased from May to July and peaked during the week of 24–28 July at both Phantom Creek and Lagins Creek (Tables 1 and 2, Figs. 1 and 2). At Phantom Creek, numbers of detections increased from May to June ($r^2 = 0.59$, $P < 0.0001$, $n = 32$) and were similar in June and July ($r^2 = 0.19$, $P = 0.060$, $n = 19$). At Lagins Creek, numbers of detections were similar in May and June ($r^2 = 0.01$, $P = 0.67$, $n = 20$), and increased from June to July ($r^2 = 0.50$, $P < 0.0001$, $n = 23$). The number of detections were slightly more numerous at Lagins Creek than at Phantom Creek in May but not in June or July when they were higher at Phantom Creek (Table 1, Figs. 1 and 2). Differences between the two stations were not significant, even in July when the mean difference was 22.1 detections (paired t-test, $t_8 = 1.95$, $P = 0.087$). Activity decreased abruptly during the second week of August at Phantom Creek (Tables 1 and 2, Fig. 1).

The mean number of detections per survey was higher on cloudy days than clear days at Phantom Creek (58.3 ± 3.9 vs. 40.8 ± 5.0) and Lagins Creek (55.6 ± 3.5 vs. 46.1 ± 3.8), though the effect of weather was significant only at Phantom Creek (Table 2).

Number of calls. The mean number of calls >10 that were actually counted per detection were 25.6 ± 0.6 ($n = 553$) at Phantom Creek and 24.0 ± 0.9 ($n = 201$) at Lagins Creek. To analyze total keer calls per survey, a value of 25 was used to replace all records of "multiple" calls. Numbers of calls per detection were not affected by weather and were similar in May, June and

TABLE 1. Marbled Murrelet activity during morning surveys at fixed stations at Phantom Creek and Lagins Creek in 1990.

	Phantom Creek				Lagins Creek			
Date	Cloud cover (%)	No. of detections	No. of keer calls	Duration (min)	Cloud cover (%)	No. of detections	No. of keer calls	Duration (min)
07 May	90	23	318	37				
08 May	100	23	393	51				
09 May	100	24	386	63				
10 May	100	31	527	51				
11 May	90	33	489	60				
12 May	100	36	587	66				
14 May	60	17	282	42				
15 May	100	21	321	64				
16 May	100	41	648	120				
17 May	60	17	325	37				
18 May	100	27	463	63				
19 May	90	21	260	54				
21 May	100	33	272	82				
22 May	0	35	322	63	0	21	163	43
23 May	100	24	191	65	0	36	350	92
24 May	98	19	209	53	100	56	953	72
25 May	10	19	264	71	10	23	355	52
26 May	50	16	130	44	100	38	542	56
29 May	100	32	537	83	100	42	710	110
30 May	25	40	759	80	100	34	711	66
31 May	0	29	516	68	0	48	678	72
01 Jun	0	21	342	43	0	36	697	47
02 Jun	100	46	595	99	100	64	946	99
12 Jun	100	78	1,430	150	100	31	575	73
13 Jun	0	42	559	68	0	39	575	47
14 Jun	0	35	538	68	0	15	255	35
15 Jun	100	82	975	146	100	25	380	84
16 Jun	100	48	864	123	100	26	340	75
19 Jun						49	816	89
20 Jun					100	99	1,946	127
21 Jun					100	47	440	84
22 Jun					100	29	235	96
23 Jun					100	28	351	70
27 Jun	100	92	963	154				
28 Jun	0	56	508	50				
29 Jun	100	48	550	67				
30 Jun	100	78	1,219	113				
01 Jul	100	68	531	86				
11 Jul	100	57	882	66	100	56	711	72
12 Jul	100	78	1,644	85	100	56	534	92
13 Jul	100	106	1,918	131	50	45	753	76
14 Jul	40	87	1,420	103	100	57	987	70
18 Jul					0	63	1,308	56
19 Jul					0	63	908	61
20 Jul					0	79	1,347	62
21 Jul					0	74	1,289	63
24 Jul	40	130	2,064	100	0	88	1,727	84
25 Jul	40	100	1,740	99	0	72	1,466	70
26 Jul	100	155	2,429	150	100	88	1,813	91
27 Jul	1	42	725	101	50	59	1,242	84
28 Jul	0	46	626	61	0	81	1,798	90

TABLE 1. Continued.

	Phantom Creek				Lagins Creek			
Date	Cloud cover (%)	No. of detections	No. of keer calls	Duration (min)	Cloud cover (%)	No. of detections	No. of keer calls	Duration (min)
07 Aug	100	28	256	98				
08 Aug	95	19	44	61				
09 Aug	100	4	14	30				
10 Aug	0	8	60	33				
11 Aug	0	6	25	27				
21 Aug	70	14	124	22				
23 Aug	100	6	17	15				

July at each station (ANCOVA, $P > 0.05$ for all comparisons). They dropped sharply from 24 July to 23 August at Phantom Creek ($r^2 = 0.74$, $P = 0.001$, $n = 12$).

Numbers of calls showed similar seasonal patterns as numbers of detections, increasing from May to July, reaching a maximum during the week of 24–28 July at Phantom Creek and Lagins Creek, and decreasing abruptly in the second week of August at Phantom Creek (Tables 1 and 2, Figs. 1 and 2). We were unable to detect an effect of weather on numbers of calls (Table 2).

Duration of activity. The duration of the Marbled Murrelet morning activity period ranged between 15 and 154 min at Phantom Creek and between 35 and 127 min at Lagins Creek. There was an increase in the duration of activity from May to July at Phantom Creek but not at Lagins Creek (Tables 1 and 2, Figs. 1 and 2). Over the entire season, duration was significantly longer at Phantom Creek than at Lagins Creek (paired t-test, $t_{23} = 2.50$, $P = 0.020$). Duration was similar in both areas in May ($t_7 = -0.64$, $P = 0.54$) and July ($t_8 = 1.91$, $P = 0.093$) but differed in

TABLE 2. Type I error estimates for rejection of null hypotheses of no change in Marbled Murrelet activity due to date and weather. Dependent variables were number of detections, number of calls and duration of activity period per survey at Phantom Creek and Lagins Creek in 1990. Date was treated as a continuous variable and weather was dichotomous (see Methods). Null hypotheses were tested using ANCOVA. An interaction term, Weather·Date, was included in initial models. If the interaction was not significant, it was dropped from the model to test main effects of weather and date. Values for r^2 are from initial models and have 3 degrees of freedom. Where indicated, measurements have been log transformed to meet assumptions of homoscedasticity and normality.

		Weather			Date			Weather·Date		
	r^2	df	F	P	df	F	P	df	F	P
Phantom Creek—morning surveys 7 May to 26 July (n = 40)										
Log # of detections	0.82	1	10.29	0.003	1	148.87	0.000	1	2.29	0.139
Log # of calls	0.67	1	4.04	0.052	1	69.05	0.000	1	1.28	0.265
Log duration	0.50	1	10.27	0.003	1	29.61	0.000	1	0.00	0.991
Phantom Creek—morning surveys 24 July to 23 Aug (n = 12)										
Log # of detections	0.70	1	0.03	0.879	1	18.75	0.002	1	0.20	0.665
Log # of calls	0.72	1	0.41	0.538	1	18.28	0.002	1	0.39	0.548
Log duration	0.88	1	3.41	0.098	1	52.66	0.000	1	1.82	0.214
Lagins Creek—morning surveys 22 May to 28 July (n = 33)										
Log # of detections	0.44	1	0.68	0.416	1	21.67	0.000	1	1.10	0.303
Log # of calls	0.44	1	0.18	0.678	1	19.06	0.000	1	2.68	0.112
Log duration	0.34	1	14.33	0.001	1	1.81	0.189	1	0.40	0.530
Lagins Creek—evening surveys 22 May to 27 July (n = 19)										
Log # of detections	0.71	1	0.29	0.601	1	21.22	0.000	1	0.91	0.355
Number of calls	0.89	1	1.91	0.190	1	41.88	0.000	1	7.32	0.018
Duration	0.42	1	0.63	0.439	1	10.95	0.004	1	0.00	0.984

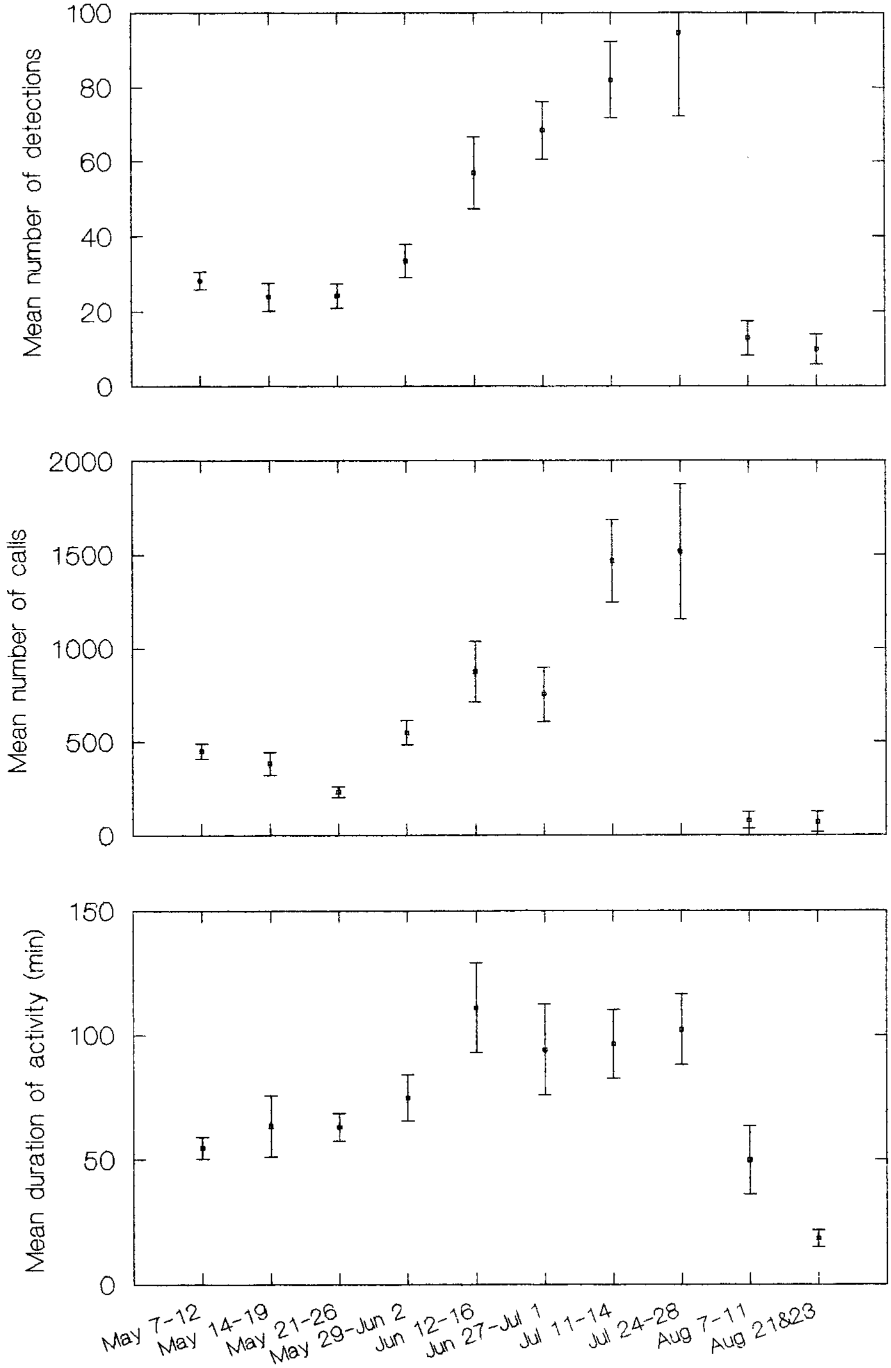

FIGURE 1. Weekly mean (±SE) numbers of Marbled Murrelet detections, keer calls and duration of activity period per survey at Phantom Creek in 1990.

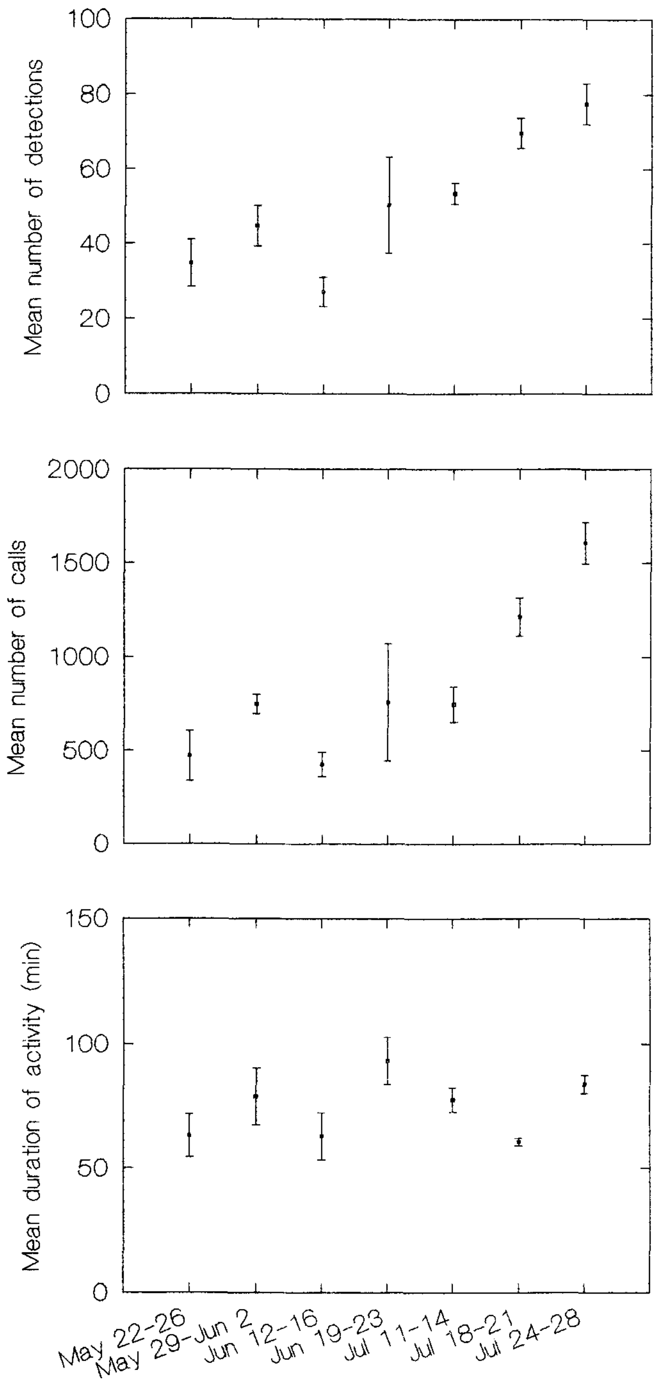

FIGURE 2. Weekly mean (±SE) numbers of Marbled Murrelet detections, keer calls and duration of activity period per survey at Lagins Creek in 1990.

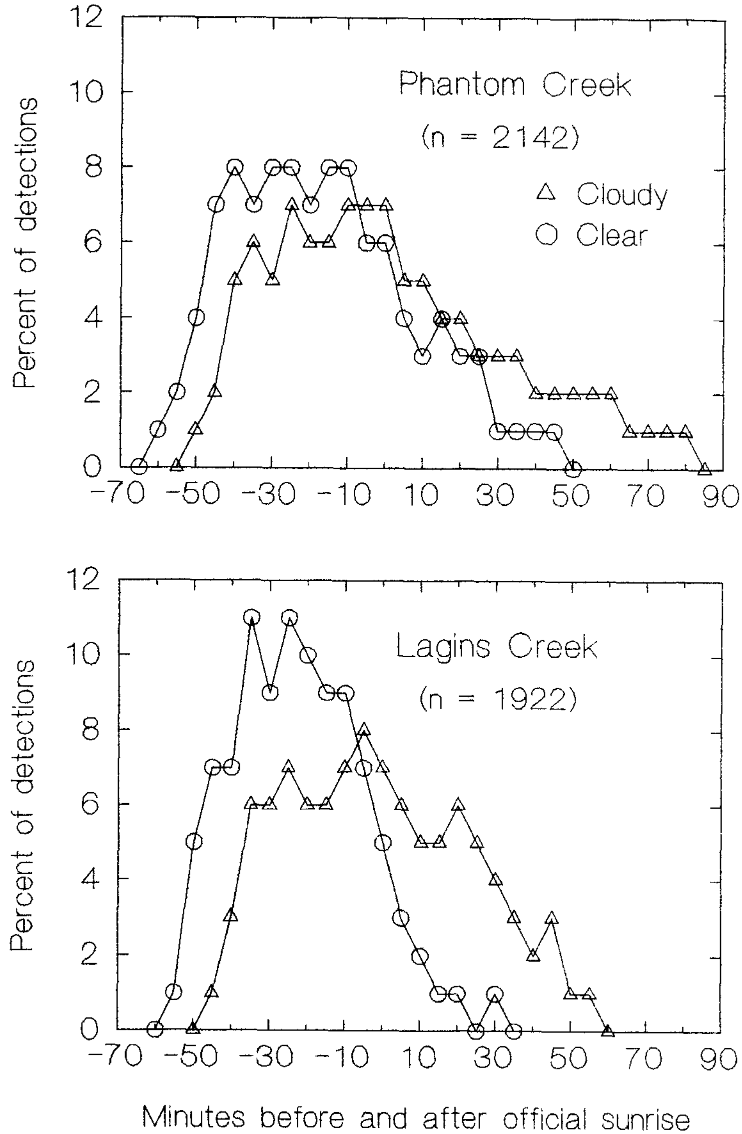

FIGURE 3. Timing of Marbled Murrelet detections in relation to sunrise and weather from May through July 1990 at Phantom Creek and Lagins Creek.

June, being longer at Phantom Creek than at Lagins Creek (t_6 = 2.93, P = 0.026). As with numbers of detections and calls, the duration of activity dropped considerably in August (Tables 1 and 2, Fig. 1).

Activity started later and lasted longer in cloudy weather (Fig. 3). At Lagins Creek, 80% of detections occurred within 47 to 0.5 min before sunrise on clear days (median = 25 min before sunrise), and 35 min before to 30 min after sunrise on cloudy days (median = 5 min before sunrise). The range of times varied from month to month, but differences in mean detection times relative to sunrise on clear and cloudy days existed during all months at both stations (t-test: $P < 0.0001$ for all comparisons). The mean duration of activity was longer on cloudy than on clear days at Phantom Creek (95.7 ± 4.6 vs. 61.1 ± 5.9 min) and Lagins Creek (82.5 ± 3.8 vs. 64.7 ± 4.1 min; Table 2), though at Phantom Creek the av-

TABLE 3. Pearson correlation matrix for measures of Marbled Murrelet morning activity over the entire season at Phantom Creek and Lagins Creek in 1990 ($n = 49$ at Phantom Creek, 33 at Lagins Creek and 24 for comparisons between Phantom Creek and Lagins Creek).

	Phantom Creek			Lagins Creek		
	Detections	Calls	Duration	Detections	Calls	Duration
Phantom Creek						
Detections	1.000					
Calls	0.954***	1.000				
Duration	0.787***	0.740***	1.000			
Lagins Creek						
Detections	0.586**	0.565**	0.153	1.000		
Calls	0.578**	0.547**	0.206	0.942***	1.000	
Duration	0.336	0.335	0.407*	0.444*	0.360*	1.000

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

erage difference (35 min) was nearly twice as long as at Lagins Creek (18 min).

CORRELATIONS BETWEEN MEASURES OF ACTIVITY

Over the season, and at both stations, number of detections per survey were highly correlated with number of keer calls per survey (Table 3). Correlation between number of detections and duration of activity and between numbers of calls and duration of activity were weaker, especially at Lagins Creek, though still significant at both stations (Table 3). At Phantom Creek, correlations between these variables were also significant within each month ($P < 0.05$ for all pairwise comparisons). At Lagins Creek, correlations between detections and calls were significant within each month ($P < 0.005$), and correlations between detections and duration and calls and duration were significant only in June ($P < 0.05$). On a weekly basis, correlations between detections and calls were significant in three of nine weeks at Phantom Creek and in four of seven weeks at Lagins Creek. Significant correlations were found between numbers of detections and duration in six of nine weeks at Phantom Creek and in zero of seven weeks at Lagins Creek, and between number of calls and duration in three of nine weeks at Phantom Creek and in zero of seven weeks at Lagins Creek.

CORRELATIONS IN ACTIVITY LEVELS BETWEEN STATIONS

The number of detections recorded on concurrent surveys at Phantom Creek and Lagins Creek were significantly correlated over the entire season (Table 3). The number of calls and the duration of activity were also correlated between the two stations over the entire season (Table 3). On a monthly basis, and at smaller time scales, there was a lack of correlation between the two stations for all measures of activity (Table 4). On a daily and weekly scale, activity often increased at one station while decreasing at the other (Table 1, Figs. 1 and 2).

DAILY VARIABILITY

At both Phantom Creek and Lagins Creek, variability was highest for number of calls (CV ± SE = 88.3 ± 14.3 and 59.5 ± 9.6%, respectively) and number of detections (CV = 75.6 ± 14.8 and 43.2 ± 6.2%) and lowest for duration of activity (CV = 46.6 ± 5.6 and 26.7 ± 3.5%). Variance was higher at Phantom Creek than at Lagins Creek for numbers of detections ($F_{48,32} = 2.29$, $P = 0.008$) and duration ($F_{48,32} = 3.08$, $P = 0.001$) and similar for numbers of calls ($F_{48,32} = 1.25$, $P = 0.255$). The variability of these measures changed during the summer and showed different patterns at the two stations. At Phantom Creek, variance was lowest in May for all measures, increased from May to June for detections ($F_{10,20} = 8.39$, $P < 0.001$), calls ($F_{10,20} = 4.35$, $P = 0.003$) and duration ($F_{10,20} = 4.86$, $P = 0.001$), increased from June to July for calls ($F_{9,10} = 3.87$, $P = 0.023$) and was similar in June and July for detections ($F_{9,10} = 2.67$, $P = 0.071$) and duration ($F_{9,10} = 2.35$, $P = 0.107$). Variances of all measures were low in August, similar to those in May, but the low variances in August were a function of smaller means in that month and coefficients of variation were much higher in August (72.2 ± 27.6, 113.4 ± 57.3 and 71.1

TABLE 4. Pearson correlation matrix for measures of Marbled Murrelet morning activity on a monthly basis at Phantom Creek and Lagins Creek in 1990.

	Phantom Creek			Lagins Creek		
	Detections	Calls	Duration	Detections	Calls	Duration
May (n = 21 at Phantom Creek, 8 at Lagins Creek and 8 for comparisons between Phantom Creek and Lagins Creek)						
Phantom Creek						
Detections	1.000					
Calls	0.802***	1.000				
Duration	0.721***	0.544*	1.000			
Lagins Creek						
Detections	−0.236	0.023	−0.210	1.000		
Calls	−0.059	0.310	0.024	0.877**	1.000	
Duration	0.116	0.233	0.442	0.510	0.420	1.000
June (n = 11 at Phantom Creek, 12 at Lagins Creek and 7 for comparisons between Phantom Creek and Lagins Creek)						
Phantom Creek						
Detections	1.000					
Calls	0.817**	1.000				
Duration	0.837**	0.855**	1.000			
Lagins Creek						
Detections	−0.140	−0.217	−0.115	1.000		
Calls	−0.187	−0.208	−0.195	0.949***	1.000	
Duration	0.580	0.447	0.695	0.735**	0.623*	1.000
July (n = 10 at Phantom Creek, 13 at Lagins Creek and 9 for comparisons between Phantom Creek and Lagins Creek)						
Phantom Creek						
Detections	1.000					
Calls	0.930***	1.000				
Duration	0.783**	0.757*	1.000			
Lagins Creek						
Detections	0.455	0.293	0.089	1.000		
Calls	0.347	0.163	0.171	0.887***	1.000	
Duration	0.085	0.089	0.056	0.201	0.198	1.000
August (n = 7 at Phantom Creek)						
Phantom Creek						
Detections	1.000					
Calls	0.863*	1.000				
Duration	0.899**	0.772*	1.000			

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

± 26.9% for detections, calls and duration, respectively) than in May (29.0 ± 4.8, 41.7 ± 7.5 and 29.9 ± 5.0% for the same measures). At Lagins Creek, numbers of detections were more variable in June than in both May ($F_{11,7}$ = 3.67, P = 0.048) and July ($F_{11,12}$ = 2.75, P = 0.048). Variance in number of calls was similar from May to June ($F_{11,7}$ = 3.38, P = 0.058) and from June to July ($F_{11,12}$ = 1.24, P = 0.357). Duration was less variable in July than in June ($F_{11,12}$ = 4.23, P = 0.010) and May ($F_{7,12}$ = 3.09, P = 0.042).

COMPARISON OF MORNING AND EVENING DETECTIONS

The number of detections recorded during evening surveys was always less than the number recorded the following morning ($\bar{x}$ = 18.9 ± 3.8 vs. 59.7 ± 4.2, n = 19 at Lagins Creek and $\bar{x}$ = 6.1 ± 2.1 vs. 67.0 ± 8.5, n = 7 at Phantom Creek; Tables 1 and 5, Fig. 4). At Lagins Creek, the number of evening detections increased from May to July (Table 2). Small numbers of evening detections were recorded in June and July at Phantom Creek (Table 5). The seasonal increase

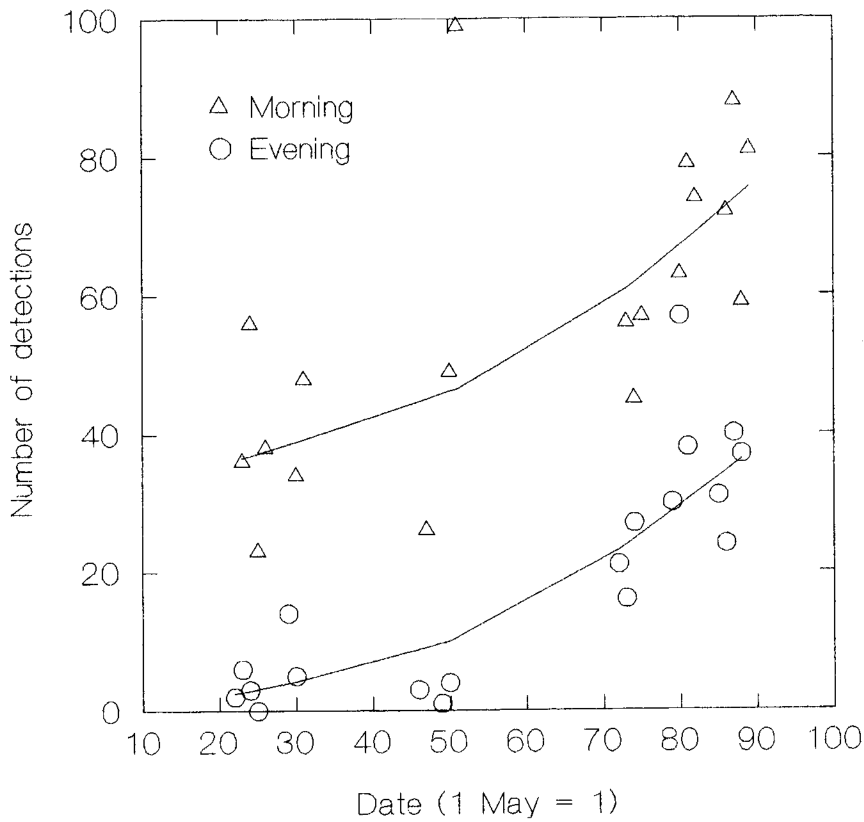

FIGURE 4. Numbers of detections recorded on evening and following morning surveys at Lagins Creek in 1990. Lines were produced by LOWESS smoothing (Cleveland 1981) used in the SYSTAT graphics program (Wilkinson 1990).

in evening activity at Lagins Creek paralleled the increase observed in morning activity (Fig. 4), although, proportionately, evening detections were 7.6 times more numerous in July ($\bar{x}$ = 32.1 ± 3.7, n = 10) than in May and June ($\bar{x}$ = 4.2 ± 1.4, n = 9), compared to morning detections which were only 1.5 times more numerous (67.4 ± 4.3 vs. 45.4 ± 7.6). Numbers of detections in the evening and following morning at Lagins Creek were weakly correlated seasonally (r = 0.56, P = 0.012) but not within each month.

Numbers of detections per evening survey were correlated with numbers of calls (r = 0.96, P < 0.001) and duration of activity (r = 0.72, P = 0.001) which also increased from May to July at Lagins Creek (Tables 2 and 5). Evening detections were rare before sunset (two of 359) and 95% of detections occurred between sunset and 45 min after sunset. Mean duration of evening activity was 26.2 ± 3.3 min (range: 0–51 min).

BEHAVIOR AND GROUP SIZE

Proportion of visual detections. Most detections were auditory, but birds were seen in 25.6% of detections at Phantom Creek and 12.1% of detections at Lagins Creek. The proportion of detections that were visual increased from May to July at both Phantom Creek (15.0 to 32.0%; ANCOVA with weather: r^2 = 0.24, $F_{1,39}$ = 12.03, P = 0.001) and Lagins Creek (1.7 to 18.7%; r^2 = 0.39, $F_{1,30}$ = 16.77, P < 0.001) and decreased in August at Phantom Creek (8.2%; r^2 = 0.79, $F_{1,8}$ = 21.61, P = 0.001). However, this trend was suspect at Lagins Creek because of the low proportion of visual detections recorded by the observer there in May and early June (see above). Excluding records by that observer, birds were seen in 19.8% of detections at Lagins Creek from 21 June to 28 July. No trend was apparent in the proportion of visual detections recorded during

TABLE 5. Marbled Murrelet activity during evening surveys at fixed stations at Phantom Creek and Lagins Creek in 1990.

	Phantom Creek				Lagins Creek			
Date	Cloud cover (%)	No. of detections	No. of keer calls	Duration (min)	Cloud cover (%)	No. of detections	No. of keer calls	Duration (min)
22 May					0	2	50	18
23 May					0	6	128	27
24 May					30	3	75	14
25 May					0	0	0	0
29 May					100	14	265	31
30 May					100	5	125	12
12 Jun	0	1	0	1				
15 Jun	100	1	0	1	100	3	75	7
18 Jun					100	1	*	1
19 Jun					100	4	*	27
29 Jun	100	4	19	39				
30 Jun	100	15	23	25				
11 Jul					50	21	373	51
12 Jul					100	16	227	39
13 Jul	0	13	167	27	100	27	373	32
18 Jul					0	30	622	37
19 Jul					0	57	835	47
20 Jul					0	38	818	37
24 Jul	0	5	51	8	0	31	662	23
25 Jul					100	24	494	31
26 Jul					0	40	821	31
27 Jul	30	4	121	9	15	37	746	32

* Not recorded.

that period at Lagins Creek (r^2 = 0.20, $F_{1,13}$ = 0.42, P = 0.530) or Phantom Creek (r^2 = 0.02, $F_{1,16}$ = 0.29, P = 0.596). There was no evidence that weather affected the proportion of birds sighted at Phantom Creek (ANCOVA with date: r^2 = 0.30, $F_{1,39}$ = 0.85, P = 0.364) or Lagins Creek (r^2 = 0.39, $F_{1,30}$ = 2.27, P = 0.143). A greater proportion of visual detections were recorded at Phantom Creek than at Lagins Creek in July (ANOVA: r^2 = 0.16, $F_{1,25}$ = 4.77, P = 0.039). This probably relates to the greater visibility at the Phantom Creek station.

Birds were calling in 50.3 and 45.5% of visual detections at Phantom and Lagins creeks, respectively. Detections that were visual only comprised 12.9% of all detections at Phantom Creek and 8.2% of detections recorded from 21 June to 28 July at Lagins Creek.

Group size. Group size of sighted Marbled Murrelet flocks ranged from one to seven birds. Single birds were most frequent in May and June, and groups of two were most prevalent in July at both stations (Fig. 5). The relative frequency of larger flocks was similar in May and June at Phantom Creek and increased from June to July at Phantom Creek (χ^2_4 = 45.6, P < 0.0001) and Lagins Creek (χ^2_4 = 23.4, P = 0.0001). The proportion of birds seen in flocks larger than two was 8.1% in May and 53.2% in July at Phantom Creek (Fig. 5). The seasonal increase in average flock size from 1.4 in May and 1.6 in June to 2.4 in July meant that the same number of detections represented 1.7 times as many birds in July as in May.

The majority of single birds sighted were silent in all months at both stations (Fig. 6). Proportions of silent birds were more variable for groups of two, with silent birds dominating only in June. The ratio of silent to calling flocks was greater for small flocks than large flocks at both Phantom Creek (χ^2_4 = 135.8, P < 0.0001) and Lagins Creek (χ^2_4 = 37.9, P < 0.0001). All sighted flocks larger than two were calling, except for one detection of three silent birds at Lagins Creek.

Height of flight. Most visual detections were above tree-top at Phantom Creek (75.1% above vs. 24.9% below tree-top, n = 461) and Lagins Creek (89.2% above vs. 10.8% below tree-top, n = 166). At Phantom Creek, those proportions changed through the season, with the greatest proportion of birds flying below tree-top (42.8% of detections) occurring in June, and the largest

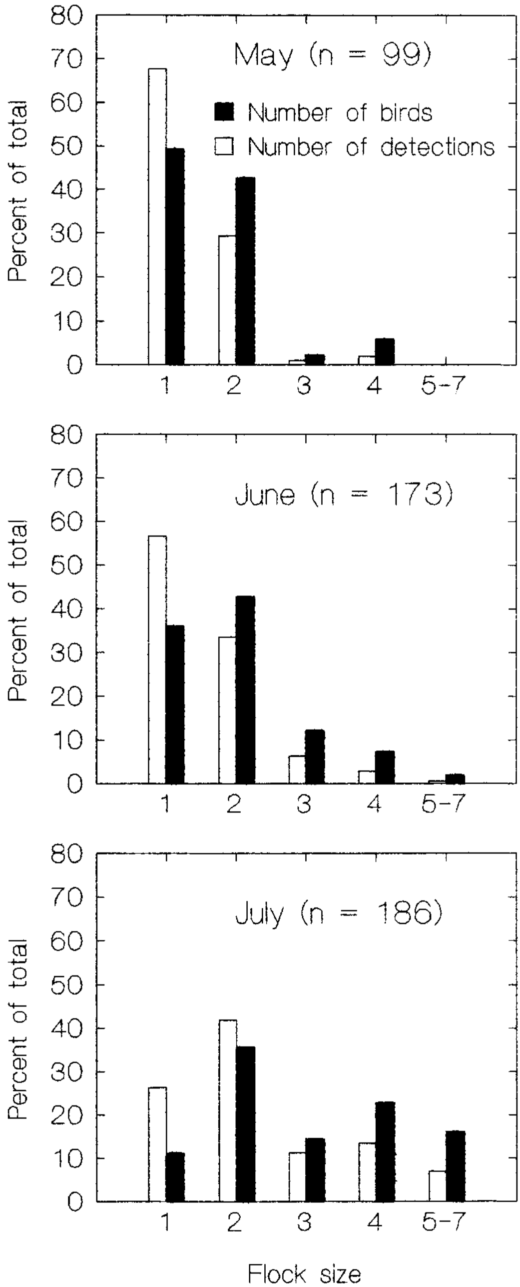

FIGURE 5. Proportion of detections and of total birds seen in different flock sizes of Marbled Murrelets by month at Phantom Creek in 1990.

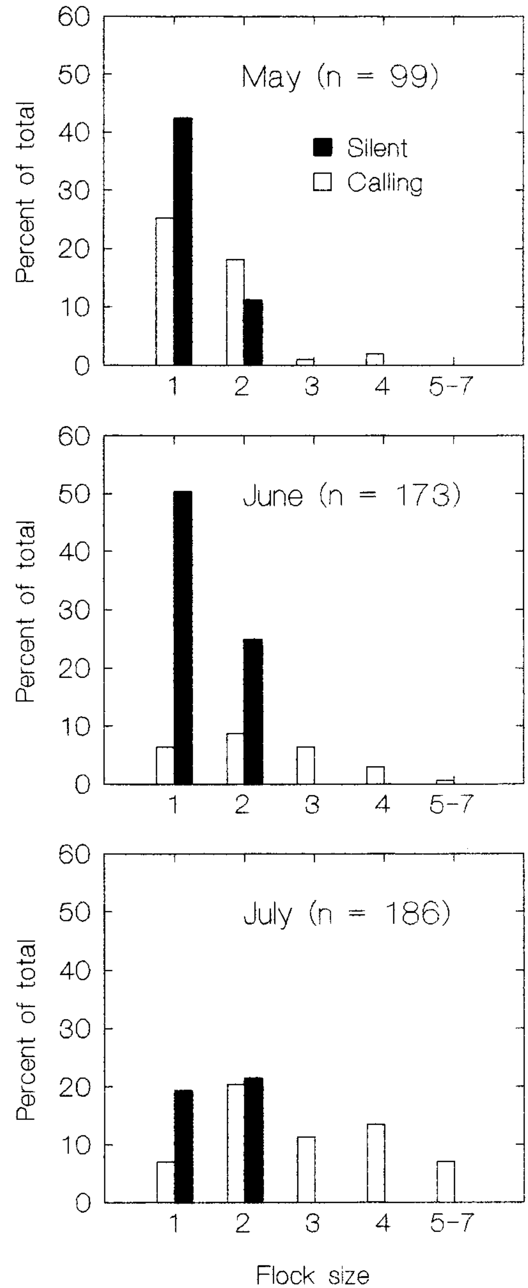

FIGURE 6. Proportion of calling and silent flocks in relation to group size of Marbled Murrelets by month at Phantom Creek in 1990.

proportion of birds flying above tree-top (86.4% of detections) recorded in July (Fig. 7; $\chi^2_2 = 71.6$, $P < 0.0001$).

Greater proportions of small flocks than large flocks were sighted below tree-top in all months at Phantom Creek (Fig. 7; $\chi^2_4 = 34.2$, $P < 0.0001$) and Lagins Creek ($\chi^2_4 = 22.0$, $P = 0.0002$). Most birds flying below tree-top were silent. The ratio

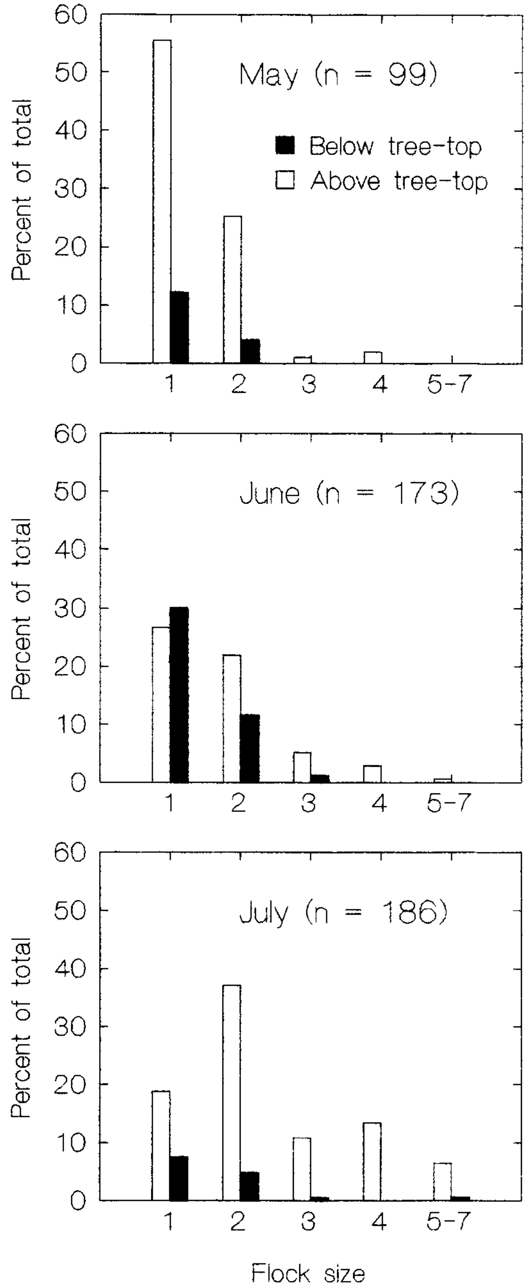

FIGURE 7. Proportion of flocks flying above and below tree-top in relation to group size of Marbled Murrelets by month at Phantom Creek in 1990.

of silent to calling birds was larger in flocks flying below tree-top than in flocks flying above tree-top at Phantom Creek (86.0% of 115 flocks below vs. 46.5% of 246 flocks above; $\chi^2_1 = 54.9$, $P < 0.0001$) and Lagins Creek (86.4% of 22 flocks below vs. 48.6% of 148 flocks above; $\chi^2_1 = 11.0$, $P = 0.0009$).

Flight path. The proportions of straight, turning, and circling flight behavior were similar in May, June and July at Phantom Creek ($\chi^2_4 = 6.28$, $P = 0.179$). Overall proportions from May to July were 34.3% straight, 15.2% turning, and 50.5% circling. A greater percentage of straight flight was recorded at Lagins Creek (68.4%, $n = 155$) than at Phantom Creek (36.8%, $n = 239$) in July ($\chi^2_2 = 53.3$, $P < 0.0001$). This may have been due to the more limited visibility at Lagins Creek, which made it more difficult to observe circling behavior than at Phantom Creek.

There were no consistent differences in the types of flight paths observed for different group sizes or for silent and calling birds. A higher proportion of calling flocks circled than silent flocks at Phantom Creek in June ($\chi^2_2 = 8.79$, $P = 0.012$) and at Lagins Creek in July ($\chi^2_2 = 13.0$, $P = 0.002$). This difference was not seen in May ($\chi^2_2 = 0.80$, $P = 0.670$) or July ($\chi^2_2 = 1.52$, $P = 0.467$) at Phantom Creek. A higher proportion of large flocks circled than small flocks at Lagins Creek in July ($\chi^2_6 = 21.6$, $P = 0.001$) but not at Phantom Creek ($\chi^2_8 = 5.72$, $P = 0.678$).

DISCUSSION

SEASONAL PATTERNS

The seasonal pattern of increased activity in July has been observed in other studies. Nelson (1989) in Oregon, noted highest numbers of detections between 12 July and 9 August with a peak in late July. She also noted that activity levels dropped off abruptly in early August and that most sites were devoid of murrelets in mid to late August. Ralph et al. (1989) observed similar activity patterns in California.

There seems to be some variation in activity patterns between areas. Nelson (1989) reported a minor peak in detections in late May to early June, whereas Manley et al. (1992) reported a peak in late June. In our study we observed differences between our two permanent stations. Both stations had a slight rise in number of detections in late May, but number of detections decreased in early June at Lagins Creek while increasing at Phantom Creek. A possible difference between the two sites is the likelihood that Phantom Creek is on a flight path for murrelets while Lagins Creek, being located at the end of an inlet, is less likely to serve as a flight corridor. If this is the case then patterns observed at Lagins Creek may reflect more closely what could be observed at breeding areas.

EFFECT OF WEATHER

Murrelets were detected more frequently on cloudy days and were active for longer periods than on clear days. Nelson (1989) also noted that the number of detections varied with weather conditions. However, she found that most detections occurred on clear and completely overcast days and that fewer detections were recorded on moderately cloudy days. Paton et al. (1988) and Ralph et al. (1989) found that murrelet activity tended to start later on foggy and misty mornings but continued for a longer period of time and appeared to be more intense than on clear days. The trend in our study and that of Paton et al. (1988) and Ralph et al. (1989) indicate a relationship between light conditions and the intensity and duration of murrelet activity. Reduced activity when light intensities are high may serve to minimize risks of predation as has been suggested for Leach's Storm-Petrels (*Oceanodroma leucorhoa*; Watanuki 1986, Bryant 1993) and Ancient Murrelets (*Synthliboramphus antiquus*; Jones et al. 1990). Weather is a major factor contributing to daily variability in the number of murrelet detections at a given site, and should be taken into consideration when comparing murrelet activity between sites.

CORRELATIONS BETWEEN MEASURES OF ACTIVITY

The strong correlation on a seasonal and monthly basis between numbers of detections and total numbers of keer calls recorded per survey suggests that they provide similar measures of Marbled Murrelet activity at those time scales. Thus, just counting total calls during a survey period may be an alternative to counting numbers of detections if a comparable measure of activity is all that is desired. Observers must be trained to discriminate detections, and counting or recording calls may be simpler and less subjective. Counts of calls plus careful records of visual detections would provide detailed measures of activity patterns. The duration of the activity period was correlated with numbers of detections on a seasonal basis but not always on a monthly basis and is probably not as useful as detections or calls as a measure of activity.

CORRELATION IN ACTIVITY LEVELS BETWEEN STATIONS

Although there was a significant correlation in murrelet activity between our two permanent stations over the entire season, there was a lack of correlation at smaller temporal scales (monthly or weekly). Local weather patterns sometimes differed and may have contributed to differences in activity levels, but we cannot pinpoint at this time the factors besides weather that may have accounted for the different patterns observed in the two areas.

DAILY VARIABILITY

The wide variation in activity levels on a daily and weekly basis recorded in this study has been noted before (Nelson 1989, Manley et al. 1992). The causes of this variation are still unknown but may include weather factors, vocalization behavior and flight patterns of breeding and nonbreeding birds, and the effects these have on observations. Because of this large variability in detection levels from day to day, caution must be taken when comparing different areas, especially when surveyed on different days or under different conditions. Large samples are required to obtain statistical power when making comparisons between sites or attempting to interpret trends in activity levels at particular sites.

MORNING VS. EVENING SURVEYS

Several other studies have documented lower numbers of detections in the evening than in the morning (Manley et al. 1992, Eisenhawer and Reimchen 1990, Paton and Ralph 1990, Paton et al. 1990, Nelson 1989). The lack of correlation within months found in this study between the numbers of detections recorded on evening and morning surveys suggests that they are more or less independent events. Morning surveys are more efficient for detecting murrelet activity.

The seasonal increase in evening activity may reflect shifts in behavior as the breeding season progresses. Exchange of incubation duties occurred at dawn at all monitored nests but feeding of young occurred at various times (Singer et al. 1991; Simons 1980; Nelson, pers. comm.).

FLIGHT BEHAVIOR AND VOCALIZATION

Most murrelets sighted were either flying alone or in pairs. Single birds flying below the canopy may be close to nest sites. This is supported by the high frequency of single birds that were silent (see Singer et al. 1991). We would expect murrelets to be silent in proximity to their nests to minimize the danger of nest detection by predators. Ten of the 23 tree nests found to date in North America were depredated (Nelson, pers. comm.). Predators at nest sites include Common Raven (*Corvus corax*), Steller's Jay (*Cyanocitta stelleri*) and Great Horned Owl (*Bubo virginianus*; Singer et al. 1991; Nelson, pers. comm.). The high frequency of silent single or paired birds stresses the importance of selecting observation stations in areas maximizing the chances of visual detections, i.e., with large sections of open sky. Several studies (Nelson 1989, Paton and Ralph 1988, Varoujean et al. 1989) have indicated that visual detections are crucial in identifying potential nesting areas. Birds flying below the canopy, birds landing in trees, and silent birds flying through the forest all could indicate potential nesting and roosting sites. Sightings in May and June may represent mostly breeding birds and may provide a better indication of nesting sites. Larger groups were more often seen in July, possibly involving non-breeding birds inspecting potential nest sites and familiarizing themselves with breeding areas. Several seabirds prospect for nest sites in the year(s) preceding first breeding (Manuwal 1974a, Sealy 1976, Gaston 1990). The seasonal increase in the proportion of large flocks, and thus in the average number of birds per detection, means that results of surveys conducted at different times during the breeding season may not be directly comparable in terms of the numbers of birds using an area.

Nothing is known about the pairing behavior of Marbled Murrelets or when they select nesting sites. Cassin's Auklets (*Ptychoramphus aleutica*) and Ancient Murrelets have elaborate displays in their breeding colonies at night, and pairing may occur there (Manuwal 1974b, Thorensen 1964, Sealy 1976, Jones et al. 1989, Gaston 1990). Some of the aerial displays observed over the forest may be associated with pairing behavior, pair bond maintenance, prospecting for nest sites, or spacing behavior. It is likely that some of the circling behavior observed permits birds to familiarize themselves with the location of the nest or nesting groves. Renesting has not been documented in the Marbled Murrelet, however the large spread of the breeding season and the seemingly high predation pressure on the species suggest that it may occur. If so, then renesting birds may prospect for new nesting sites during the breeding season. The two nests found in California in 1989 had been depredated and were not reused by murrelets in 1989 or 1990 (Singer et al. 1991; Singer, pers. comm.).

The results of this study indicate that caution must be used when comparing numbers of detections at different sites, taking into consideration the high levels of daily and seasonal variability, effects of weather, the amount of visibility at specific survey stations, and changes in group size and behavior over the breeding season. Setting priorities for habitat protection based on relative activity levels is problematical because we as yet have no gauge with which to relate measures of activity to breeding population. Behavioral studies in the vicinity of known breeding sites and known nesting densities are required to determine the significance of behaviors observed during surveys and the relationship between activity levels and habitat use.

ACKNOWLEDGMENTS

This research was funded by B.C. Ministry of Forests, B.C. Ministry of Environment, B.C. Ministry of Parks, Canadian Wildlife Service, Canadian Parks Service, Fletcher Challenge Canada, Husby Trucking Ltd., MacMillan Bloedel, Western Forest Products, and World Wildlife Fund. We would like to acknowledge the foresight and genuine concern of the forest companies involved. Research committee members included: Fred Bunnell, Forestry U.B.C.; Wayne Campbell, Royal B.C. Museum; Bill Dumont, Western Forest Products; Gary Kaiser, Canadian Wildlife Service; Dave Lindsay, Fletcher Challenge; Ron McLaughlin and Bill Pollard, MacMillan Bloedel; Bob Moody, B.C. Conservation Foundation; Dale Seip, Ministry of Forests; Bob Redhead and Doug Burles, Canadian Parks Service. Research assistants included Don Garnier, Moira Lemon, and Audrey Pearson. Field work by Heidi Regehr was funded by Malcom Ramsay of the University of Saskatchewan. Special thanks to the volunteers Kerry Baker, Julie Stoneman, Inez Weston and Tom Weston for their generous help and wonderful company. Thanks to Gene Matchitt, Lorne McIntosh, Keith Moore and Ken Morgan for help with logistic problems. Administrative support was provided by Bob Moody and Deborah Gibson of the B.C. Conservation Foundation. The B.C. Conservation Foundation also helped in entering the field data on the computer, a monumental task. We especially thank Dianne Rose-Talarico for her efforts in that regard. C. J. Ralph, D. C. Schneider and S. W. Singer provided many helpful comments on the manuscript.

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