The Condor 102:275–285

ACTIVITY PATTERNS OF MARBLED MURRELETS IN DOUGLAS-FIR OLD-GROWTH FORESTS OF THE OREGON COAST RANGE[1]

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Abstract. We monitored activity patterns of Marbled Murrelets (*Brachyramphus marmoratus*) on a near-daily basis using audio-visual surveys during three breeding seasons at five forest stands in the Oregon Coast Range. Three measures of activity were recorded: number of daily detections, number of daily vocalizations, and duration of daily activity. Each measure was highly variable within and among stands and years, and we recorded greater variability than has been previously reported for this species. The three measures of activity were strongly correlated within a day at each survey station, but correlative relationships at temporal and spatial scales greater than this were inconsistent. Activity varied greatly from one day to the next during all portions of the breeding season, and we did not identify any month when variability in activity was consistently higher or lower than any other month. Multivariate analyses revealed that weather and date variates explained little of the variability in daily activity. Given the extreme levels of variability in Marbled Murrelet activity and our lack of understanding as to which factors drive that variability, it is critical that conclusions about activity or behavior not be drawn from data sets not specifically designed to answer the questions of interest.

Key words: activity patterns, alcids, attendance, Brachyramphus marmoratus, *canonical correlation, Marbled Murrelet, survey methodology.*

INTRODUCTION

Daily surveys of seabird nest-site attendance have revealed important aspects of species' reproductive, foraging, and social behavior, and have been used to design population monitoring plans (Byrd et al. 1983, Hatch and Hatch 1989, Jones et al. 1990). However, survey efforts of such intensity are rare for Marbled Murrelets (*Brachyramphus marmoratus*), a species considered threatened outside of its Alaskan breeding range (Kaiser et al. 1994, USFWS 1997). Although prone to disturbance at sea from oil spill events and gill net fisheries (Carter and Kuletz 1995, Carter et al. 1995), the foremost threat to this species is loss of and disturbance to its primary nesting habitat, coastal old-growth coniferous forest (FEMAT 1993, Ralph et al. 1995b). Therefore, to aid in management of nesting habitat, a survey protocol was developed that relies on visual and aural detections of birds as they exchange nesting duties, provision young, and fly about forest stands during early morning hours. Because the protocol was developed primarily to assess nesting status within a stand and not to measure abundance, density, behavior, or reproductive success, low intensity efforts were sufficient (Ralph et al. 1994, Paton 1995).

These protocol surveys revealed that duration of daily murrelet activity and counts of daily murrelet detections and vocalizations were highly variable at multiple time and space scales and much of this variability was attributed to weather and date (Naslund and O'Donnell 1995, O'Donnell et al. 1995). It is unclear, however, if this conclusion is accurate because protocol surveys were not designed with sufficient power or detail to examine such relationships. Because inland survey data are being used increasingly to develop complex management plans and answer specific questions about the inland ecology of the species (Ralph et al. 1995a), it is critical that a more complete and reliable examination of activity patterns be undertaken.

Our goal was to examine Marbled Murrelet activity levels and behavior in forest stands in relation to date and weather by using single ob-

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server, high intensity audio-visual surveys. Our objectives were to: (1) examine correlative relationships among three activity measures (duration of activity and numbers of detections and vocalizations) at multiple temporal scales, (2) examine linear and nonlinear relationships among the three activity measures and both date and weather, (3) examine correlative relationships of each activity measure within and among stands on a daily, weekly, seasonal, and interannual time scale, and (4) describe flight behaviors of Marbled Murrelets and determine influential factors.

METHODS

STUDY AREA

Five survey stations were located in Douglas-fir (*Pseudotsuga menziesii*) old-growth forest stands of the Oregon Coast Range. Each stand was in the Coast Range Province and western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1988). The Valley of the Giants Meadow (Giant 1; 44°56′N, 123°43′W, 365 m above sea level, asl) and Valley of the Giants Upper Plateau (Giant 2; 44°55′N, 123°42′W, 535 m asl) stands were ~2 km apart and ~25 km inland. Marbled Murrelet nests have been located in each of these stands (Hamer and Nelson 1995). The Spencer Creek Main Fork (Spencer 1; 43°49′N, 123°51′W, 100 m asl) and Spencer Creek Upper Fork (Spencer 2; 43°49′N, 123°52′W, 100 m asl) stands were ~1.5 km apart and ~23 km inland. The 2x4 Creek stand (2x4; 42°52′N, 124°08′W, 425 m asl) was ~25 km inland. With the exception of Spencer 2, surveys were conducted at each stand for at least two years prior to our study and results indicated Marbled Murrelets were likely nesting in each stand. None of the stands surveyed were harvested, and all but Giant 2 were located along rivers or creeks. Stands or survey stations located in the same general area (Giant 1 and 2, Spencer 1 and 2) are referred to as "proximal."

FIELD TECHNIQUES

We conducted audio-visual surveys on a near-daily basis between 1 May and 4 August 1994 (Giant 1 and 2, Spencer 1 and 2), 1996 (Giant 1 and 2), and 1997 (Giant 1 and 2, Spencer 1, and 2x4). We followed survey guidelines from the Marbled Murrelet Inland Survey Protocol and all surveyors were trained prior to data collection to standards set by the protocol (Ralph et al. 1994). Surveys began 45 min prior to sunrise and ended 75 min after sunrise or 15 min after the last detection, whichever was later. Surveys were not conducted during heavy rain or wind, which would interfere with visual or aural observations of birds. One survey station was located in each stand. Each station was surveyed by the same observer during the entire breeding season to eliminate effects of inter-observer variability on within-stand activity data. Two exceptions were Giant 1 in 1996 and Spencer 1 in 1997. Here, we conducted simultaneous surveys with the original and replacement surveyor. Daily tallies of each activity measure and timing of murrelet observations from these simultaneous surveys were similar.

The activity we recorded was based upon the primary sampling unit of the "detection," which was defined as "the sighting or hearing of one or more murrelets acting in a similar manner" (Ralph et al. 1994). For each detection, we recorded time of day, type of detection as audio only, audio-visual, or silent-visual, and number of "keer" calls (the primary vocalization). For visual detections, we also recorded height of birds in relation to the canopy, behavior of birds (categorized as flying over canopy in a straight line, circling over canopy, circling below the canopy, flying through or below the canopy in a straight line, landing in or departing from tree, or stationary), and group size. We summarized daily survey data by calculating the duration of activity in minutes (duration = time of last detection − time of first detection) and tallying all detections and keer calls. We refer to these three measures as the daily activity metrics.

We recorded weather every 20 min during surveys. We estimated cloud and fog cover to the nearest 25%. Height of cloud ceiling was estimated relative to the forest canopy to standardize measurements among stations. Ceiling below canopy was recorded as <1 and ceiling above canopy as the nearest multiple of the canopy height, up to 5. We classified precipitation as none, drizzle, or steady rain. Wind was recorded on a modified Beaufort scale. We averaged weather data for each survey day to create a daily summary value.

STATISTICAL ANALYSIS

We examined the relationship between Marbled Murrelet activity and both date and weather with canonical correlation analyses (PROC CANCOR; SAS Institute 1990). We chose this multivariate approach because all daily activity metrics were strongly correlated ($r_s > 0.7$). Canonical correlation is an extension of multiple regression that examines the linear relationship between multiple X and Y variables by creating linear combinations (i.e., variates) for each data set that best express the correlation between the two data sets. The first canonical correlation explains the maximum relationship between the canonical variates, and each successive canonical correlation is estimated so as to be orthogonal yet still explain the maximum relationship not accounted for by the previous canonical correlation.

We assessed the relationship between the Xs and Ys with canonical correlation coefficients (CC) and canonical redundancy indices (CRI), the latter measuring the average proportion of variance in the Y variables explained by the X variables. We examined the canonical correlation structure with canonical loadings, which estimate the influence of each independent variable on the newly created variate, and canonical cross-loadings, which estimate the strength of the correlation between each dependent variable and the independent variate set (Hair et al. 1995). Squaring the cross loadings provides a measure of the proportion of variability in a dependent variable explained by the independent variate.

Multicollinearity among the dependent variables cloud cover, ceiling, and fog prohibited them from being included in the canonical correlation analysis simultaneously. We used principal components analysis to assess the relationship between the weather variables and determined that cloud, ceiling, and fog each weighted the first principal component evenly. We created a new variable, termed CLCEFO, by summing the daily, standardized values of each of these three variables (Hair et al. 1995).

We examined nonlinear relationships between activity and date with locally weighted regression and smoothing scatterplots (LOWESS). We plotted counts of daily detections from each stand and year as a proportion of the maximum daily detection count (for LOWESS plots only). Tension was set at 0.2 for each plot.

We investigated relationships among group size of murrelets visually observed during a detection and behavior, date, and time of day with Poisson regression (PROC GENMOD; SAS Institute 1993). We performed these analyses on visual detections only. We ran three Poisson regression models in an effort to keep the data relatively balanced among years and sites. We included all survey data from Giant 1 and 2 in one model; data from Spencer 1 and 2 in 1994 in a second model; and data from 2x4 1997 in a third model. We used a forward, single-best-predictor process with an F-to-enter value of 4.0 to select variables. Explanatory variables available for inclusion in the models were time of day (categorized by 20-min blocks beginning at the start of the survey period and labeled as time periods 1–6), month, height of birds detected in relation to the canopy (above or below canopy), detection type (silent-visual or audio-visual), and all possible second-order interaction terms. We chose final models based on drop-in-deviance tests and Bayesian information criteria (SAS Institute 1993). Mean responses are presented for Poisson regression models.

We did not use August detection data in analyses unless otherwise stated because sample sizes from that month at all sites and in all years were <5. August detection data were used for calculation of overall means, however. Means are presented $\pm$ SD.

RESULTS

SURVEY EFFORT AND SUMMARY STATISTICS

We conducted 572 daily surveys for Marbled Murrelets. At least one Marbled Murrelet was detected on 517 mornings, although 7 of 10 site-by-year combinations had at least one day with no detections. A total of 10,848 Marbled Murrelets were sighted during 4,148 silent-visual and 1,840 audio-visual detections. The mean percentage of detections that were audio, silent-visual, and audio-visual when pooled among all sites and years were 58.4 $\pm$ 20.8, 12.3 $\pm$ 4.8, and 29.3 $\pm$ 19.6, respectively. Summaries of daily murrelet activity data from each site-by-year combination appear in Table 1.

TEMPORAL AND SPATIAL VARIABILITY IN ACTIVITY

There was considerable variation in each daily activity metric within and among stations and years (Table 1). For example, monthly estimates of coefficients of variation (CVs) for daily detections ranged from 38–210%, and we were unable to identify any month when CVs were con-

TABLE 1. Means and coefficients of variation (%) of daily counts of detections, daily counts of keer calls, and duration of daily activity (min) for Marbled Murrelets at five survey stations, Oregon Coast Range, 1 May–5 August 1994, 1996, 1997. n = number of survey days.

Activity metric	2 × 4	Spencer 1		Spencer 2	Giant 1			Giant 2		
	1997	1994	1997	1994	1994	1996	1997	1994	1996	1997
Detections	51.3	32.4	10.6	162	27.3	7.7	15.3	36.1	14.1	14.7
	(69.5)	(130.0)	(152.5)	(134.1)	(68.4)	(113.4)	(87.4)	(49.3)	(72.1)	(121.6)
Keer calls	505.1	101.6	25.1	149.9	167.2	36.3	94.0	457.4	106.74	168.6
	(529.4)	(157.2)	(213.2)	(172.7)	(102.2)	(143.7)	(126.2)	(73.3)	(14.13)	(29.45)
Duration (min)	71.9	44.2	18.6	48.6	52.7	24.3	43.3	68.0	36.1	36.4
	(46.2)	(94.6)	(114.8)	(65.8)	(41.1)	(96.1)	(55.8)	(44.2)	(55.6)	(70.1)
n	62	66	61	58	55	50	58	55	51	56

sistently higher or lower than any other month within or among sites and years. Daily activity metrics within each stand were moderately to strongly correlated ($0.53 \leq r_s \leq 0.87$). Correlation between identical activity metrics from proximal stands on the same day were weaker and more variable ($-0.38 \leq r_s \leq 0.64$). Correlative strength of weekly means for each activity metric also varied greatly among stands ($-0.42 \leq r_s \leq 0.79$), and proximity of survey stations was not indicative of correlative strength. Seasonal timing of activity also varied among years within stations. Correlation coefficients were weak to moderate within sites among years for daily detections ($-0.46 \leq r_s \leq 0.47$) and for duration of daily activity ($-0.18 \leq r_s \leq 0.48$).

RELATIONSHIPS BETWEEN ACTIVITY AND BOTH WEATHER AND DATE

The degree of weather-related visibility at a stand, represented by the summed variable of cloud, ceiling, and fog (CLCEFO), differed significantly among months (ANOVA, $F_{2,518} = 7.8$, $P < 0.001$) but not among stations ($F_{4,518} < 0.1$, $P > 0.9$) or site-by-month interactions ($F_{8,518} = 0.5$, $P = 0.8$). Tukey-Kramer post-hoc comparisons revealed July was clearer (i.e., cloud and fog cover less, ceiling higher) than May or June.

Weather and date variates explained little of the variability in murrelet activity. Although canonical correlation coefficients (CC) between the first independent and dependent variates were as high as 0.75 and likelihood-ratio P-values were <0.05 for all survey stations except Giant 1, canonical redundancy indices (CRIs) indicated that first CCs explained an average of 20% of the variability in the activity data at the survey stations. The second CCs explained <7% of the variability at all survey stations although likelihood-ratio P-values were <0.05 at all stations except Giant 1 and Spencer 1. Therefore we interpreted only the structure of the first CCs for each survey station.

The canonical loadings (CLs; Table 2) show the influence of each weather and date variable on the independent variate. The interpretation for independent variate 1 (V1) differed among stands based on these loadings. Weather influenced V1 strongly at 2x4, date influenced V1

TABLE 2. Canonical loadings for the first independent variates from canonical correlation analyses of daily Marbled Murrelet activity metrics and both weather and date variables from five survey stations, Oregon Coast Range, 1 May–31 July, 1994, 1996, 1997.

	Survey stations				
	2 × 4	Spencer 1	Spencer 2	Giant 1	Giant 2
CLCEFO[a]	0.66	0.03	−0.25	0.53	0.33
Month	0.16	0.59	0.96	−0.37	0.05
Precipitation	0.67	0.19	−0.35	0.24	−0.32
Wind	0.64	0.17	−0.15	0.42	0.16
Year[b]	—	−0.69	—	−0.65	−0.95

[a] CLCEFO = combined weather variable from daily cloud, ceiling and fog measures.
[b] 2 × 4 and Spencer 2 had only one year of data, so year was not available for inclusion in the models.

TABLE 3. Canonical cross-loadings from canonical correlation analyses of daily Marbled Murrelet activity metrics and both weather and date variables from five survey stations, Oregon Coast Range, 1 May–31 July, 1994, 1996, 1997.

	Survey stations				
	2 × 4	Spencer 1	Spencer 2	Giant 1	Giant 2
Detections	0.12	0.46	0.74	0.24	0.49
Keer calls	0.17	0.47	0.70	0.19	0.45
Duration (min)	0.49	0.43	0.55	0.27	0.43

strongly at Spencer 1, Spencer 2, and Giant 2, and all variables influenced V1 moderately at Giant 1. The strongest CLs for V1 were date influenced (month at Spencer 2 and year at Giant 2), whereas the weakest CLs were CLCEFO at Spencer 1 and month at Giant 2.

Canonical cross-loadings (CXLs; Table 3) demonstrate the correlation strength between each activity metric and each independent variate. CXLs were the most uneven at 2x4 where V1, predominantly a weather effect, had a greater correlation with duration of activity than counts of detections or counts of vocalizations. At Spencer 1 and 2, V1 (predominantly month and year effects) explained 18–54% of the variability in activity. At Giant 1, V1 (a mixed weather and date effect) explained only 3.7–7.5% of the variability in each activity metric, whereas at Giant 2, V1 (a strong year-effect) explained 18.3–23.6% of the variability in each activity metric. The strongest correlation between activity metrics and V1 occurred at Spencer 2 where V1 was predominantly a month effect. The weakest correlation between activity metrics and V1 occurred at 2x4 where V1 was predominantly a weather effect.

We also conducted canonical correlation analyses without date variables to maximize the potential of observing a relationship between weather and activity. Results indicated a weak relationship between activity and weather. Two of the 10 site-by-year combinations had significant first canonical correlations (likelihood-ratio $P < 0.05$), and the independent variates explained 1–13% of the variability in activity data

We evaluated patterns in seasonal and interannual activity with raw and smoothed plots of daily detections (Fig. 1 and 2). We restricted these analyses to counts of detections to simplify the display and because the correlation among all daily activity metrics was high ($r_s > 0.7$). We chose counts of daily detections as it is typically the metric considered when working with Marbled Murrelets. Graphical analyses showed that near-maximum and near-minimum numbers of daily detections occurred throughout the breeding season and were often recorded during the same week within a stand (Fig. 1). Smoothed plots revealed an underlying pattern where activity was consistently higher over time during July at most stations during most years (Fig. 2). However, secondary peaks in activity that were not temporally consistent among stands also occurred.

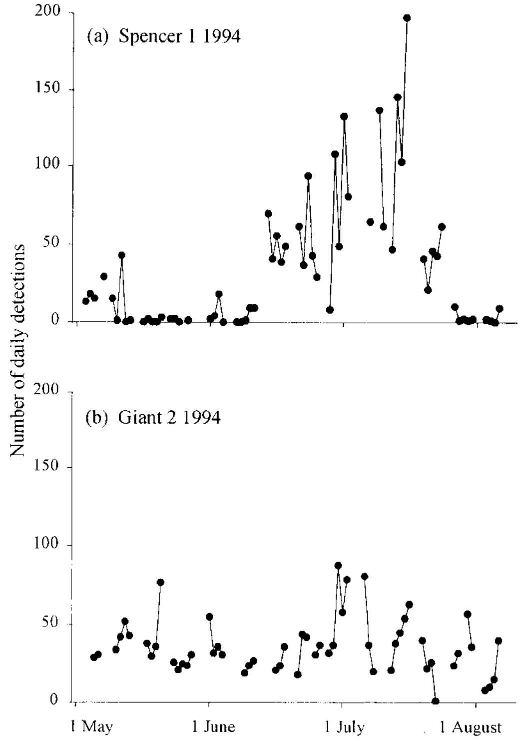

FIGURE 1. Examples of counts of daily detections of Marbled Murrelets from survey stations in the Oregon Coast Range with (a) high daily variability (Spencer 1, 1994) and (b) low daily variability (Giant 2, 1994), 1 May–5 August 1994.

BEHAVIOR AND GROUP SIZE

Mean group size of Marbled Murrelets detected during surveys was 1.8 ± 0.8 (data pooled from all visual detections). Groups of murrelets visually detected beneath the canopy were smaller

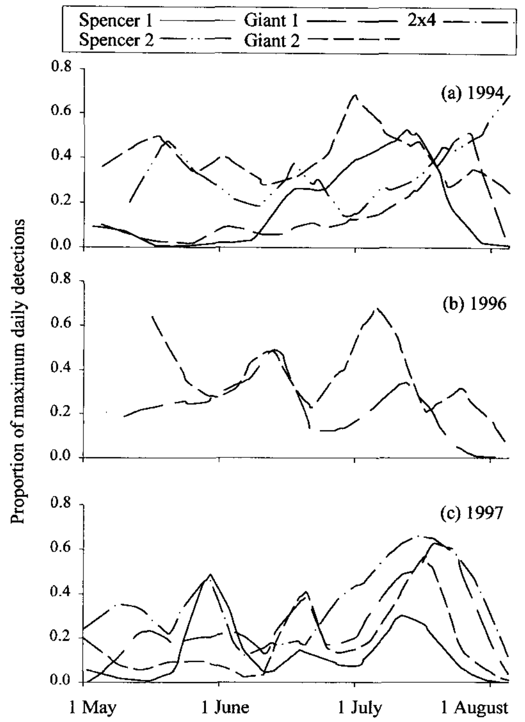

FIGURE 2. Smoothed plots of daily detections of Marbled Murrelets from five survey stations in the Oregon Coast Range, 1 May–5 August (a) 1994, (b) 1996, and (c) 1997. Data at each station during each year were standardized as a proportion of the maximum detection count for that station during that year. Smoothing was done with locally weighted regression and smoothing scatterplots (LOWESS) with tension = 0.2.

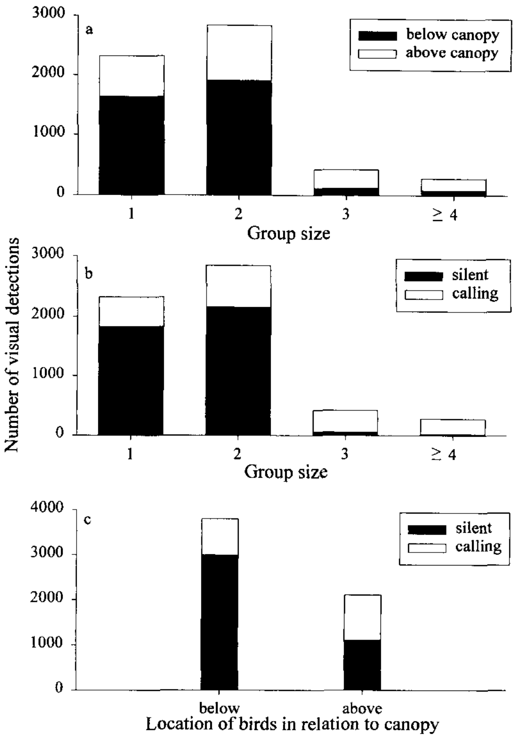

FIGURE 3. Number of visual detections of Marbled Murrelets in relation to (a) height of detection and group size, (b) vocal behavior and group size, and (c) height of detection and vocal behavior at five survey stations in the Oregon Coast Range, 1 May–5 August 1994, 1996, and 1997. Data from group sizes of 4–8 were pooled for display as the sample size for each was small and hence bars were too low to distinguish categories.

and silent, whereas groups visually detected above the canopy were larger and vocal (Fig. 3). Although the final generalized linear models for group size included a slightly different set of variables for each model, some patterns within the explanatory variables were consistent. Detection type was most strongly related to group size for each model ($175.1 < F_{1,1493\text{–}2116} < 335.0$, $P < 0.001$). Average group size increased by about 1.4 birds group^{-1} when murrelets were calling versus silent at all stations (Table 4; mean responses). Detection height also was significant for each model ($19.5 < F_{1,1493\text{–}2116} < 31.0$, $P < 0.001$). Average group size decreased by about 0.9 birds group^{-1} when detections occurred below canopy versus above canopy (Table 4). Time of day also was significant for each model ($15.8 < F_{4,1493\text{–}2116} < 61.1$, $P < 0.001$) as group size increased between time period two and three at all stations (Table 4).

DISCUSSION

FACTORS POTENTIALLY RELATED TO ACTIVITY

High temporal variability in daily activity levels of Marbled Murrelets occurred across all stations and years during this study, although the forces driving that variability remain unclear. We observed greater variability in daily activity than has been previously reported for this species (Rodway et al. 1993) or for other alcids (e.g., Jones et al. 1990, Piatt et al. 1990), and we failed to observe consistent seasonal patterns in activity. Similar to patterns reported by Rodway et al. (1993) in British Columbia, we also

TABLE 4. Poisson regression model estimates of the mean change (with 95% confidence intervals)[a] in a group size of Marbled Murrelets at each of three survey areas when visual detections occur in the indicator level versus the reference level for each explanatory variable (e.g., a mean response <1 indicates mean group size decreases by that amount in the indicator level). n = number of visual detections used in each survey area's Poisson regression model.

Explanatory variable	Reference level	Indicator level	Giant 1 & 2 mean response (95% CI)	Spencer 1 & 2 mean response (95% CI)	2 × 4 mean response (95% CI)
Height of detection	above canopy	below canopy	0.89* (0.85–0.93)	0.89* (0.85–0.93)	0.90* (0.86–0.94)
Month	June	May	n/s[b]	n/s	0.91* (0.86–0.96)
	July	June	n/s	n/s	0.97 (0.91–1.03)
Time period	3	2	0.87* (0.83–0.91)	0.83* (0.80–0.87)	0.83* (0.79–0.88)
	4	3	0.91* (0.86–0.96)	0.89* (0.84–0.93)	1.03 (0.97–1.10)
	5	4	1.03 (0.95–1.12)	1.01 (0.96–1.06)	0.92 (0.86–1.01)
Type of detection	visual-silent	visual-audio	1.32* (1.27–1.38)	1.27* (1.23–1.31)	1.50* (1.43–1.56)
Year	1996	1994	1.20* (1.12–1.28)	n/a[b]	n/a
	1997	1996	0.82* (0.77–0.87)	n/a	n/a
n detections			1,801	2,124	1,503

[a] A 95% confidence interval that includes 1.0 indicates that the change in mean response is not significant (flock size is not affected by that explanatory variable). * indicates significant mean responses.
[b] n/s = variable not selected for final Poisson regression model for that survey area; n/a = variable has only one level and so is not available for inclusion in the Poisson regression model.

observed inconsistent relationships between identical activity metrics on the same day at proximal survey stations. Variability in daily activity patterns of Marbled Murrelets has previously been attributed to both weather conditions at the nest stand and breeding phenology (see reviews in Naslund and O'Donnell 1995, and O'Donnell et al. 1995). We discuss the relationship of each of these factors to daily activity.

Reviews of Marbled Murrelet survey data suggest that daily measures of each Marbled Murrelet activity metric are positively related to cloud or fog cover (Naslund and O'Donnell 1995). However, most of the data used in these analyses were not collected from studies specifically designed to address this question. Alternatively, surveys specifically designed to test for a relationship between activity and weather show inconsistent relationships between these two sets of variables. For example, Rodway et al. (1993) report that counts of daily detections significantly increased on days with >80% cloud cover at only one of their two survey stations, and counts of keer calls did not differ with cloud cover at either station. However, duration of murrelet activity significantly increased on days with >80% cloud cover at both of their survey stations. Similarly, our analyses showed a weak and inconsistent relationship between weather and levels of murrelet activity and, when weather was a significant factor, daily duration of activity was affected more than daily counts of detections or vocalizations. We also observed that although absolute maximum levels of activity occurred on overcast days, minimum, moderate, and near-maximum levels of activity occurred across the entire range of weather conditions. Furthermore, if murrelet activity patterns at our survey stations had been strongly related to weather, then activity recorded on the same day at proximal survey stations experiencing the same weather should have been similar. This was not the case. Therefore, the relationship between weather and activity levels of Marbled Murrelets as determined by observer-based surveys is not consistent or strong.

Another factor that may be related to seasonal patterns in Marbled Murrelet activity is breeding phenology. For example, many alcids display high and highly variable attendance during early breeding (pre-laying), lowered attendance and variability during incubation, and increased and often highest attendance and variability during chick rearing and colony departure (Gaston and Jones 1998). Activity levels of Marbled Murrelets at our sites were often intermediate in May, least in June, and highest in July. These months generally correspond to the stages of murrelet laying, incubation, and chick-rearing, respectively (Nelson and Hamer 1995). Variability in timing of these stages within and among geographic areas may account for some of the variability we observed in activity patterns among sites and years. However, because we observed maximum and near-maximum levels of activity in at least one station during each month we surveyed, and because all stations displayed high daily variability during all portions of the breeding season, factors other than breeding phenology must also have influenced activity.

An additional factor that may have affected daily activity patterns at forest stands is foraging behavior at sea. In other alcids, when foraging conditions improve and foraging consumes a smaller proportion of an individual's daily activity budget, breeding and nonbreeding individuals each invest more time in colony visits (Gaston and Nettleship 1982, Jones et al. 1990, Zador and Piatt 1999). We have no direct evidence of a link between foraging conditions and Marbled Murrelet activity at inland nest sites. However, a moderate yet significant negative correlation ($r_s = -0.47$, $P < 0.05$) was observed in 1996 between the mean number of daily detections at Giant 1 and 2 and the percent time radiotagged Marbled Murrelets offshore of that stand spent diving versus resting on the surface during foraging bouts (Jodice 1999). Although not conclusive, these observations suggest a negative relationship between murrelet activity levels at the nest site and energy expended during foraging that would be consistent with those observed in other alcids.

Similarly, annual differences in foraging conditions may have affected annual differences in activity patterns. For example, Nelson (1987) attributed higher annual attendance of Pigeon Guillemots (*Cepphus columba*) to improvements in foraging conditions. Although we have no direct data on murrelet foraging conditions during survey years, we do know that sea surface temperature (SST) was coolest in 1994 and warmest in 1996, and regional upwelling was greatest in 1994 and least in 1996 (National Buoy Data Center 1997, Pacific Fisheries Environmental Group 1997). SST and upwelling are typically negatively and positively correlated with alcid foraging conditions, respectively (Gaston and Jones 1998). Coincidentally, we observed that annual mean and annual maximum counts of Marbled Murrelet detections at Giant 1 and 2 were highest in 1994 and lowest in 1996. These observations, therefore, suggest a positive relationship between murrelet activity at inland forest stands and improved foraging conditions.

Another factor that accounts for a proportion of variability in annual and daily activity of other alcids is irregular attendance of nonbreeders (Gaston and Nettleship 1982, Nelson 1987, Jones et al. 1990). For example, daily attendance of nonbreeders was variable and accounted for as many as 23% of the Pigeon Guillemots at a colony during pre-laying (Ewins 1985) and 50% of Least Auklets (*Aethia pusilla*) at a colony during incubation (Piatt et al. 1990). Although we were not able to determine the breeding status of Marbled Murrelets during our surveys, there was some evidence that a high proportion of the birds we recorded were not breeding. For example, approximately 74% of the detections we recorded included behaviors not indicative of nesting according to the Marbled Murrelet survey protocol. Furthermore, breeding murrelets typically approach the nest silently and during the earliest portions of the survey period (Nelson and Peck 1995, Singer 1995). Approximately 70% of our detections, however, included an audio component and were recorded after sunrise. Therefore, many of our detections likely recorded nonbreeding birds, and thus much of the variability we recorded may have been due to inconsistent attendance patterns of nonbreeders.

Irregular attendance patterns of nonbreeding birds also may account for the weak correlation we observed between activity levels at proximal stands on the same day. For example, if the proportion of nonbreeding murrelets attending stands accounts for a significant portion of the variability in daily activity as we have suggested, then the weak correlation we observed between activity at proximal stands could occur if nonbreeders alternated which stands they visited on which days. It is unlikely that this weak correlation in activity between proximal stands would be due to differences in foraging conditions encountered by murrelets because individuals that attend proximal stands typically forage at the same or nearby marine locations (C. Lougheed, pers. comm.). Rodway et al. (1993) also failed to document a strong correlation in daily activity between nearby stands.

BEHAVIOR AND GROUP SIZE DURING DETECTIONS

Flight behavior of Marbled Murrelets at inland forest stands appears to be similar across much of their range. Maximum group size varies from 6–8 and average group size is <2 (Manley et al. 1992, O'Donnell et al. 1995). Similarly, most studies including ours noted that murrelets detected below canopy were silent and occurred as singles or pairs, whereas birds detected above canopy were vocal and occurred in groups >2. Because nesting adults typically approach and depart the nest singly, silently, and below the canopy, larger groups of murrelets flying above the canopy during the middle and later portions of surveys are likely to be nonbreeding adults that may be displaying or prospecting.

As with numbers of daily detections, variability in mean group size among years during our study may have been related to foraging conditions. Group sizes at Giant 1 and 2 were least during 1996, which, of the three years we surveyed, likely represented the year of poorest foraging conditions at sea. If nonbreeding birds made up a significant proportion of birds attending nest stands, as has been demonstrated with other alcids and as discussed previously, and if the proportion of nonbreeding birds attending nest sites was directly related to foraging quality at sea, then lowered average group sizes in 1996 may have been due in part to fewer nonbreeding birds attending the forest stands. This effect on group size would be consistent with other annual differences in activity patterns.

Our study demonstrated that daily activity patterns of Marbled Murrelets at forest stands as determined by audio-visual surveys was highly variable at all temporal and spatial scales and greater than previously reported. Given the extreme levels of variability present in Marbled Murrelet activity data and our lack of understanding as to which factors drive that variability, it is critical not to infer relationships about behavior or activity patterns from small data sets or audio-visual studies not specifically designed to explore these issues. Further study of Marbled Murrelet activity using radar techniques (Burger 1997) and a direct comparison of data collected simultaneously using radar and intensive observer-based surveys such as ours would provide valuable information on many of the issues addressed herein. Further study of activity patterns of radiotagged birds at nest stands also would provide valuable information on daily activity patterns and flight behavior. Additional multiyear, high intensity surveys are needed throughout the species' range. Data from such survey efforts could be used to determine how attendance at nesting areas varies spatially and temporally, how activity patterns are related to forest habitats and marine foraging conditions, and, potentially, how activity patterns recorded during surveys are related to nesting effort.

ACKNOWLEDGMENTS

This research was funded by the Oregon State Office of the Bureau of Land Management, the USGS Biological Resources Division, and the USGS Forest and Rangeland Ecosystem Science Center. We are grateful to the following field technicians who endured many rainy mornings collecting survey data: Betsy Arden, Tracey Arensberg, Brad Buckley, Kemper Carlsen, Kelley Goocher, Lyndia Hammer, Rick Hatcher, Barry Hughes, Chris Knauf, Molly Monroe, Dana Morley, Mike Reardon, Rob Schneider, and Katerine Schletz. Special thanks to BLM biologists Joe Lint, Barb Hill, Wayne Logan, Kevin Kritz, and Gary Likata for their much appreciated support, advice, and assistance with field logistics. Lisa Ganio and Manuela Huso provided statistical support. Thanks to Steve Garman, Brian Cooper, Diane Evans, Anne Harfeneist, Bob Jarvis, Laura Jodice, Fred Ramsey, Walter Koenig, and two anonymous referees for constructive reviews of the manuscript.

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