Chapter 12
Daily Patterns of Marbled Murrelet Activity at Inland Sites

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Abstract: Patterns in the daily activity of Marbled Murrelets (*Brachyramphus marmoratus*) at inland sites has been studied throughout their range from California to Alaska. Murrelets are most active at inland sites around dawn, and to a lesser degree, at dusk. Throughout their range, peak levels of activity (detections) occur in the hour around dawn, but detections begin progressively earlier as one moves from south to north, corresponding to changing daylight regimes (e.g., California: 45 minutes before to 75 minutes after sunrise; Alaska: 90 minutes before to 40 minutes after sunrise). Timing of dawn detections also varies seasonally in relation to changing sunrise times. The duration of morning activity periods varies seasonally, being longest (2 hours) during summer and shortest (<1 hour) in winter. In all areas, weather conditions affect the timing, duration, and level of murrelet activity. In general, activity tends to begin later, last longer, and reach peak levels on cloudy or foggy mornings. The frequency of different behaviors varies throughout the morning period of activity. Murrelets tend to fly below the canopy more before sunrise than after, and group sizes become larger after sunrise. Early detections tend to include more silent birds, solitary calls, and wing sounds than later detections.

The relatively predictable changes in diurnal activity of birds have been well documented. Patterns of daily activity and behavior can vary widely between species. Knowledge of these activity patterns helps us understand avian ecology, develop appropriate survey techniques, and ultimately to manage threatened or endangered species. Relevant research questions include: How do activity levels and behaviors change between different times of the day? What are reasonable interpretations of temporal variation in behaviors? How should factors influencing variation in daily activity be used to interpret survey results? In this chapter, we examine the daily patterns of Marbled Murrelet (*Brachyramphus marmoratus*) activity at inland sites and how they are influenced by season, geographic location, and environmental conditions. Where applicable, patterns of subcanopy behaviors (i.e., murrelets occurring below canopy level), thought to be indicative of nesting, are also examined (see Ralph and others 1994).

Methods and Results

Data were collected primarily using general and intensive survey techniques (see Paton and others 1990, Ralph and others 1994). During these surveys, each time one or more murrelets were seen or heard, the event was recorded as a "detection" (see Paton and others 1990). Additional results from other research activities in murrelet nesting habitat (e.g., nest searches, observations at nests) are presented. For example, data from Alaska are from intensive surveys and from "stake-outs." During the latter, only those murrelet detections that occurred within 100 m of the observer were recorded (see Kuletz and others 1994c, Naslund and Hamer 1994). Only visual observations of murrelets were used in analyses of behavior (i.e., flying above or below canopy) and murrelet group size. All detections were used in other analyses.

General Patterns of Daily Activity

Murrelets are primarily active at inland sites around dawn and dusk. However, activity levels in the evening are lower and more sporadic than those during the morning. Nelson (1989) recorded that 12 percent of detections occurred at dusk and that murrelets were present on only 36 percent of dusk surveys in Oregon during the breeding season. In northern California, dawn activity was about five to six times greater than at dusk (Paton and Ralph 1988). Similar trends have been observed during the breeding season in British Columbia, Alaska, and at known nest sites in central California (Eisenhawer and Reimchen 1990, Kuletz 1991, Manley and others 1992, Naslund 1993a, Rodway and others 1993b). Anecdotal evidence for California and Alaska indicates that dusk activity also occurs during winter but may be less frequent than during the breeding season (Naslund, unpubl. data; Piatt, pers. comm.; Westphal, pers. comm.).

In central California, two murrelet nests were monitored using video equipment and night viewing devices. Murrelets were not observed visiting nests during the night (i.e., 1 hour after sunset through 1 hour before sunrise; Naslund 1993a). Radar studies on Vancouver Island found no detectable flight activity by murrelets through the middle of the night (Burger 1994, Burger and Dechesne 1994).

Timing and Duration of Morning Activity

In California and Oregon, murrelets were generally active between 45 minutes before and 75 minutes after official sunrise although most activity occurred during the hour around sunrise (Nelson 1989, Paton and Ralph 1988, Sander 1987). Murrelets occasionally were detected prior to 45 minutes before sunrise, but rarely more than an hour before (*fig. 1*; Naslund 1993a, Nelson 1989, Paton and Ralph 1988). Activity in Washington probably began earlier and lasted later than activity further south, and the peak activity period also occurred slightly earlier (Hamer and Cummins 1990, Hamer and others 1991). Murrelets in British Columbia typically became active up to about 75 minutes before sunrise (*fig. 1*; Manley and others 1992, Rodway and others 1993b). In southeast Alaska, most murrelets were detected between

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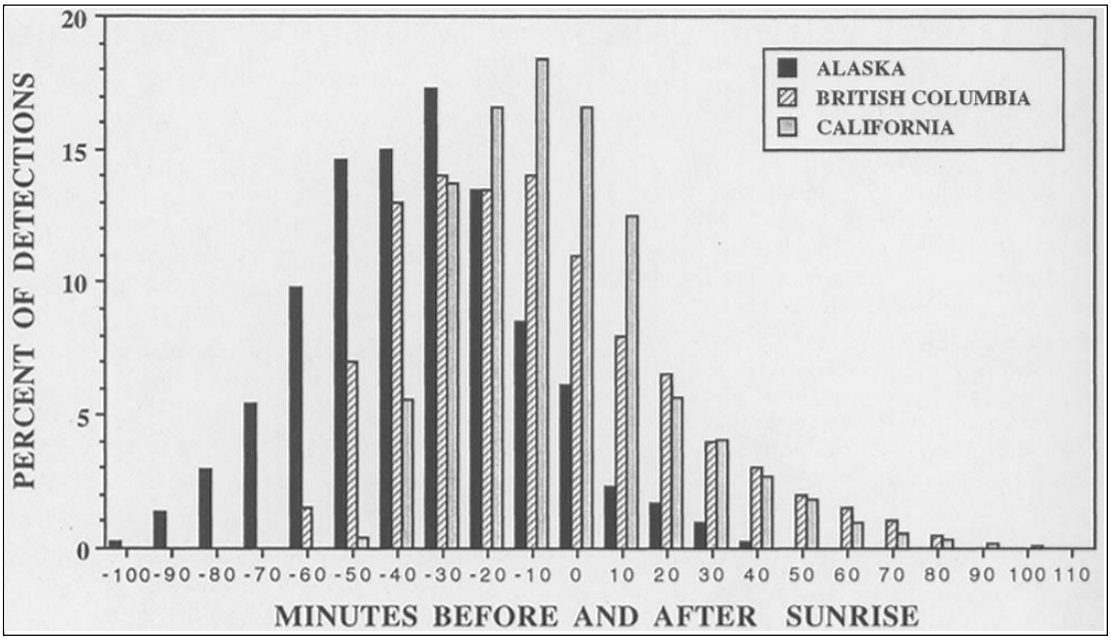

Figure 1—Timing of Marbled Murrelet detections relative to sunrise in California (*n* = 9764; Big Basin Redwoods State Park, 1989–1991; Naslund, unpubl. data), British Columbia (*n* = 2142; Phantom Creek, May-August 1990; Rodway and others 1991), and Alaska (*n* = 1649; Naked Island, May–August 1991; Kuletz and others 1994c)

1 hour before and 1 hour after sunrise (Walsh, pers. comm.). In southcentral Alaska, murrelets were generally active between 90 minutes before and 40 minutes after sunrise, although the majority were detected during the 75 minutes before sunrise (*fig. 1*; Kuletz 1991, Kuletz and others 1994c). However, they sometimes were detected 120+ minutes before sunrise (Kuletz 1991; Naslund, unpubl. data). In Alaska, the timing of first detections varied during the breeding season. Murrelets were active earliest around the beginning of summer (*fig. 2*; Kuletz and others 1994c).

In California, the duration of murrelet activity was longest during the breeding season (*fig. 3*; Naslund, unpubl. data; O'Donnell, unpubl. data). Conversely, their winter activity period was compressed and typically ended before sunrise (*fig. 3*). Murrelet activity occasionally began slightly earlier during winter than during summer (*fig. 3*). Murrelets tended to be active later in the morning and for shorter periods of time during August than in other summer months, in both California and Alaska (*fig. 3*; Kuletz, pers. comm.; Naslund, unpubl. data; O'Donnell, unpubl. data).

Timing and Duration of Evening Activity

In California and Oregon, most evening detections occurred from about 20-30 minutes (but up to 90 minutes) before, through about 20-30 minutes after, official sunset (Fortna, pers. comm.; Nelson 1989; Paton and Ralph 1988). Murrelets have been detected up to 45 minutes past sunset in Oregon, and were rarely heard during the middle of the night in California (Nelson 1989; Strachan, pers. comm.). Timing of evening activity in British Columbia was slightly later than that observed farther south, with 95 percent of detections occurring between sunset and 45 minutes after sunset (Rodway and others 1993b). Elsewhere in British Columbia, murrelets were most active >45 minutes after sunset in early June (Eisenhawer and Reimchen 1990). Virtually all evening activity in Alaska has been detected after sunset, and murrelets occasionally fly inland throughout the relatively bright nights around the summer solstice (Kuletz, pers. comm; Naslund, unpubl. data).

Weather Effects on Timing and Levels of Activity

Weather has been observed to affect the timing and duration of activity throughout the murrelet's range. Murrelet activity tends to begin later and last longer on cloudy or foggy mornings than on clear mornings (Kuletz, pers. comm; Manley and others 1992; Naslund, unpubl. data; Nelson 1989; Nelson and Hardin 1993a; Paton and Ralph 1988; Rodway and others 1993b; Sander 1987). However, Nelson (1989) noted that murrelet activity in Oregon also began earlier and lasted longer on clear mornings than on mornings with intermediate cloud cover, though not longer than on mornings with 100 percent cloud cover. In Alaska, activity several hours after sunrise was associated with heavy fog at ground level or mist (Kuletz 1991; Walsh, pers. comm.).

Environmental conditions can also affect levels of murrelet activity. At nest sites in central California, total numbers of detections and numbers of subcanopy behaviors tended to be higher when cloud cover was >80 percent, but was variable between sites (Naslund 1993a, unpubl. data). Rodway and others (1993b) also found that activity levels

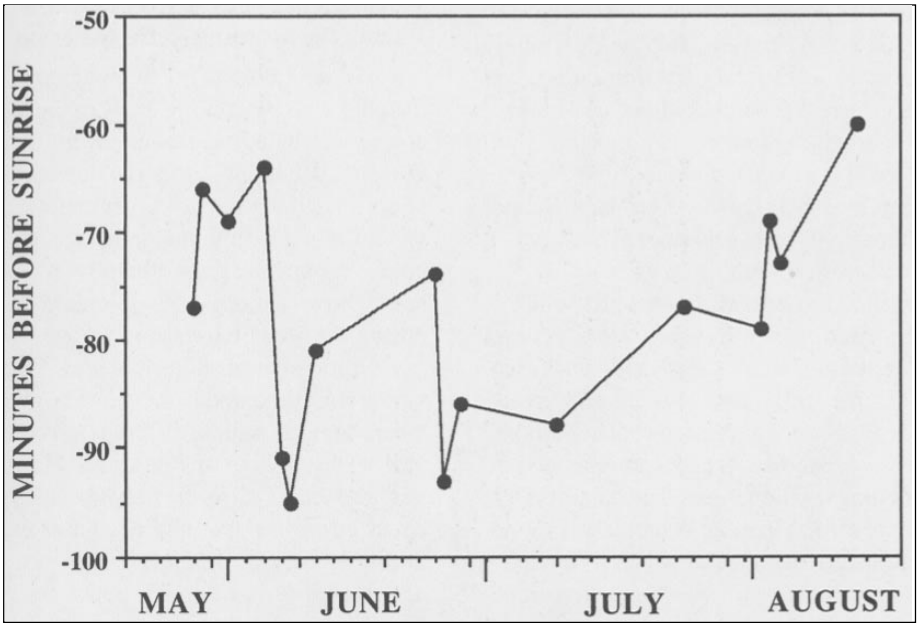

Figure 2—Timing of first Marbled Murrelet detections relative to official sunrise on Naked Island, Prince William Sound, Alaska, in May–August 1991 (Kuletz, pers. comm.)

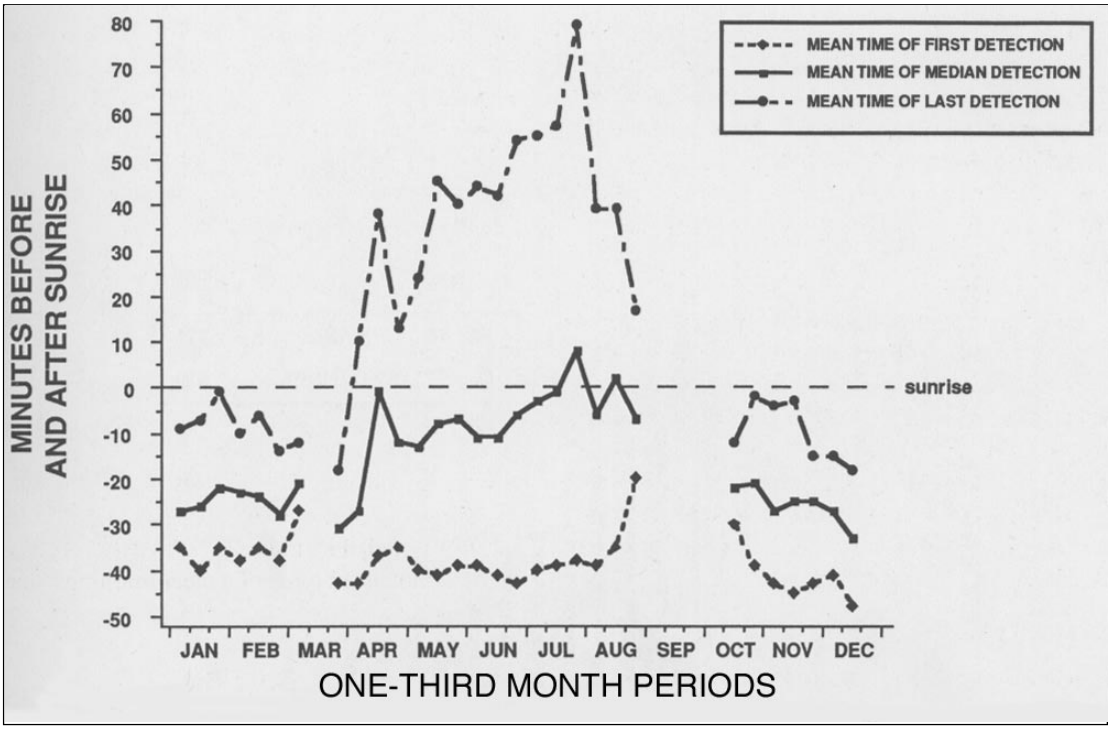

Figure 3—Timing of first, median, and last detections of Marbled Murrelets relative to sunrise at Lost Man Creek in northwestern California, 1989–1991 (O'Donnell, unpubl. data)

were higher on cloudy (≥80 percent cloud cover) than on clear (<80 percent cloud cover) days in British Columbia. Conversely, highest activity levels and detection rates have been recorded during clear (<25 percent cloud cover) and mostly cloudy (>75 percent cloud cover) mornings in Washington and Oregon (Hamer and Cummins 1990, Nelson 1989, Nelson and Hardin 1993a). However, Hamer and Cummins also noted that activity (mean number of detections) was greatest during conditions of light drizzle.

Other environmental factors also affect murrelet activity. Activity levels were high during periods of low cloud ceiling and decreased with increased wind speed and decreased temperatures during summer in Alaska (Kuletz and others 1994c). Mean detection rates were highest during conditions of poor visibility (i.e., low visibility ratings corresponded to days with low cloud ceilings) (Hamer and Cummins 1990). When examining weather effects in more detail, it was found that murrelets in Oregon were most active when it rained at the beginning of the survey, or when it was foggy at the end (Nelson and Hardin 1993a). In Alaska, murrelets sometimes exhibited high activity levels during snowstorms, when cloud ceilings were low and wind was negligible (Naslund, unpubl. data; Piatt, pers. comm.).

Weather may also influence the occurrence of activity around dusk. Although activity at dusk is infrequent in Alaska, murrelets were detected circling inland on two extremely foggy evenings (Kuletz 1991).

Variation in Behaviors, Vocalizations, and Group Size During the Morning Activity Period

Murrelet detections below canopy were more frequent than those above canopy, early in the morning activity period during the breeding season in northern California (*fig. 4*; O'Donnell, unpubl. data). The opposite was true after sunrise. It appears that this pattern remains intact throughout the year. The mean time that murrelets were seen in nest stands below canopy was significantly earlier than flight activity seen above canopy year-round in central California and during the breeding season in Alaska (*table 1*).

Group size of murrelets seen flying in forested stands varies with time of day. In central California and Alaska, the mean time at which different group sizes were observed varied throughout the morning during the breeding and nonbreeding (California only) seasons (*table 1*). Individuals occurred earliest, pairs somewhat later, and groups (i.e., ≥3) latest. However, this trend was not apparent during the transitional period. Similar trends have been noted in British Columbia and Oregon. In these regions, most observations before 20 minutes before sunrise were single birds, whereas later detections included larger groups (Manley and others 1992, Nelson and Hardin 1993a).

Numbers of vocalizations made by murrelets also exhibit temporal variation during the morning activity period. Single calls were heard earlier than calls involving ≥6 calls/detection, although this was only significant during the breeding season

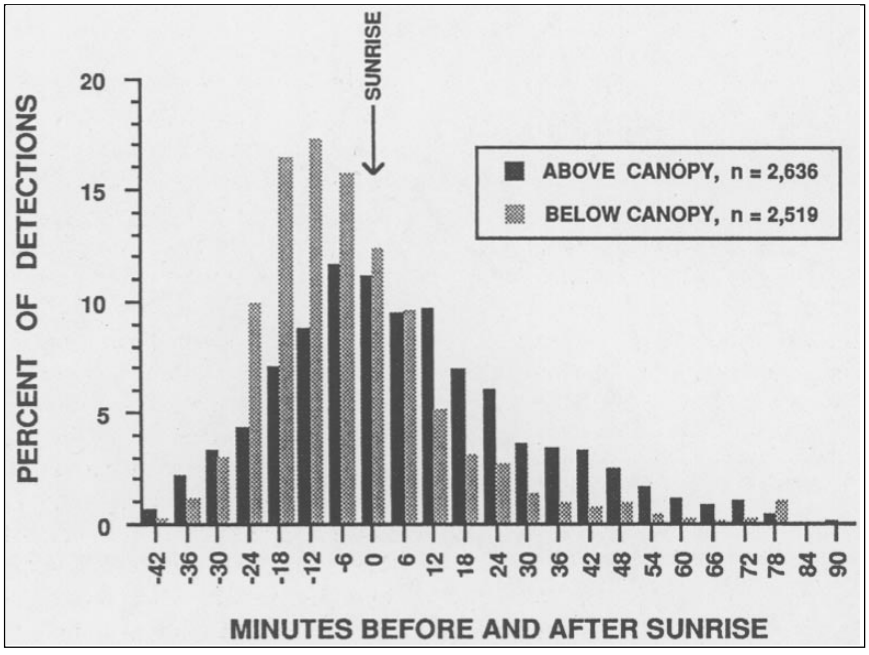

Figure 4—Timing of detections of Marbled Murrelets above and below the canopy relative to sunrise. Data presented are from Lost Man Creek in northwestern California, 1989–1991. *n* is the number of detections for each behavior class (O'Donnell, unpubl. data)

Table 1—Mean detection times ($\bar{x}$) and their standard deviation (sd), in minutes, relative to sunrise of Marbled Murrelet detection categories at Big Basin Redwoods State Park, California from 1989-1991, and at Naked Island, Alaska during 1992. Results of Tukey-Kramer range tests are shown. Means with different letters (in parentheses) are significantly (P < 0.05) different from each other

	Breeding						Nonbreeding			Transitional		
	California[1]			Alaska[2]			California[1]			California[1]		
Variable	*n*	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*
Bird height												
Below	714	-4(a)	19.9	252	-37(a)	21.5	7	-28(a)	8.0	63	-3(a)	14.
Above	1251	8(b)	20.4	297	-18(b)	25.4	33	-17(b)	10.1	100	3(b)	15.1
Group size												
1	1005	-1(a)	19.7	226	-34(a)	22.3	16	-25(a)	9.8	94	2(a)	16.7
2	737	6(b)	22.5	258	-26(b)	24.2	13	-19(ab)	8.0	55	-1(a)	12.4
≥3	259	10(c)	18.2	68	-8(c)	29.2	13	-13(b)	11.2	17	1(a)	12.4
No. calls												
0	1248	3(a)	21.8	126	-38(a)	18.9	9	-27(a)	12.1	106	2(a)	16.4
1	1761	-4(b)	23.6	231	-38(a)	22.5	291	-27(a)	15.4	299	-13(b)	16.3
2-5	2376	-2(bc)	23.5	490	-33(ab)	25.6	332	-25(a)	13.8	274	-10(bc)	15.2
6-9	824	0(c)	23.6	190	-29(b)	27.0	148	-23(a)	12.8	83	-8(c)	15.4
>9	4171	0(c)	22.6	1004	-29(b)	24.5	859	-25(a)	12.1	457	-10(bc)	14.7
Type												
Wings[3]	74	-13(a)	14.2	36	-48(a)	13.0	7	-32(a)	7.0	7	-19(a)	8.6
Heard[4]	8415	-1(b)	23.4	944	-33(b)	21.8	1602	-25(ab)	13.2	1054	-12(ab)	15.3
Both[5]	751	4(bc)	19.5	80	-18(c)	26.6	31	-16(ab)	8.9	60	-1(bc)	11.8
Seen[6]	1174	4(c)	21.8	83	-32(b)	17.5	2	-11(b)	14.1	99	3(c)	15.9

[1] Naslund (unpubl. data)
[2] Kuletz (pers. comm.)
[3] Wings heard only, not seen
[4] Heard calling, not seen
[5] Seen and heard calling
[6] Seen, not calling

(*table 1*). In British Columbia, solitary calls were most frequent before sunrise (Manley 1992). Murrelets making only wing sounds were heard earlier than those heard vocalizing or those seen (*table 1*). This pattern was consistent year-round but was significant only during the breeding seasons in California and Alaska. Silent murrelets were also seen relatively earlier in Alaska than in California. This may partially be a function of greater light levels before dawn in Alaska, thereby making murrelets easier for observers to see. In British Columbia, Manley (1992) found that the occurrence of silent murrelets (including both single birds and pairs) peaked 20 minutes before sunrise.

Discussion

Daily Patterns of Activity and Behaviors

Murrelets exhibit a primary period of inland activity around dawn and a secondary period around dusk. That murrelets are most active during the low light levels of dawn and dusk presumably reflects adaptation to predation pressures in the forest. Nesting murrelets and their chicks and eggs are vulnerable to a variety of avian predators including corvids and raptors (Brown, pers. comm.; Marks and Naslund 1994; Naslund and others, in press; Nelson and Hamer 1992, this volume b; Singer and others 1991). Crepuscular activity also allows for maximum diurnal foraging time.

Variation in activity levels during the day appears to mirror aspects of murrelet nesting biology. Murrelets exchange incubation duties and exhibit peak feeding rates of young chicks around dawn (Hamer and Cummins 1991; Naslund 1993a; Nelson and Hamer, this volume a; Nelson and Hardin 1993a; Nelson and Peck, in press; Singer and others 1991, 1992). Murrelets also sometimes exhibit flight behaviors around nests and feed chicks around dusk. They visit nests with young chicks infrequently mid-day, though diurnal feedings increase when chicks get older (Fortna, pers. comm.; Hamer and others 1991; Naslund 1993a; Nelson and Hamer, this volume a; Singer and others 1991).

Low detection levels at dusk may result from temporal differences in the composition and behavior of murrelets at inland sites. Fewer nonbreeders may fly inland during the evening activity period. Murrelets appear to fly silently while

carrying fish and are generally silent when visiting or flying around nests during the evening and are thus less easily detected (Naslund 1993a, unpubl. data).

Activity levels relative to sunrise are notably earlier at northern latitudes (i.e., British Columbia and Alaska) than at more southern latitudes. This difference in activity periods results from differing light regimes. Pre-dawn light levels are greater and occur earlier, relative to sunrise, in Alaska. In this region, the seasonal variation in timing of first murrelet detections appeared to track changes in light levels. Murrelets were heard earliest, and occasionally throughout the "night", around the summer solstice when light levels were greatest (Kuletz and others 1994c). As summer advanced and light levels decreased, murrelet activity occurred increasingly later. Similarly, early activity in Washington and British Columbia is thought to result from longer twilight periods (Eisenhawer and Reimchen 1990; Hamer and Cummins 1990; Rodway and others 1991, 1993b).

Cloudy or foggy weather results in lower light levels than clear mornings and may thus be affecting the timing of murrelet activity similar to changes in twilight regimes. In addition, murrelets may respond to periods of low fog or clouds, light rain, or snow by flying lower and calling more frequently and are thus detected more frequently under these conditions. However, on at least some occasions, murrelets fly above the fog, then drop below the fog just before entering the forest canopy (Kristan, pers. comm.). The influence of weather on murrelet activity is further evidenced by observations of murrelets exchanging incubation duties later on cloudy mornings and mornings with low cloud ceilings than on clear mornings, as well as changes in behaviors at nests with changes in weather conditions (Naslund 1993a, Nelson and Peck, in press).

Although weather conditions apparently affect many aspects of murrelet activity, murrelets exhibit variable responses to conditions observed inland. This variability may reflect differences between weather conditions at survey sites and conditions that murrelets respond to down drainages and other flight corridors, or at the coast. Timing and duration of activity inland also reflects seasonal variation in environmental conditions. For example, activity is earlier and shorter in winter when days are shorter and environmental conditions more extreme than in summer. This presumably reduces the time available to murrelets for foraging, and may increase the effort required to obtain food. Consequently, less time and energy may be available for inland flights. Differences may also correspond to changes in social behavior or reduced numbers of birds in winter (see Naslund 1993a,b; O'Donnell and others, this volume). The late and reduced duration of activity observed in August corresponds to a time when detections become sporadic and decrease overall (Kuletz and others 1994c, Naslund 1993a, Nelson and Hardin 1993a).

Temporal variation in behavior, group size, and vocalization patterns of murrelets during the morning activity period reflects features of nesting biology. The early timing of single birds and birds flying below canopy coincides with the typical times that murrelets exchange incubation duties and display around nest sites (Naslund 1993a; Nelson and Hamer, this volume a; Nelson and Peck, in press; Singer and others 1991, 1992). Similarly, murrelets make single calls and wing sounds early in the morning. These behaviors have also been associated with incubation exchanges, chick feedings, and possible displays in nesting territories (Naslund 1993a; Naslund and Hamer 1994; Nelson and Hamer, this volume a; Nelson and Hardin 1993a). Conversely, the larger and more vocal groups that are more frequent later in the morning may represent murrelets engaged in social interactions or joining together for flights to sea.

Survey Implications

Based on the daily activity patterns described here for murrelets, it is clear that current guidelines, which recommend that surveys be conducted during the dawn activity period, will provide the most consistent information on use of inland habitat by nesting murrelets (see Ralph and others 1993, 1994). Evening surveys may furnish additional information useful for interpreting stand-use or furthering our understanding of murrelet biology. It is evident that survey start-times should be shifted earlier as one moves north to compensate for changes in light levels relative to sunrise. Exact timing for some areas (e.g., southwest Alaska) may require further evaluation.

It is difficult to standardize surveys in a manner which eliminates the contribution of weather conditions to daily variation in activity patterns. Variability in activity is further confounded by the effects of weather conditions on the ability to detect murrelets. For example, fog and rain may reduce observers' abilities to see or hear murrelets. However, Rodway and others (1993b) found no evidence that some weather conditions (e.g., cloud cover) affect the proportion of detections that are seen. Avoiding surveys during certain conditions (e.g., heavy rain), as recommended by current guidelines (Ralph and others 1993, 1994), will reduce variation in recorded activity due to differences in visibility. This can be particularly important when evaluating subcanopy behaviors, which relies primarily on the visual detection of murrelets. In Alaska, where inclement weather prevails, surveys may be conducted on all days except those with high winds and extreme rain. Weather effects should be considered accordingly when making temporal and spatial comparisons between surveys.

Collection of data on group size, behaviors, and vocalizations during surveys provides information that is important for interpreting stand-use by murrelets. These data may also prove useful for unraveling various aspects of the ecology of this enigmatic species.

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