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WHY DO MARBLED MURRELETS ATTEND OLD-GROWTH FOREST NESTING AREAS YEAR-ROUND?

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ABSTRACT.—The attendance of Marbled Murrelets (*Brachyramphus marmoratus*) in old-growth forest in central California was studied from January 1989 through July 1991. Five nesting areas were surveyed ($n = 216$ survey mornings) by recording the number of times murrelets were detected (by sight or sound) during a 2-h period at dawn. Presence or absence of murrelets was determined during an additional 123 morning surveys. Murrelets were active in nesting areas nearly year-round. Detection levels in fall and winter (nonbreeding season) were about one-half those in spring and summer (breeding season). Murrelets were absent, or detections were minimal and most variable, during August–October and March. These transitional periods of low murrelet activity coincided with periods of molt. Detection levels were least variable in November and December. Marbled Murrelets in central California attended nesting areas during the nonbreeding season more frequently than murrelets in other regions, and more often than most other alcids. Wintering murrelets may be year-round resident breeders and attendance during the nonbreeding season may be important for maintenance of nest sites, nesting territories, or pair bonds. Nesting areas should be managed throughout the year. Winter may be an ideal time to conduct long-term monitoring studies, as variability in attendance is low. *Received 4 November 1992, accepted 31 May 1993.*

MEMBERS OF THE Alcidae typically breed in large colonies on coastal cliffs and islands. Following the breeding season, alcids are no longer tied to colonies, and most migrate or disperse to winter foraging areas. However, some species (e.g. Common Murre [*Uria aalge*], Black Guillemot [*Cepphus grylle*]) attend colonies during fall and winter, particularly those breeding at the southern reaches of their range (Greenwood 1987, Harris and Wanless 1989). Presumably, such behavior is beneficial despite the possibly higher energetic costs incurred by remaining within foraging distance of the colony during harsh winter months.

Compared to other alcids, the Marbled Murrelet is unique because it usually nests solitarily on branches of old-growth coniferous trees up to 100 km inland (Binford et al. 1975, Carter and Sealy 1986, Quinlan and Hughes 1990, Singer et al. 1991; see Carter and Morrison 1992). Few nests have been found and most inland records are of murrelets heard calling as they fly above the forest. Only a few birds are actually seen. Typically, murrelets fly from marine foraging areas to nest sites around dawn and, to a lesser extent, at dusk (Eisenhawer and Reimchen 1990, Paton and Ralph 1990, Manley et al. 1992). During the chick-rearing period, they occasionally visit nests during the day (Carter and Sealy 1990, Naslund 1993).

Little is known about the inland activity patterns of the Marbled Murrelet in nesting areas during the nonbreeding season. Anecdotal observations of murrelets calling over forested stands, or of murrelets found injured on the forest floor, suggest that they sometimes visit nesting habitat during fall and winter (for Alaska, Willet 1926, Dick 1979, M. McAllister pers. comm., Naslund and Piatt unpubl. data; for California, Singer and Verardo 1975, Carter and Erickson 1992). Murrelets were frequently observed on winter surveys conducted at inland forests in California and Washington (Sander unpubl. manuscript, Cross unpubl. report). Finally, Carter and Sealy (1986) compiled records of murrelets at inland lakes and found that about one-fifth occurred during the nonbreeding season. They speculated that the association of murrelets with nesting habitat during winter may be important in courtship, pair-bond maintenance, and prospecting for nest sites.

I studied the breeding behavior and seasonal activity patterns of Marbled Murrelets at an inland forest along the central coast of California. The area represents the southernmost breeding

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range of the species (Sowls et al. 1980, Carter and Erickson 1992) and is one of the few locations where murrelet nests have been found (Binford et al. 1975, Singer et al. 1991). Murrelets in central California typically breed from mid-April through mid-August, but nesting may begin as early as the beginning of April and extend through September in some years (Carter and Erickson 1992, unpubl. data). In this paper, I describe the annual cycle of Marbled Murrelets in nesting areas and consider the implications of winter attendance with respect to behavioral ecology and habitat requirements.

METHODS

I surveyed Marbled Murrelets in Big Basin Redwoods State Park, Santa Cruz County, California, from January 1989 through July 1991. The park is located in the Santa Cruz mountains and is comprised largely of old-growth forest dominated by coast redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*). Singer et al. (1991) have described the habitat of the study area in detail.

Five sites were examined during both the breeding and nonbreeding seasons: Bloom's Creek Campground (BCCG), Hihn-Hammond Road (HHRD), J Camp (JCAM), Opal Creek Picnic Area (OCPA), and Redwood Loop-Mother of the Forest (RLMF). Hereafter "site" refers to a specific area, approximately 100 × 100 m, where murrelet surveys were conducted. Each site contained confirmed nest trees (HHRD, OCPA, JCAM, RLMF; Binford et al. 1975, Singer et al. 1991, 1992) or suspected nests (based on murrelet behavior and the presence of grounded nestlings; Carter and Sealy 1987, unpubl. data). All five sites were approximately 8 to 9 km from the ocean, between 286 and 315 m in elevation, and within 1.25 km of each other.

Levels of murrelet activity were quantified during 216 morning surveys using a modified version of the intensive inventory (hereafter referred to as "intensive survey") method described by Paton et al. (1990). Surveys were conducted from 1 to 10 times per month at each site during all or part of the study period. A murrelet "detection" was defined as "the sighting or hearing of a single bird or a flock of birds acting in a similar manner" (Paton et al. 1990:2). Activity was quantified by recording the total number of detections that occurred during the peak activity period for murrelets (between about 45 min before, and 75 min after, official sunrise). Because some birds may be detected repeatedly, and calling birds are more likely to be detected than silent birds, detection rates provide only an index of relative activity. However, lower detection rates probably indicate that fewer birds are using an area. For each detection, personnel recorded the number of birds, their behavior, numbers and types of calls, flight directions, distance, and height of birds seen. Intensive surveys were modified to include counts from stationary and grid surveys.

Stationary surveys were conducted from a single station within each site for the entire survey period. Grid surveys were conducted from four stations, about 50 to 100 m apart, within each site. During grid surveys, data were collected for 20 min at a station before moving to the next station, rotating between stations for the duration of the survey period (see Ralph et al. 1990). Few, if any, detections were missed while traveling between stations, owing to the ease of moving through the relatively open understory of the forest. Total counts from both types of surveys were pooled for analyses.

To compensate for differences in maximum activity levels between sites, surveys were standardized at each site. This was done by calculating the ratio of the number of detections per survey to the highest count at that site. Data from each site and from all sites combined were then averaged by month to examine overall seasonal trends in attendance. Proportional data were arcsine transformed and analyzed using a test for equal variances (see TTEST; SAS Institute 1985).

To determine frequency of murrelet attendance, intensive survey data were augmented with an additional 123 morning surveys (where presence or absence was recorded) in or adjacent to the five intensive survey sites. Survey days ($n = 339$) were not randomly selected but sampled the full spectrum of weather (excluding hard rain) and other environmental (e.g. moon and tide phase) conditions. Most mornings were surveyed during the breeding season. Nonbreeding-season surveys were conducted once or twice a week.

RESULTS

Data (grouped by week) from Blooms Creek Campground illustrate the typical pattern of activity throughout the year at Big Basin Redwoods State Park (Fig. 1). Peaks of activity occurred from May through July (and occasionally in April at other sites; see Table 1). Activity then decreased and became sporadic in August and ceased in September. Detection levels rose again in October and continued throughout the winter. The number of detections per survey at this site peaked ($n = 177$) in early May and weekly means ranged from 0 to 144. The highest number of detections per intensive survey at any site was 309.

Survey counts varied between sites and seasons, and were influenced by environmental

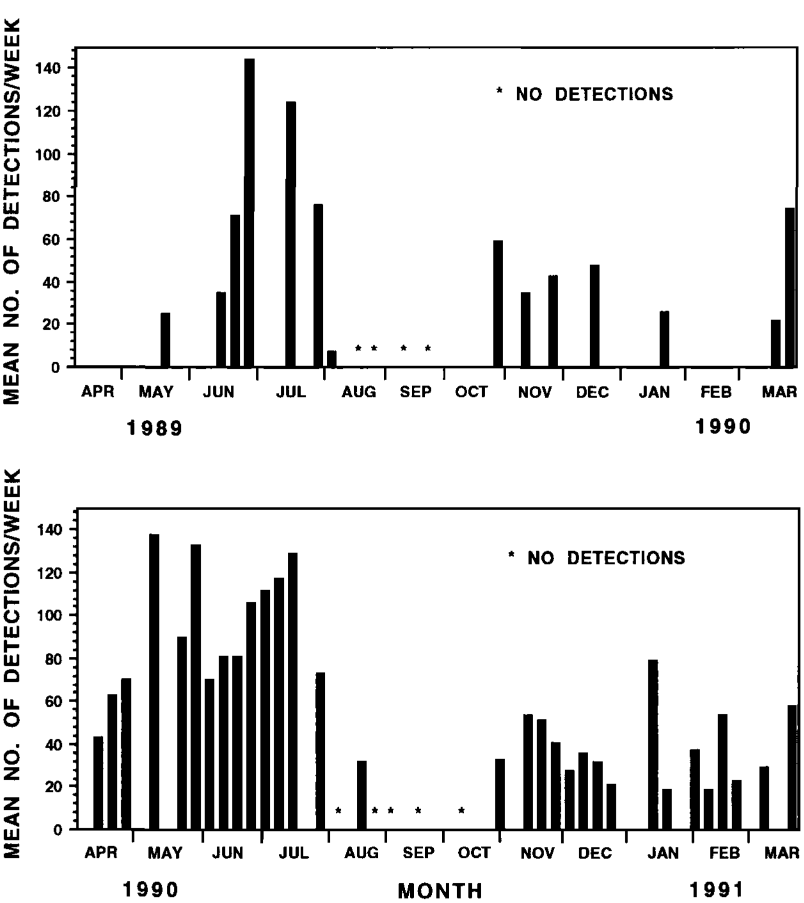

Fig. 1. Mean number of Marbled Murrelet detections per week at Bloom's Creek Campground in 1989–1990 (upper) and 1990–1991 (lower). Each weekly mean calculated from one to three intensive dawn surveys (see Methods). Asterisks (*) indicate that survey conducted, but no murrelets detected; all other blank columns represent weeks in which data were not collected.

conditions (Naslund 1993). At all sites, activity levels during winter (November through February) were lower than during summer (April through July; Fig. 2). Seasonal means ranged between 17–80 and 49–158 detections during winter and summer, respectively. The ratio of winter-to-summer detections varied between sites and ranged from 0.35 to 0.80 (Table 1). Sites with low summer variability had high winter/summer ratios; those with high summer variability had low ratios; and one site was intermediate for both (average of monthly coefficients of variation [CV] for April–July at BCCG = 35%, HHRD = 61%, JCAM = 27%, OCPA = 28%, RLMF = 49%). Sites with high summer variability and low winter-to-summer ratios (HHRD, RLMF) contained what appeared to be display areas (i.e. individuals or pairs of murrelets repeatedly joined, separated, and circled low over the ground). On average, winter activity levels were about one-half those of summer (unweighted mean ratio of winter-to-summer detections for all sites combined was 0.514).

Standardized data from all sites and years combined shows that mean monthly detections were consistently highest in summer and lower during the remaining months (Fig. 3). Detection rates were significantly more variable in summer than in winter (test for equality of variance, df = 109 and 36, $P < 0.0001$; Table 1). On average, activity was least variable in November and December and most variable in March, August, and October. Some individual sites also exhibited low variability in activity levels in April, May, and July (Table 1).

Combining presence-absence and intensive-

TABLE 1. Numbers of Marbled Murrelet detections (per survey) by month at five study sites in Big Basin Redwoods State Park, California, 1989-1991.

	BCCG		HHRD		JCAM		OCPA		RLMF		Total
Month	n	$\bar{x}$ ± CV (range)	n	$\bar{x}$ ± CV (range)	n	$\bar{x}$ ± CV (range)	n	$\bar{x}$ ± CV (range)	n	$\bar{x}$ ± CV (range)	CV[a]
January	3	41 ± 79 (19-79)	1	15	1	37	0		1	75	34
February	6	32 ± 50 (10-54)	0		1	73	0		1	39	35
March	6	44 ± 61 (5-75)	1	15	1	57	4	55 ± 103 (0-121)	1	0	67
April	3	59 ± 24 (43-70)	4	81 ± 82 (32-176)	3	79 ± 19 (63-93)	2	112 ± 19 (97-127)	1	149	38
May	6	102 ± 50 (25-177)	6	47 ± 59 (27-91)	5	83 ± 17 (65-101)	4	102 ± 36 (64-151)	2	79 ± 11 (73-85)	38
June	11	86 ± 41 (35-151)	9	47 ± 41 (27-76)	7	90 ± 36 (55-156)	8	95 ± 32 (69-159)	1	168	34
July	9	107 ± 25 (53-138)	14	42 ± 61 (18-112)	5	101 ± 36 (66-152)	5	103 ± 25 (59-124)	5	189 ± 37 (127-309)	38
August	8	21 ± 171 (0-94)	9	19 ± 107 (0-49)	7	8 ± 178 (0-37)	4	2 ± 200 (0-6)	8	4 ± 212 (0-27)	130
September	4	0	4	0	4	0	2	0	0		—
October	2	30 ± 141 (0-59)	2	3 ± 141 (0-6)	1	63	1	40	0		93
November	8	46 ± 25 (33-65)	1	19	3	59 ± 26 (44-75)	2	80 ± 28 (64-96)	0		25
December	7	35 ± 28 (21-51)	0		2	60 ± 25 (50-71)	0		0		23
Winter/summer ratio[b]		0.415		0.345		0.649		0.799		0.360	

[a] Total CV determined from proportions of individual survey counts to maximum counts (see Methods).

[b] "Winter" months include November-February and "summer" months are April-July. Ratios calculated by dividing mean number of detections during winter-month surveys by mean number of detections during summer-month surveys. Average ratio for five sites was 0.514.

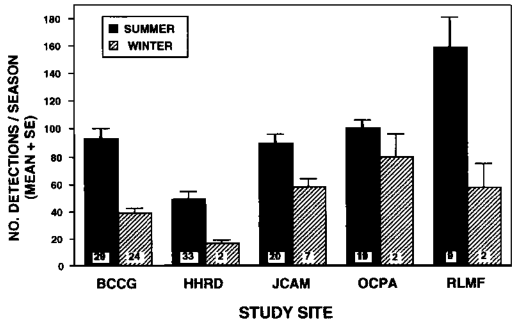

Fig. 2. Mean number of Marbled Murrelet detections by season at five study sites. "Summer" includes April-July and "winter" includes November-February. Study-site codes explained in Methods. Sample sizes (number of surveys) indicated in histogram bars.

survey data, murrelets were present during 306 of 339 (90%) morning surveys. They were detected during all surveys in all months except March and August-October (Fig. 3). The proportion of surveys in August-October with murrelets present was much lower than for surveys in summer ($X^2 = 110.82$, df $= 1$, $P < 0.0001$), winter ($X^2 = 29.79$, df $= 1$, $P < 0.0001$), or March ($X^2 = 4.91$, df $= 1$, $P = 0.027$). Similarly, murrelets were observed on a smaller proportion of surveys in March than during summer (Fisher's exact test, $X^2 = 30.70$, df $= 1$, $P = 0.0036$) or winter (Fisher's exact test, $X^2 = 6.65$, df $= 1$, $P = 0.0532$). Overall, murrelets were active on 94% of surveys ($n = 66$) conducted during the entire nonbreeding season (October through March).

DISCUSSION

Ecological implications of attendance behavior.—Marbled Murrelets visited nesting areas in central California in most months. They exhibited the highest peaks of inland activity during the breeding season (April-September), but also visited nesting areas throughout the nonbreeding season (October-March). Two transitional periods of reduced or no murrelet activity were evident. The most pronounced of these corresponds to the cessation of nesting and the onset of the pre-basic molt (Sealy 1975, Carter and Sealy 1987, Carter and Erickson 1992, G. Strachan pers. comm.). The second transitional period occurred approximately four to six weeks prior to egg laying and coincides with the prealternate body molt (Carter and Erickson 1992, unpubl. data). Activity inland may have been reduced during these periods because the prebasic molt limits flying ability and because both molts, as well as egg formation, place high energetic demands on the birds.

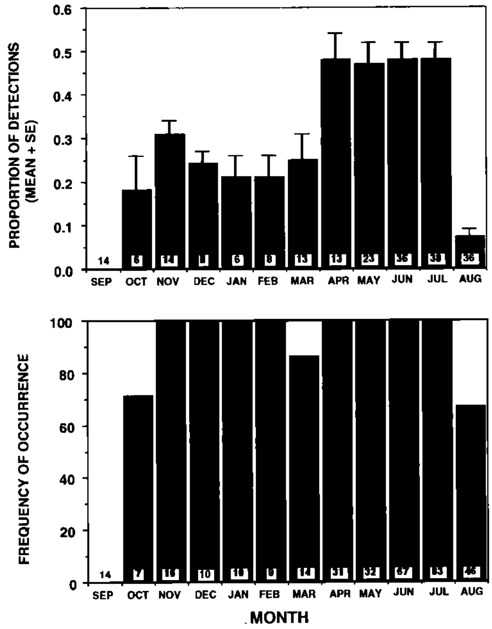

Fig. 3. Average levels of Marbled Murrelet activity (upper) and frequency of Marbled Murrelet occurrence (lower) by month at all study sites combined. Sample sizes (number of surveys) indicated in histogram bars.

The pattern of fall and winter activity I observed agrees with Carter and Erickson's (1992) summary of anecdotal murrelet observations for California and is similar to attendance patterns of most other alcids that visit colonies during the nonbreeding season. Similarities between murrelets and other alcids include: (1) spring and summer peaks of activity generally correspond to features of breeding phenology; (2) attendance during the prelaying period is variable (Bayer and Herzing 1985); and (3) the postbreeding return follows the end of a flightless wing molt (Greenwood 1987, Harris and Wanless 1990a).

Winter attendance in Big Basin Redwoods State Park occurred with greater regularity than in other areas where murrelet attendance has been examined in winter. In Washington and northern California, murrelets attended nesting areas only 61% and 66%, respectively, of winter mornings (Cross unpubl. report, Sander unpubl. manuscript). Variation in weather, oceanographic conditions, and prey availability may contribute to variation in murrelet attendance patterns, as it does for other alcids (Ainley and Boekelheide 1990). The distance between nest sites and foraging areas (e.g. about 35 km at the Washington site studied by Cross vs. 8 to 9 km in central California) may also influence attendance in winter. Additional studies are needed to determine whether the patterns observed are representative of murrelet attendance on a larger temporal and spatial scale.

The reduced level of activity in central California during fall and winter probably represents a reduction in the number of individuals flying inland and suggests that part of the population had dispersed from nesting areas. Based on the distribution of murrelets at sea following the breeding season, it appears that some California murrelets disperse south in some years and that there is little movement of northern murrelet populations to the central coast of California (Sealy et al. 1991, Carter and Erickson unpubl. report).

For a variety of non-seabird taxa that exhibit partial migration, evidence indicates that winter residency confers a reproductive advantage by enabling residents to: (1) secure optimum breeding sites early in the season; (2) have greater success in securing mates or being recruited into the breeding population; or (3) have more familiarity with home ranges (Adriaensen and Dhondt 1990, Warkentin et al. 1990, Ulenaers and Dhondt 1991). Fall and winter attendance has also been documented at several alcid colonies, generally at the southern end of each species' range (Thoresen 1964, Taylor and Reid 1981, Harris 1985, Greenwood 1987, Harris and Wanless 1989, 1990a, Ainley and Boekelheide 1990, Sydeman 1993). This attendance is most pronounced in dense or saturated colonies, and birds tend to return earlier as populations grow. It appears that autumn return is important for maintaining established nest sites or pair bonds and that this translates into increased reproductive success. For example, in the few colonies for which breeding histories of individual Common Murres were known, fall and winter populations were comprised primarily of breeding and site-holding adults (Harris and Wanless 1989, 1990b, W. Sydeman pers. comm.). Further, Harris and Wanless (1989) found that, over a six-year period, the degree of fall visitation by Common Murres was highly correlated with reproductive success in both the previous and subsequent summers.

Murrelets that visit nesting areas in winter probably represent a portion of the breeding population that is resident year-round. The question is whether they derive reproductive advantages similar to those observed in other taxa and other alcids. The degree of nest-site fidelity exhibited by murrelets is unknown. However, they sometimes nest in the same tree in successive years (Nelson 1992, Singer et al. 1992); they appear to maintain loose territories during summer (Naslund et al. 1993), and behaviors that are typically associated with nesting areas during summer (e.g. flights through or low over the forest canopy, chases) are occasionally seen in fall and winter (Naslund 1993). Fall and winter attendance may increase the likelihood that pairs will retain nest sites or territories in the subsequent summer. I hypothesize that high-quality nest sites are rare, despite the apparent abundance of possible nest branches within forests. Based on nest records (Binford et al. 1975, Quinlan and Hughes 1990, Singer et al. 1991, Nelson and Hamer 1992, Naslund et al. 1993), optimal nest characteristics appear to include: (1) a large platform to support the nest; (2) sufficient moss cover or debris to contain and insulate a nest depression; (3) cover from predators and inclement weather; and (4) easy flight accessibility. The availability of such nest sites depends on the age and physical structure of individual trees as well as the forest stand. Conditions affording the optimum characteristics for high-quality nest sites are probably limited. In addition, available nesting habitat for murrelets has greatly diminished because of extensive logging of old-growth forests, and competition for nest sites may have increased. Winter attendance could enhance the murrelet's ability to retain or secure high-quality nests.

Implications for management and conservation.— Most survey work on Marbled Murrelets and other alcids is directed towards monitoring populations during the breeding season. A common problem is that the interpretation of survey results is confounded by the presence of nonbreeding adults and subadults among the breeding population. These birds contribute significantly to seasonal and annual variability in attendance rates and may comprise up to 50% of the population present at some colonies during summer (Gaston and Nettleship 1982, Nelson 1987, Jones 1992). I observed the greatest variability in murrelet attendance in summer at sites in central California that contained possible display areas (HHRD, RLMF), which probably reflected attendance by displaying nonbreeders. Indeed, breeders may contribute little to daily variability in detections because they are typically silent and secretive around their nests, they may fly directly between nests and foraging areas, and they probably spend most daylight hours during the nestling period meeting the demands of feeding chicks (Varoujean et al. unpubl. report, unpubl. data).

As the winter population may consist of a high proportion of resident breeders and because variability is lowest during November and December, winter could be an ideal time to conduct long-term monitoring studies of murrelets in central California. Winter surveys would be advantageous for three reasons: (1) they may track the most important component of the population (i.e. breeders); (2) there would be less competition for personnel and resources required for other biological studies; and (3) in some regions (e.g. Alaska) there would be fewer landbird species calling and flying at dawn to confuse with murrelets. Winter monitoring should complement summer studies. Application elsewhere would require further evaluation.

The Marbled Murrelet was recently listed as federally threatened in California, Oregon, and Washington, primarily because of substantial reductions in available nesting habitat due to the logging of old-growth forests (Stein and Miller 1992). Fall and winter attendance at nesting areas has important implications for the conservation of murrelets. Some current management recommendations advise that potential disturbances (excluding logging) around nest sites may be allowed during the nonbreeding season (Interagency Marbled Murrelet Guidelines Committee). My study indicates that protection should be extended year-round (at least during the dawn activity period) to insure minimal disturbance to local breeders. Furthermore, murrelets in California forage near shore and adjacent to breeding areas throughout the year. These small, localized populations are particularly at risk from oil pollution and gill-net mortality (Carter and Erickson 1992). Chronic oiling, in association with larger oil spills, is contributing to the decline of Marbled Murrelets in central California (Piatt et al. 1990, Carter and Erickson 1992). Long-term impacts would be more significant if winter residents are high-quality breeders. Throughout the murrelet's range, there is a need to monitor mortality and to identify and protect primary wintering areas at sea.

Conclusions.—Attendance of nesting areas during the nonbreeding season is an important component of Marbled Murrelet ecology. In the population I studied, fall and winter attendance was similar in pattern to that of other alcids that attend colonies during the nonbreeding season. More so than other alcids (with the possible exception of Cassin's Auklet [*Ptychoramphus aleuticus*]; Ainley and Boekelheide 1990), Marbled Murrelets regularly visit nesting areas in fall and winter throughout their range in North America. By inference from detailed studies on other species, this suggests that some murrelet populations that winter near nesting areas may be comprised of experienced breeders, and that winter attendance could be important for maintenance of pair bonds and nest sites. The nearly year-round attendance of nesting areas by Marbled Murrelets has important ecological, management, and conservation implications and warrants further study.

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