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ABSTRACT—Marbled Murrelets (*Brachyramphus marmoratus*) nest predominantly in the canopies of large old-growth conifers, and are listed as Threatened in Canada and 3 US states mainly as a consequence of reductions in this habitat due to logging. We assessed the re-use of nest sites (nest trees) by murrelets in British Columbia using 3 types of data: 1) evidence of return of adults to the same nest site; 2) evidence of multiple nests within the same tree; and 3) re-checking known nest trees in subsequent seasons for evidence of re-use. All 3 methods showed evidence of re-use of nest trees in different years, but there were marked regional differences in the degree of re-use. Re-use of nest trees was most frequent in regions with extensive loss of nesting habitat due to logging (Southern Mainland Coast and East Vancouver Island), and rare in a less disturbed region (West Vancouver Island). Overall, 26 of 143 (18%) nest trees climbed showed evidence of multiple nesting in separate seasons. Management of nesting habitat should incorporate these results by providing greater protection of habitat in regions where habitat is sparse, and by minimizing predation risk where murrelets more frequently re-use nest sites. Since re-use of nest sites is infrequent, managers should aim to provide murrelets with multiple choices for nest sites, such as maintaining large tracts of old-growth forest with many large trees containing potential nest platforms.

Key words: Marbled Murrelet, *Brachyramphus marmoratus*, nest re-use, British Columbia, conservation, habitat selection

Most species of the family Alcidae (auks or alcids), in common with many other seabirds, exhibit high nest site fidelity, with individuals returning to the same burrows or cliff-ledges used in previous breeding seasons (Gaston and Jones 1998). As in most seabirds, the majority of alcid species are colonial and nest on islands, cliffs or other sites relatively free of predators. In contrast, Marbled Murrelets (*Brachyramphus marmoratus*) are non-colonial, typically nesting in low densities with widely dispersed nests; most nests south of Alaska are located high in the canopies

of old-growth conifers (Nelson 1997). Such highly dispersed nesting habitat, along with cryptic breeding plumage and secretive visits to nest sites in twilight hours, has probably evolved to reduce predation at nest sites. Predation of adults, eggs, and chicks at nest sites has been widely documented and is the most common cause of nest failure (Nelson and Hamer 1995; Nelson 1997; Burger 2002; Piatt and others 2006).

Marbled Murrelets typically nest in a simple depression (about 10 cm dia; 0.5–8 cm deep) in the moss on a large canopy limb or deformity, but sometimes on large limbs or deformities with no epiphyte cover (Nelson 1997). Evidence of nesting includes flattened and brown moss, eggshell fragments, chick down, and in recently

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occupied nests, chick excreta which often forms a conspicuous white fecal ring bordering the nest cup.

Although there is evidence of some re-use of nest sites by murrelets (Singer and others 1995; Nelson 1997; Hebert and Golightly 2006, 2007), the frequency and geographic variation of this behavior is not well known. Such information is important for 3 reasons: first, it helps to understand the biology of the species, including the selection pressures under which its nesting behavior evolved; second, as murrelets increasingly nest in highly fragmented and dwindling old-growth forests it is important to understand the flexibility and limitations of their habitat use, and their response to these anthropogenic changes; third, this information is important in formulating management and conservation policy. Repeated occupancy of forest stands by murrelets from year to year is well documented (Divoky and Horton 1995; Nelson 1997; Burger 2002), but it is not known if pairs return to the same stand in each year. Most occupied stands contain large numbers of potential nest platforms (Burger 2002) and hence re-use of a stand does not imply re-use of the same tree or nest site.

Information on nest site re-use is urgently needed to help formulate management policies in British Columbia. The Species at Risk Act (SARA; <http://www.sararegistry.gc.ca/>) enacted by the federal Canadian government in 2003 enables protection of the "residence" of a listed species, such as the Marbled Murrelet. SARA defines a residence as: "a dwelling-place, such as a den, nest or other similar area or place, that is occupied or habitually occupied by one or more individuals during all or part of their life cycles, including breeding, rearing, staging, wintering, feeding or hibernating". A key aspect in allocating and protecting residences is the extent to which the species returns to re-use the residence sites, such as murrelet nest trees. Government agencies and the lumber industry therefore need to know the extent and geographical variation of nest site re-use in British Columbia. In the most obvious application, forest managers need to know whether to protect known nest sites for use in subsequent breeding seasons.

In this paper we collate and review information on nest site re-use by Marbled Murrelets in 3 regions in British Columbia and recommend implementation of this information in manage-

ment and conservation policy. The data available are sparse and geographically clumped, but since there is so little published information on this topic from anywhere in the species' range and there is currently very little effort aimed at discovering and monitoring nest sites, it is worth summarizing what is known, taking into account the small samples. Our results will be valuable for refining management policies in the US too, where murrelets use similar nesting habitats and have experienced significant changes in the extent and configuration of nesting habitat (Ralph and others 1995; McShane and others 2004; Piatt and others 2006).

METHODS

Of the 6 Marbled Murrelet conservation regions recognized in British Columbia (see map in CMMRT 2003), most research and nest searches have been concentrated on the southern coast. Consequently, data were available from 3 regions: the Southern Mainland Coast (SMC); East Vancouver Island (EVI); and in the western portion (WVI) of the West and North Vancouver Island region. We collated published and unpublished information on the re-use of nest sites, focusing on the re-use of nest trees (that is, trees known to contain a nest), but also considered the re-use of nest cups at the finest spatial scale and re-use of nest stands at a coarser level. There were 3 types of data available.

Observations of Birds at Nest Trees or Nest Stands

This information came from the extensive radio-telemetry studies undertaken by Simon Fraser University (SFU) in 2 locations: Desolation Sound (UTM: Zone 10U, 381000E, 5549000N, NAD 83) on the Sunshine Coast (SMC region), and Clayoquot Sound (UTM: Zone 9U, 715000E, 5465000N, NAD 83) on southwestern Vancouver Island, in the WVI region (for example, Bradley and Cooke 2001; Bradley and others 2004; McFarlane Tranquilla and others 2003). Additional information came from Manley's (1999) study of murrelet nesting in the Bunster Range (UTM: Zone 10U, 384000E, 5545000N, NAD 83) on the Sunshine Coast, where visual observations combined with extensive tree-climbing provided some information on murrelets returning to known nest sites. Jones (2001) provided observations at 2 nests on the nearby Caren Range (UTM: Zone 10U,

436000E,5496000N,NAD 83) on the Sunshine Coast.

Evidence from Tree Climbing of Multiple Nesting in a Single Tree

Tree-climbing by specialist climbers has been extensively used in British Columbia to search for nests or confirm the location of nests identified from ground survey (visual) or telemetry methods (for example, Manley 1999; Bradley 2002; Conroy and others 2002). We also used unpublished information which the authors had collected over the past 18 y while researching murrelets in southern British Columbia. In situations where the climbers systematically searched the canopy for evidence of nests, we extracted information on the number of trees that contained more than 1 nest, either on the same or on different limbs. Tree climbers checking the canopy for nests visually scanned every likely limb. In some cases recent nesting activity was "clearly evident (for example, clear nest depression; feces deposited by chick; fresh eggshell or egg membrane fragments, or chick down), but many nests were also identified on the basis of past nesting activity that might have occurred earlier in the season, or in past seasons (for example, clear nest cup with dead or recovering epiphytes; old and discolored eggshell fragments or chick down; see results). Consequently we did not attempt to differentiate between nests made in previous years and those active in the season that the tree was climbed. Some trees with multiple nests were therefore used in different years.

Evidence of Re-use based on Monitoring Known Nests in Subsequent Years

In the Bunster Range, SMC region (IAM, unpubl. data) and in the Carmanah (UTM:Zone 10U,377000E,5393000N,NAD 83) and Walbran (UTM:Zone 10U,382500E,5393000N,NAD 83) watersheds, WVI region (AEB and KMJ, unpubl. data), tree climbers re-visited known nest sites for 1 to 5 y after the nest was discovered to document re-use of the nest and the same tree. Climbing was done at the end of the breeding season to reduce the chance of disturbing active breeders. Two nests located by telemetry on southwestern Vancouver Island (southern boundary of the WVI region) were re-visited 1 y after discovery; one nest was clearly visible

from the ground and it was not deemed necessary to climb the tree and the second was visited by both ground observers and a tree climber (US Forest Service study; TDB and MGR, unpubl. data).

RESULTS

Re-use of Nest Stands based on Radio-telemetry

During the 3-y radio-tracking study at Desolation Sound, only 1 bird was tracked in multiple years (1999 and 2001). Two nests used by this bird were found in separate trees located within 200 m of each other (Simon Fraser University: DBL and MS, unpubl. data). In the same study, Bradley (2000) documented the re-use of the same forest stand by a radio-tagged male murrelet which re-nested later in the same season after a failed 1st attempt, but he was unable to confirm whether the bird used the same tree within the stand.

Re-use of the same Nest Cup or Limb

In the Bunster Range (SMC), Manley (1999) used a combination of audio-visual watches and tree-climbing to provide evidence of nest re-use between 1995 and 1997. Inter-annual re-use of nest trees occurred at 12% ($n = 8$) and 11% ($n = 27$) of nest trees in 1996 and 1997, respectively. Of the 4 nest trees re-used, the same limb and nest cup was re-used in 2 trees and a different limb in 2 trees. In the nearby Caren Range (SMC), Jones (2001) documented the re-use of 1 nest cup in 2 successive years but did not report further observations at this nest or at a 2nd nest site. At 1 of the 2 nest sites monitored on southwestern Vancouver Island (WVI) by the US Forest Service, there was evidence of re-use of the same nest cup in successive years (2006 and 2007; TDB and MGR, unpubl. data).

Multiple Nesting in a Single Tree - Tree-climbing Data

We obtained data from 143 nest trees documented by climbers from a total of 1628 trees climbed in British Columbia (Table 1). The table shows evidence of multiple use of a tree based on single visits by a climber, such as multiple nest sites within the tree or other evidence that the tree was used more than once (for example, old eggshell fragments or chick down from a previous nesting attempt within a fresh nest).

TABLE 1. Evidence of multiple nests or re-use of nest sites by Marbled Murrelets within trees checked once by climbers in British Columbia.

Marbled Murrelet Conservation Region	Method for locating nests	No. of years sampled	No. of trees climbed	No. of nest trees in sample	No. of trees with multiple use	Site location	Source
Southern Mainland Coast (SMC)							
	Ground Surveys and tree climbing	4	721	52	10	Bunster Hills, Sunshine Coast	Manley 1999, IAM (unpubl. data)
	Telemetry and tree climbing	4	54	40	11	Desolation Sound area, Sunshine Coast	DBL (unpubl. data)
	Total SMC		775	92	21		
East Vancouver Island (EVI)							
	Tree Climbing	1	32	2	1	Sooke Hills	Burger and others 2000
West & North Vancouver Island (WVI)							
	Ground Surveys and tree climbing	6	320	11	0	Carmanah & Walbran Valleys	AEB (unpubl. data)
	Ground Surveys and tree climbing	1	1	1	0	Bulson Valley, Clayoquot Sound	Jordan and others (in Burger and others 1997)
	Tree Climbing	1	467	5	0	Ursus Valley, Clayoquot Sound	Conroy and others 2002
	Telemetry and tree climbing	3	27	27	3	Clayoquot Sound	DBL (unpubl. data)
	Telemetry and tree climbing	3	6	5	1	Southwest Vancouver Island	TDB and MGR (unpubl. data)
	Total WVI		821	49	4		
Total all regions			1628	143	26		

Overall, 26 (18%) of the nest trees showed evidence of multiple nesting, but there were regional differences in these trends.

Of the 92 nest trees checked by climbers on the Sunshine Coast (SMC), 21 (23%) showed evidence of multiple use. These data came from 2 separate studies. Manley (1999) reported 19% of nest trees had more than 1 nest indicating use in more than 1 season ($n = 52$ nest trees: 9 trees each had 2 nest sites and 1 tree had 3 nest sites). In the SFU telemetry study (DBL and MS, unpubl. data), 28% of nest trees had multiple nests indicating use in more than 1 season ($n = 40$ nest trees: 9 trees each had 2 nests, 1 tree had 3 nests, and 1 tree showed re-use of the same nest cup). Of these 11 nests in the SFU study considered to be possible re-use of the same tree, 5 had strong evidence of murrelet nesting (eggshells, feces, and/or down), and 6 had no

evidence of occupation apart from the formation of a depressed cup in the epiphyte layer. Four of the 11 were on different branches, 6 were on the same branch, and 1 was not recorded.

In a small sample of nest trees found in the EVI region, 1 of the 2 nest trees discovered in the Sooke Hills near Victoria had 2 separate nest sites (Table 1). All 3 of these nests appeared to have been active 1 to 2 y prior to discovery (Burger and others 2000).

Evidence of multiple nests was found in 4 (8.2%) of the 49 nest trees climbed in the WVI region in 5 separate studies (Table 1). These 4 trees were all in the sample of active nests located by telemetry: 1 tree had an additional nest 25 cm from the active nest on the same limb, with eggshell fragments and feces from a previous year; 1 nest which failed appeared to have been used in a previous year (old downy feathers

TABLE 2. Evidence of re-use of nest trees in Marbled Murrelets in British Columbia from known nests re-checked in subsequent years. Data were available from the Bunster Range, Southern Mainland Coast (SMC) region (23 nests; Manley 1999, IAM, unpubl. data), and from the Carmanah and Walbran valleys (6 nests; AEB, unpubl. data) and Cullite and Hemmingson valleys (2 nests; TDB and MGR, unpubl. data) in the West and North Vancouver Island (WVI) region.

No. of years after nest found	Bunster Range (SMC)		WVI watersheds	
	No. trees checked	No. (%) re-used	No. trees checked	No. (%) re-used
1	23	3 (13)	7*	1 (14)
2	13	3 (23)	6	0
3	3	1 (33)	4	0
4	-	-	4	0
5	-	-	2	0
6	-	-	1	0

* 1 nest was not checked a year later but was checked 2 y after use.

worked into the moss); and in the 3rd tree the climber reported "possible multiple use" with no further details. Overall, the re-use of nest trees in highly disturbed (see Discussion) regions (SMC and EVI; 22 of 94 trees) was significantly higher than in the less disturbed region (WVI; 4 of 49 trees; $X^2 = 5.03$, $df = 1$, $P < 0.05$).

Evidence from Nests Checked in Multiple Years

Samples in this category were too small for statistical testing among regions. In the Bunster Range (SMC), tree-climbers checked 23 known nest trees for evidence of re-nesting for 1 to 3 y after nest discovery; re-nesting was discovered in 7 trees (23%) and in all 3 y sampled (Table 2). Nest trees re-used were not necessarily used in each year; IAM (unpubl. data) documented gaps of 1 to 2 y between re-use of a nest tree.

Of the 8 nests in the WVI region that were re-checked in subsequent years, likely re-use of the same tree (and same nest cup) was found in only 1 nest (Table 2). The re-used nest site was in the Hemmingson Valley on southwestern Vancouver Island; the chick fell from the nest in the year the nest was found and there was inconclusive but suggestive evidence of recent nesting (thick fecal ring) when the nest was checked in the following season. There was no sign of re-nesting in 6 nest trees in the Carmanah and Walbran valleys (WVI) which were checked annually 1 to 6 y after discovery (Table 2).

TABLE 3. Persistence of nesting evidence documented by a tree climber in the Carmanah and Walbran watersheds on southwest Vancouver Island. The number of nests showing clear evidence of each nest feature in the active year (Year 0) and in subsequent years (Years 1–4) is shown.

Nest feature	Year 0	Year 1	Year 2	Year 3	Year 4
Fecal ring	4	0	0	0	0
Fishy odor	4	0	0	0	0
Eggshell fragments	5	3	2	1	1
Cup depression	5	5	4	2	1
Moss damage	5	5	4	2	1

Detailed observations and photographs made in successive years at the Carmanah and Walbran nests by the climber (KMJ) also provide information on the persistence of evidence of nesting in murrelet nests in this region (Table 3). The limb bearing 1 nest fell the winter after the nest was found. In the remaining nests, the fecal ring and fishy odor resulting from the feces, which are evidence of a chick in the nest, were no longer discernable (to a human) the year after nesting. Eggshell fragments persisted in 1 nest for 4 y, but were not found in most nests after 3 y. Evidence of the flattened nest depression and damage to moss within the nest cup persisted for 3 y in 2 of the 5 nests, and for 4 y in 1 of the nests. Most nests remained evident to human observers for at least 2 y after occupancy and some for much longer.

DISCUSSION

Extent of Nest Tree Re-use in the British Columbia Data

We found that a portion of the nest sites used by Marbled Murrelets in British Columbia were re-used in subsequent years, although there is no evidence in this sample that the same individual birds were re-using any nest site. We also had insufficient data to test whether re-use of nest sites was affected by the success or failure of nesting attempts. There was, however, a marked regional difference in the extent of re-use, which appeared to be linked to the amount of suitable nesting habitat available to the birds and the history of clearcut logging in the surrounding area. On the Sunshine Coast (Bunster Range and Desolation Sound; SMC region) re-use of nest trees appeared to be relatively common (25% of trees contained more than 1 nest site; 23% of

known trees were re-used within 1 to 3 y of discovery). The small sample from East Vancouver Island showed evidence of re-use (1 of the 2 nest trees had 2 nests). Both the Sunshine Coast forest district and EVI have experienced extensive clearcut logging over the past 150 y (reviewed by Burger 2002). Demarchi and Button (2001a, b; summarised in Burger 2002) estimated that 70% of the apparently suitable forest in the Sunshine Coast forest district had been removed, and within this area the reduction in the Desolation Sound area was independently assessed as 80% (Zharikov and others 2006). Similarly, on East Vancouver Island, the Demarchi and Button (2001a, b) data suggest a decline of 77% of suitable forest habitat in the Duncan forest district (Burger 2002).

In contrast, we found infrequent re-use of nest sites in the West & North Vancouver Island region; however, most of our work was done in the southwestern portion of this region. Only 8% of trees climbed showed evidence of multiple use, and repeated use was found in 1 of the 8 nest trees checked 1 to 6 y after discovery (maximum re-use was 14%, recorded 1 y after the nests were discovered; Table 2). Loss of the old forests likely to provide nesting habitat has been much less widespread in this region than on the Southern Mainland Coast or East Vancouver Island. The Demarchi and Button (2001a, b) data suggest a decline of 47 and 41%, respectively, in the Port Alberni and Campbell River forest districts which include the study areas (Burger 2002). Habitat loss was less than this in the watersheds where most nest trees were located. The Carmanah and Walbran valleys and the large relatively unmodified watersheds of Clayoquot Sound provide many thousands of hectares of likely nesting habitat, much of it protected in parks (Burger 2001, Chatwin 2002).

Documentation of nests by tree climbers without complementary information on nest attendance is likely to under-estimate nest site re-use because re-use might not be detectable if failure occurs early. For example, Hebert and others (2007) recorded removal by corvids of eggs at 2 nests leaving no evidence that nesting had occurred. In addition, recent nesting might obscure evidence of past nesting if the same nest cup was used (Manley 1999). Nevertheless, the marked regional differences in nest re-use in British Columbia, supported by 2 different

methods (Tables 1 and 2), suggest that these are real differences and not sampling artifacts.

We tentatively conclude that nest re-use by Marbled Murrelets in British Columbia is more likely in areas where nesting options have been curtailed by large-scale clearcut logging. Even in these areas, the proportion of nest trees which were re-used within 1 to 3 y appeared low, suggesting fidelity to nest trees is extremely low. This does not rule out site fidelity at a larger spatial scale; murrelets might return to a particular forest stand to nest, but select a different tree within the stand, as was found in our sole example from the radio telemetry work. Replacement laying within a season has been documented in British Columbia (McFarlane Tranquilla and others 2003) and there is evidence from British Columbia (Bradley 2000) and California (Hebert and others 2003) that 1st and 2nd nests in a season are sometimes within the same stand, but repeated use of the same nest tree within the same season has not yet been documented.

Evidence from Elsewhere in the Species Range

In areas where there are few suitable trees with nest platforms, Marbled Murrelets appear to re-use nest trees and even nest cups quite frequently. In the redwood forests of California, where up to 95% of historical likely nesting habitat has been removed by logging (Noss 1999; Ricketts and others 1999), nest re-use by murrelets appears to be common. In central California (Big Basin State Park, Santa Cruz County), 1 tree was used for 5 successive seasons with 2 different limbs used (Singer and others 1995; Nelson 1997). Similarly in northern California (Redwoods National and State Parks, Humboldt County), re-use was reported of 1 nest site in 4 successive years (2001-2004) and repeated use of nests at 2 other nest sites (Hebert and Golightly 2006, 2007). These authors concluded that nest sites were limited in northern California. In the same area, Hebert and others (2003) documented repeated use of the same forest stand by a radio-tagged murrelet re-nesting within the same season after breeding failure, but they did not confirm the re-use of the same tree or limb. One tree in Oregon was used in 1991 and 1993 but not in 1992, and a different limb was used in each year (Nelson 1997). There is also additional evidence for re-use of nest trees in Oregon and

Washington (TDB and MGR, unpubl. data; SK Nelson, unpubl. data).

Nest Fidelity in an Evolutionary Context

Marbled Murrelets differ from most other alcids in many aspects of their breeding and it is not surprising therefore that they do not display the same nest site fidelity that is characteristic of their colonial-nesting relatives (Gaston and Jones 1998). Marbled Murrelets, along with their close relatives the Kittlitz's Murrelet (*B. brevirostris*) and the Asian Long-billed Murrelet (*B. perditus*), are the only alcids to display camouflage alternate (breeding) plumage and nest in scattered, widely dispersed sites (Gaston and Jones 1998). For all 3 *Brachyramphus* murrelets, many nest sites are on mainland locations exposing nesting birds to a wide range of potential predators, and predation risk has obviously been a strong selection force in the evolution of plumage, nest site selection, and nesting behavior.

Avoidance of previously used nest sites can be explained as an anti-predator strategy. Tree climbers frequently noted a strong fish odor at nest cups in which chicks had been raised, which might attract mammalian predators (most likely squirrels and mice; Nelson 1997; Flaherty and others 2000; Bradley and Marzluff 2003). Although this was not evident to humans a year later, arboreal mice or squirrels might still be able to detect the faint fishy scent. Corvids are the most common nest predators documented at murrelet nests (Nelson 1997; Burger 2002; McShane and others 2004). Ravens, crows, and jays have excellent spatial memories and show evidence of episodic memory whereby they recall past events to influence present activities (Bekoff and others 1999; Clayton and others 2003; Emery and Clayton 2004; Marzluff and Angell 2005). An experimental study of Steller's Jay (*Cyanocitta stelleri*) concluded that these predators were most likely to encounter a murrelet's nest incidentally while searching for their primary prey (insects and fruit), but that they did appear to retain a search image for nests (Vigallon and Marzluff 2005). Other corvids (crows and ravens) do remember the locations of nests (Sonerud and Fjeld 1987). Indeed, where repeated use of a murrelet nest site over 4 successive years was documented in northern California, most of the breeding

attempts ended in failure, with predation by a Common Raven (*Corvus corax*) and a Steller's Jay documented in 2 years (Hebert and Goughly 2007). All of the re-use attempts documented by Manley (1999) on the Sunshine Coast ended in failure and 2 of these nests had evidence of predation. It seems likely that low nest site fidelity, in combination with highly dispersed nest sites, cryptic plumage, inconspicuous nests, and secretive nest visits is part of the evolutionary response by murrelets to the high risks of predation at their inland nest sites. This behavior therefore needs to be considered for optimal management of nest habitat.

Management Implications

Our study contributes to both policy development and field management of Marbled Murrelet nesting habitat in British Columbia, and our results also will be important for management in the US. At the policy level we have confirmed that re-use of nest sites does occur frequently enough to be considered within the SARA framework. Known nest sites, whether currently active or active in past seasons, and the buffering forest stand around them should be considered as "residences" as defined by SARA. The application of this definition should certainly be enforced in the murrelet conservation regions where there has been greatest habitat loss (East Vancouver Island and the Southern Mainland Coast; Burger 2002; CMMRT 2003), and within parts of the other regions where extensive habitat loss has occurred. We recommend annual monitoring of known nest sites, especially in these highly modified regions, to increase our knowledge of long-term trends in the use of nest trees and the need to protect known nest stands as "residences" under SARA.

Relative to field management, our study reinforces the need to protect known nest sites, especially in those areas where habitat loss has been extensive. Furthermore, our results need to be incorporated into management efforts to minimize predation risk for nesting murrelets within the forests. Reduction of nesting habitat in old-growth forests by clearcut logging is acknowledged to be the greatest threat to Marbled Murrelets through most of their range, including in British Columbia (reviews by Ralph and others 1995; Nelson 1997; Burger

2002; Raphael and others 2002; McShane and others 2004; Piatt and others 2006). Increased predation risk due to habitat fragmentation, creation of edges preferred by corvid predators, and the increase of predator densities in the Pacific Northwest are related problems (see reviews cited above). Although data on the fate of breeding attempts is extremely sparse, murrelets have low reproductive output and predation is the most commonly documented cause of nest failure (see reviews above). The most detailed observations of nests re-used in subsequent years suggests that nest predation is exceptionally high in such situations (Hebert and others 2003; Hebert and Golightly 2006, 2007), although nesting success was higher in the re-used nests observed by Singer and others (1995). Clearly, additional research is needed to quantify the change in predation risk resulting from reduced habitat options where murrelets more often re-use the same nest tree in subsequent seasons.

Re-use of nest trees is relatively infrequent in British Columbia, even in regions where the murrelets seem to have limited choices. Managers should therefore aim to provide murrelets with the forest conditions with which the species has evolved, such as large tracts of old-growth forest with many large platform-bearing trees providing multiple choices for nest sites. The precautionary approach would be to provide multiple nest site options per stand. Furthermore, where habitat is reduced and nest re-use is likely, steps should be taken to minimize predation risk by, for example, reducing anthropogenic attractants to corvids and squirrels and by minimizing roads and fragmented forests which tend to benefit some nest predators (Marzluff and Restani 1999; Raphael and others 2002; Marzluff and Neatherlin 2006).

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LITERATURE CITED

- BEKOFF M, ALLEN C, GRANT M. 1999. Feeding decisions by Steller's Jays (*Cyanocitta stelleri*): the utility of a logistic regression model for analyses of where, what and with whom to eat. *Ethology* 105: 393-406.
- BRADLEY J E, MARZLUFF M. 2003. Rodents as nest predators: influences on predatory behavior and consequences to nesting birds. *Auk* 120:1180-1187.
- BRADLEY R W. 2000. Evidence of re-nesting in the Marbled Murrelet: inferences from radio-telemetry. *Pacific Seabirds* 27: 33 (Abstract only).
- BRADLEY R W. 2002. Breeding ecology of radio-marked Marbled Murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia [MSc thesis]. Burnaby, BC: Simon Fraser University. 86 p.
- BRADLEY R W, COOKE F. 2001. Cliff and deciduous tree nests of Marbled Murrelets in southwestern British Columbia. *Northwestern Naturalist* 82:52-57.
- BRADLEY R W, COOKE F, LOUGHEED W, BOYD W S. 2004. Inferring breeding success through radiotelemetry in the Marbled Murrelet. *Journal of Wildlife Management* 68:318-331.
- BURGE A E. 2001. Using radar to estimate populations and assess habitat associations of Marbled Murrelets. *Journal of Wildlife Management* 65:696-715.
- BURGER A E. 2002. Conservation assessment of Marbled Murrelets in British Columbia: review of the biology, populations, habitat associations, and conservation. Canadian Wildlife Service Technical Report Series No. 387. Delta, BC: Canadian Wildlife Service. 171 p. URL: <http://www.sfu.ca/biology/wildberg/bertram/mamurt/links.htm>
- *BURGER A E, BEASLEY B A, CHATWIN T A (editors). 1997. Clayoquot Sound Marbled Murrelet inventory for 1996. Nanaimo, BC: Ministry of Environment, Lands and Parks. 127 p.
- *BURGER A E, BAHNV, YOUNG A. 2000. Assessment of nesting habitat for Marbled Murrelets in coastal Douglas-fir forests of southeast Vancouver Island

* Unpublished report

- in 1998 and 1999. Victoria, BC: University of Victoria, Department of Biology. 36 p.
- CANADIAN MARBLED MURRELET RECOVERY TEAM (CMMRT). 2003. Marbled Murrelet Conservation Assessment 2003, Part B - Marbled Murrelet Recovery Team advisory document on conservation and management. Delta, BC: Canadian Wildlife Service. 31 p. URL: <http://www.sfu.ca/biology/wildlberg/bertra/mamurt/links.htm>
- CHATWIN TA. 2002. Management of Marbled Murrelet nesting habitat in Clayoquot Sound. In: Burger AE, Chatwin TA, editors. Multi-scale studies of populations, distribution and habitat associations of Marbled Murrelets in Clayoquot Sound, British Columbia. Victoria, BC: Ministry of Water, Land and Air Protection. p 139-162. URL: wlapwww.gov.bc.ca/wld/documents/techpub/mamuwebs.pdf
- CLAYTON NS, BUSSEY TJ, DICKINSON A. 2003. Can animals recall the past and plan for the future? *Nature Reviews Neuroscience* 4:685-691.
- CONROY CJ, BAHNV, RODWAYMS, AINSWORTH L, NEWSOM D. 2002. Estimating nest densities for Marbled Murrelets in 3 habitat suitability categories in the Ursus Valley, Clayoquot Sound. In: Burger AE, Chatwin TA, editors. Multi-scale studies of populations, distribution and habitat associations of Marbled Murrelets in Clayoquot Sound, British Columbia. Victoria, BC: Ministry of Water, Land and Air Protection. p 121-137. URL: wlapwww.gov.bc.ca/wld/documents/techpub/mamuwebs.pdf
- *DEMARCHI DA, BUTTON AA. 2001a. Marbled Murrelet nesting habitat capability in British Columbia: Map 2 - weighted average capability. Map @ 1:300,000. Victoria, BC: Resources Inventory Branch, Ministry of Environment, Lands and Parks.
- *DEMARCHI DA, BUTTON AA. 2001b. Marbled Murrelet nesting habitat suitability in British Columbia: Map 3 - weighted average suitability. Map @ 1:300,000. Victoria, BC: Resources Inventory Branch, Ministry of Environment, Lands and Parks.
- DNOKY GJ, HORTON M. 1995. Breeding and natal dispersal, nest habitat loss, and implications for the Marbled Murrelet. In: Ralph CJ, Hunt GL Jr., Raphael MG, Piatt JF, editors. Ecology and conservation of the Marbled Murrelet. General Technical Report PSW-GTR-152. Albany, CA: USDA, Forest Service, Pacific Southwest Research Station. p 83-87.
- EMERY NJ, CLAYTON S. 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* 306:1903-1907.
- FLAHERTY EA, DUBAYSA, BRADLEY I, MARZLUFF J, HAYWARD GD. 2000. The Northern Flying Squirrel (*Glaucomys sabrinus*) as a potential predator of Marbled Murrelet (*Brachyramphus marmoratus*) eggs. *Northwest Science* 74:335-339.
- GASTON AI, JONES IL. 1998. The Auks, Alcidae. Oxford, UK: Oxford University Press. 388 p.
- *HEBERT PN, GOLIGHTLY RT. 2006. Movements, nesting and response to anthropogenic disturbance of Marbled Murrelet (*Brachyramphus marmoratus*) in Redwood National and State Parks, California. Arcata, CA: Department of Wildlife, Humboldt State University. 321 p.
- HEBERT PN, GOLIGHTLY RT. 2007. Observations of predation by corvids at a Marbled Murrelet nest. *Journal of Field Ornithology* 78: 221-224.
- HEBERT PN, CARTER HR, GOLIGHTLY RT, ORTHMEYER DL. 2003. Radio-telemetry evidence of re-nesting in the same season by the Marbled Murrelet. *Waterbirds* 26:261-265.
- JONES PH. 2001. The Marbled Murrelets of the Caren Range and Middlepoint Bight. Vancouver, BC: Western Canada Wilderness Committee. 150 p.
- MANLEY IA. 1999. Behaviour and habitat selection of Marbled Murrelets nesting on the Sunshine Coast [MSc thesis]. Burnaby, BC: Simon Fraser University. 163 p.
- MARZLUFF JM, ANGELL T. 2005. In the company of crows and ravens. New Haven, CT: Yale University Press. 408 p.
- MARZLUFF JM, NEATHERLIN E. 2006. Corvid responses to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biological Conservation* 130:301-314.
- MARZLUFF JM, RESTANI M. 1999. The effects of forest fragmentation on avian nest predation. In: Rochelle JL, Lehmann LA, Wisniewski I, editors. Forest fragmentation: wildlife and management implications. Leiden, Netherlands: Brill. p 155-169.
- McFARLANE TRANQUILLAL, BRADLEY R, PARKER N, LANK D, COOKE F. 2003. Replacement laying in Marbled Murrelets. *Marine Ornithology* 31:75-81.
- MCSHANE C, HAMERT, CARTER H, SWARTZMAG G, FRIESEN D, AINLEY D, TRESSLER R, NELSON K, BURGER A, SPEAR L, MOHAGEN T, MARTIN R, HENKEL L, PRINDLE K, STRONG C, KEANY. 2004. Evaluation report for the 5-year status review of the Marbled Murrelet in Washington, Oregon and California. Report prepared for the U.S. Fish and Wildlife Service, Region 1. Portland, Oregon. Seattle, WA: EDAW, Inc. 218 p.
- NELSON SK. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). In: Poole A, Gill G, editors. Birds of North America, No. 276. Philadelphia, PA: The Birds of North America Inc. 32 p.
- NELSON SK, HAMERT E. 1995. Nest success and the effects of predation on Marbled Murrelets. In: Ralph CJ, Hunt GL Jr., Raphael MG, Piatt JF, editors. Ecology and conservation of the Marbled Murrelet. General Technical Report PSW-GTR-152.

- Albany, CA: USDA, Forest Service, Pacific Southwest Research Station. p 89-97.
- Noss R (editor). 1999. The redwood forest: history, ecology, and conservation of the coast redwoods. Washington, DC: Island Press. 366 p.
- PIATT JF, KULETZ KJ, BURGER AE, HATCHSA, FRIESEN VL, BIRT TP, ARIMITSU ML, DREW GS, HARDING AMA, BIXLERKS. 2006. Status review of the Marbled Murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia. U.S. Geological Survey Open-File Report 2006-1387. 276 p. URL: <http://pubs.usgs.gov/ofr/2006/1387/>
- RALPH CJ, HUNT GL JR., RAPHAEL MG, PIATT JF, editors. 1995. Ecology and conservation of the Marbled Murrelet. General Technical Report PSW-GTR-152. Albany, CA: USDA, Forest Service, Pacific Southwest Research Station. 420 p.
- RAPHAEL MG, EVANS MACK O, MARZLUFF JM, LUGINBUHL J M. 2002. Effects of forest fragmentation on populations of the Marbled Murrelet. *Studies in Avian Biology* 25:221-235.
- RICKETTSTH, DINERSTEIN E, OLSONOM, LOUCK SC, EICHBAUM W, DELLASALLA O, KAVANAGH K, HEDAO P, HURLEY P, CARNEY K, ABELL R, WALTERS S. 1999. Terrestrial ecoregions of North America: a conservation assessment. Washington, DC: Island Press. 508 p.
- SINGERS W, SUDDJIAN DL, SINGER SA. 1995. Fledging behavior, flight patterns, and forest characteristics at Marbled Murrelet tree nests in California. *Northwestern Naturalist* 76:54-62.
- SONERUD GA, FJELD PE. 1987. Long-term memory in egg-predators: an experiment with a Hooded Crow. *Ornis Scandinavica* 18:323-325.
- VIGALLON SM, MARZLUFF JM. 2005. Is nest predation by Steller's Jays (*Cyanocitta stelleri*) incidental or the result of a specialized search strategy? *Auk* 122: 36-49.
- ZHARIKOV Y, LANKD B, HUETTMANN F, BRADLEY R. W, PARKERN, YEN PP-W, MCFARLANE-TRANQUILLA LA, COOK EF. 2006. Habitat selection and breeding success in a forest-nesting Alcid, the Marbled Murrelet, in 2 landscapes with different degrees of forest fragmentation. *Landscape Ecology* 21: 107-120.

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