NESTING BEHAVIOR OF MARBLED MURRELETS *BRACHYRAMPHUS MARMORATUS* IN WASHINGTON AND BRITISH COLUMBIA

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ABSTRACT

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Marbled Murrelets are threatened seabirds that nest predominantly in old-growth forests in the southern part of their western North America range. Little is known about causes of nest failure, timing of parental visits, and nest reuse because it is difficult to locate and monitor nests of this cryptic species. We used radio telemetry to locate murrelet nests from 2004 to 2008 in northwestern Washington and southeastern British Columbia. We monitored four nests with video cameras to document causes of nest failure, and we visited 15 nests after the nesting season to infer nest fate. We also monitored six active nests with telemetry data loggers to determine the timing of parental visits, and eight previous-year nests to determine nest reuse. Among 20 nests, four successfully fledged and 16 failed. Among failed nests, 10 failed from unknown causes and the remaining six failed from non-predatory causes. Parental visits during the incubation period occurred exclusively before dawn (100 % of 32 visits), whereas visits during the nestling period (n = 73) occurred during the morning (70 %), afternoon (1 %), and evening (29 %). Among eight nests monitored for reuse, we observed two cases of nest reuse and two cases in which nests were briefly visited by murrelets in later years but were not reused for nesting.

Key words: *Brachyramphus marmoratus*, video surveillance, radio telemetry, nest predator, nest provisioning, nest success

INTRODUCTION

Marbled Murrelets *Brachyramphus marmoratus* are seabirds that are unique in the family Alcidae for nesting in coastal, old-growth forests in western North America. Populations from British Columbia to California are federally threatened, with consistent population decreases reported in British Columbia and Washington (Bertram *et al*. 2015, Falxa *et al*. 2016). Poor recruitment from low nest success is considered a major threat to populations (USFWS 1997). However, there is little definitive information on causes of nest failure because nests are difficult to locate and monitor. Marbled Murrelets nest solitarily, high in old-growth trees throughout their range, and on cliffs or in glaciated, mountainous terrain in the northern part of their range (Hamer & Nelson 1995, Bradley & Cooke 2001, Barbaree *et al*. 2014). Adults are secretive and crepuscular in their nesting behavior, and eggs and nestlings are extremely well-camouflaged. Adults typically visit nests once daily during the incubation period and 1–8 times daily during the nestling period (Naslund 1993, Nelson & Peck 1995, Nelson 1997, Manley 1999, Nelson & Wilson 2002).

All together, we found < 50 accounts of Marbled Murrelet nest failure in which the cause of failure was known with certainty (Appendix 1, available on the website). Corvid depredation appears to be an important issue in Oregon and California, accounting for 50 % of failed nests in these states (Singer *et al.* 1991, Peery *et al.* 2004, Hebert & Golightly 2007, Golightly & Schneider 2011; Appendix 1). Corvids have been identified as nest predators in many other studies where the act of nest predation was not observed directly or was not described explicitly by the study authors (Ford & Brown 1995, Naslund *et al*. 1995, Nelson & Hamer 1995, Nelson & Peck 1995, Manley 1999). Other causes of nest failure include egg abandonment, death of a parent, and nestlings dying from health-related problems (Appendix 1). For Washington and British Columbia, where the most pronounced murrelet population decreases have been reported (Bertram *et al*. 2015, Falxa *et al*. 2016), we found only two studies where causes of nest failure were observed or described. In one case, Hamer and Cummins (1991) retrieved a downy murrelet chick from beneath a nest, indicating that the chick fell off the nest platform. In Silvergieter (2009), three eggs failed to hatch (one egg was infertile) and one chick was found dead in the nest. In other studies, from Washington and British Columbia, the cause of nest failure was not known with certainty (e.g., Manley 1999). Overall, larger sample sizes of nests are needed to determine the predominant causes of nest failure in this population.

To address this information gap, we used radio telemetry to study Marbled Murrelet nesting behavior in Washington and British Columbia. Our primary goal was to determine causes of nest failure, but over the course of our study we also obtained data on the timing of parental nest visits and nest reuse. This information is useful for informing inland survey protocols for Marbled Murrelets, which in turn are used to guide land management decisions. The objective of this paper is to present causes of nest failure, the timing of nest visits by parents, and observations of nest reuse for Marbled Murrelet nests monitored in Washington and British Columbia.

STUDY AREA

We conducted this study in northwestern Washington and southwestern British Columbia. We captured murrelets in US waters of the Pacific Ocean, as well as the Strait of Juan de Fuca, Puget Sound, and in Hood Canal, Washington. We searched for nesting murrelets on the Olympic Peninsula and in the Cascade Range of Washington, and on Vancouver Island, British Columbia (see Methods, Locating nest sites). This area has a maritime oceanic and temperate climate with mild, rainy weather year-round, except for a dry period in late summer. Forests used for nesting by murrelets in this region are generally temperate coastal rainforests dominated by western hemlock *Tsuga heterophylla*, Douglas-fir *Pseudotsuga menziesii*, Sitka spruce *Picea sitchensis*, and western red cedar *Thuja plicata.*

METHODS

Locating nest sites

The most efficient method of locating Marbled Murrelet nests involves radio-tagging murrelets at sea and searching for radio signals of tagged breeders at inland nest sites by aircraft. From 2004 to 2008, we radio-tagged Marbled Murrelets in coastal waters of Washington State to locate nest sites. For additional details on radio-tagging methods, see Lorenz *et al*. (2017). We obtained a small sample of blood from each bird for determining sex.

We located radio-tagged murrelets primarily by aerial tracking from fixed-wing aircraft. We used ground-based telemetry for pinpointing the exact location of nest sites and for monitoring nests. We initiated aerial tracking searches within three days after the first murrelet was tagged in each year. We ended searches after the last identified nest had fledged or failed and when significant numbers of transmitters were no longer detectable within our study area, indicating post-breeding dispersal or transmitter battery failure.

Weather permitting, we conducted tracking flights daily. Tracking flights lasted up to 5 h, until all birds had been located or the aircraft needed refueling. Aerial searches included marine foraging areas and terrestrial nesting areas. If we did not locate an individual murrelet at sea or on an inland nest for 2–3 consecutive days, we expanded our search area to find the missing bird, focusing on areas beyond the location that the missing murrelet was last detected. When pilots detected a murrelet's radio signal, they circled over the source and used a global positioning system (GPS) unit to mark the location from which they heard the loudest signal.

Because we were interested in marine locations for studies of breeding season space use, we typically first detected breeding activity when radio-tagged murrelets exhibited the characteristic on-off pattern at sea, in which adults alternate 24-h incubation shifts (Bradley *et al*. 2004). When the on-off pattern was observed for a murrelet, we flew over suitable nesting habitat until the tagged bird was detected. We then visited the area on foot and located the nest by homing to the murrelet's radio signal. It often took multiple visits on foot to locate murrelet nest sites.

Nest fate

We determined nest fate using one of three techniques: (1) we set a remotely powered video camera (Sentinel MAGNUM and Sentinel for daytime footage, and ELF fixed lenses and Starlight Color Zoom lenses for recording at night; Sandpiper Technologies, Inc., Manteca, CA) at accessible nests to monitor nest activity directly; (2) we climbed nest trees after the nesting season to view nest contents; and (3) we counted the number of days murrelets exhibited incubation behavior (Bradley *et al*. 2004) or nestling visits from telemetry monitoring at sea. When we visited nests after the breeding season, some contained eggs or chick remains, which we submitted for necropsy to the Washington Animal Disease Diagnostic Lab.

We chose nests to video monitor based on ease-of-access and distance to roads; video-monitored nests also had to be viewable from a nearby tree. Most nests were located in rugged, mountainous terrain and were difficult to access. Therefore, only four of 20 nests were monitored with video: Boulder Creek, Sombrio, Hemmingsen Creek, and Rica Canyon (Appendix 2, available on the website). For these nests, we set video cameras in trees within 30–50 m of the nests. We did not climb trees with active nests. Once we located a limb on a nearby tree where the murrelet's nest could be viewed, we affixed a camera with a zoom lens to the tree limb (Fig. 1). We extended a 50-m cable from the lens to the ground and set batteries for powering the camera on the ground. Cameras were powered with marine deep-cycle batteries and video files were stored on media storage devices that we changed weekly. When we visited monitored nests, we were able to replace batteries and media storage devices without climbing the camera tree. To minimize disturbance to nesting murrelets, we took basic precautions to minimize attracting potential nest predators and affecting murrelet behavior. We also stationed one crew member on the ground to observe nesting murrelets. No murrelets flushed from nests during camera set-up. Cameras ran continuously both day and night, although night footage (from approximately 22h30 to 04h30) was not viewable due to the distance lenses were placed from nests. We reviewed all footage from video-monitored nests to note the time of day for parental visits, chick behavior, and visits by other species.

We visited all nests after the nesting season to view nest contents. For nests that were not video monitored, we considered nests

Fig. 1. Photo showing placement of a zoom lens relative to the Hemmingsen Creek Marbled Murrelet nest in 2006 (nest is indicated with arrow), on Vancouver Island, British Columbia. Zoom lenses were typically placed in nearby trees on limbs 30–50 m from the nest. A ~50-m cable cable extended from the lens to the ground. Deep-cycle batteries (for powering the camera) and a digital video recorder (for recording and storing video files) were placed on the ground below the camera tree. Thus, when we visited the nest to replace batteries we did not have to climb the camera tree. Inset photo in upper right shows the Hemmingsen Creek Marbled Murrelet incubating an egg on the nest. Photos by N.R. Hatch.

successful if the length of time a radio-tagged adult visited a nest indicated nest attendance for ~ 30-d incubation and 30-d nestling periods, or if we found a large fecal ring during our post-breeding nest visits (Nelson 1997, and references therein). We classified nests as unsuccessful if the timing of adult visits was too short for successful nesting based on known dates of nest initiation (< ~ 60 d; Nelson & Hamer 1995, McFarlane Tranquilla *et al*. 2005), if there was an under-developed fecal ring at the nest site, or if we found an egg or dead chick (Nelson & Hamer 1995, Nelson 1997).

Parental visits

We determined the time of parental visits using one of two techniques: (1) we noted the time of visits from video recordings (for video monitored nests); or (2) we monitored visits by radio-tagged parents using telemetry dataloggers (for nests with dataloggers) (n = 5 nests; Appendix 2) (R4500SD Receiver-Datalogger, Advanced Telemetry Systems, Isanti, MN). We set dataloggers on the ground along flight paths of murrelets, 1–15 km from nest sites. Dataloggers recorded continuously. Dataloggers recorded times that radio signals were detected but provided no direct information on the activities of radio-tagged murrelets. For estimating nest visitation times, we included one additional nest that was found incidentally (without radio telemetry) in 2006 in the Heart o' Hills Campground in Olympic National Park, Washington. When found, birds in this nest were in the nestling phase. We climbed the nest tree following the 2006 breeding season and found a thick fecal ring, indicative of nest success. We set a camera in a nearby tree to monitor this nest in 2007.

There are several potential biases that are unaccounted for in our analysis of nest visitation rates. First, if transmitters affected nest visitation rates, radio-tagged murrelets recorded on the dataloggers may not be a representative sample of the population of murrelets in our study. Second, visits detected by dataloggers may reflect murrelets circling over nests rather than visiting nests. Last, for video-monitored nests, murrelets may have visited nests in full dark. Our cameras were unable to detect nest activities between approximately 22h30 and 04h30 hrs.

Nest reuse among years

We monitored a total of eight nests for reuse in later years. Seven nests were located by radio-tracking murrelets and one nest was found incidentally (Heart o' Hills nest, described above). Nests were monitored for 1–3 y after their discovery. Six of these previous-year nests were video monitored. For these nests, we set up video cameras in a nearby tree or in the nest tree, 1 m above nest platforms. We recorded video opportunistically during the breeding season (May to July), when personnel and equipment could be spared from the main objective of the study, which was monitoring outcomes at active nests. For two additional nests previously reported by Burger *et al*. (2009), we visited the nest once or twice during the nesting period to look for evidence of nesting activity. One of these nests was not visible from the ground, so we also climbed the tree after the nesting period to look for evidence of nesting activity at the nest platform. We acknowledge that we likely missed nest visits and possibly nesting attempts due to our sporadic monitoring.

RESULTS

We radio-tagged 157 murrelets from 2004 to 2008. Most murrelets were captured in the Strait of Juan de Fuca (n = 113), followed by Hood Canal (n = 28) and the Pacific Ocean (n = 16). Twenty murrelets attempted nesting (14 males, six females). Nests were 4–58 km from the nearest shoreline (median distance 18 km; Fig. 2) (Wilk *et al*. 2016). One nest fledged and one nest failed before we pinpointed the nest tree. Nineteen nests were in trees and one nest was on a cliff face (North Fork Sol Duc Cliff; Fig. 2). For additional

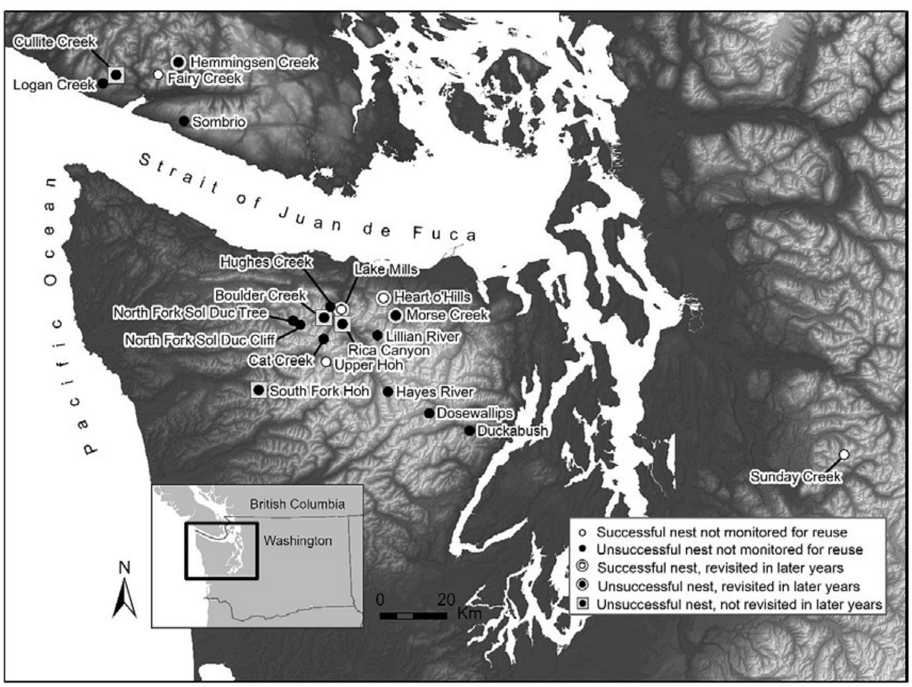

Fig 2. Study area in northwestern Washington and southwestern British Columbia from 2004 to 2008 with locations of 21 Marbled Murrelet nests. The Heart o' Hills nest was not found using radio telemetry and was excluded from our analysis of nest fate.

details on nest characteristics and locations see Wilk *et al*. (2016) and Lorenz *et al*. (2017).

Nest fate

Among 20 nests of radio-tagged murrelets, we concluded that four successfully fledged young and 16 failed (Fig. 2, Appendix 2). Among failed nests, we have information on the cause of nest failure for four nests (Table 1). Two video-monitored nests failed when the eggs did not hatch within a 35-d (Boulder Creek) or 40-d (Sombrio; Appendix 2) period, and were then abandoned. At a third video-monitored nest, the chick fell out of the nest while being fed by the adult (Hemmingsen Creek). One additional nest was abandoned during incubation based on signs left at the nest (Duckabush). At this nest, which was not video-monitored, we found an intact egg in the nest depression. Necropsy revealed that the egg contained a well-developed embryo (Appendix 2).

For three additional nests (Rica Canyon, South Fork Hoh, and North Fork Sol Duc cliff), nest predation did not appear to be the cause of failure, although the ultimate cause of chick death was not known with certainty. At the Rica Canyon nest, the chick was slow to accept fish from parents approximately 6 d post-hatching, and we observed flies (Diptera) on the chick 18 and 19 d post-hatching (05 and 06 July 2005). At 19 d post-hatching (06 July) the chick became nearly motionless. At 20 d post-hatching (07 July) the adult male visited the nest without a fish in the morning. When the adult female visited with a fish in evening of the same day, the chick did not respond and was presumed dead (Appendix 2). Necropsy was performed on the decayed remains of the chick, but soft tissues had decomposed and we could not determine cause of death. Necropsy showed no damage or fractures to the major long bones.

At the second nest (South Fork Hoh), we found a dead chick in the nest depression when we climbed the nest tree after the nesting season (Appendix 3, available on the website). The chick had a fish in its bill that apparently filled its esophagus, and a second fish was lying in the nest depression. Necropsy was conducted on the desiccated remains, but it revealed no significant gross findings, no bone fractures, no histological inflammation, and no evidence of bacterial infection (Appendix 2). The cause of death is unknown, but it is unlikely that it was from predation because the chick was intact and had no obvious signs of trauma or hemorrhage.

At the third nest (North Fork Sol Duc Cliff), evidence points to the nestling dying after being grounded while fledging. The remains of a chick in juvenile plumage were found at the base of the nest cliff after the nesting season (Appendix 3). Because murrelet nestlings retain down until 8–48 h before fledging (reviewed in Nelson 1997), this indicates that the chick died near the time of fledging.

We did not directly observe nest predation in this study. However, three video-monitored nests were visited by putative predators after they were abandoned by parents but still contained an egg or chick (Appendix 2). One nest (Rica Canyon) was visited by a Steller's Jay *Cyanocitta stelleri* around the time that the nestling murrelet died. We suspect that the chick was dead during the jay's visit, but we cannot not be certain of this. Regardless, the chick was unresponsive and the jay did not touch the chick. A Steller's Jay visited this nest again eight days later, when it pecked at the pile

TABLE 1

Causes of nest failure for 16 unsuccessful Marbled Murrelet nests monitored in Washington and British Columbia from 2004 to 2008[a]

Year	Sex of tagged bird	Site	Cause of nest failure
Nests that failed during incubation:			
2004	Female	Boulder Creek	Egg failed to hatch (reason unknown)
2007	Male	Sombrio	Egg failed to hatch (reason unknown)
2005	Male	Duckabush	Egg was abandoned (reason unknown)
2005	Male	Dosewallips	Unknown
2005	Female	Hayes River	Unknown
2005	Female	Logan Creek	Unknown
2007	Male	Cat Creek	Unknown
2007	Male	Hughes Creek	Unknown
2007	Male	Lillian River	Unknown
Nests that failed during nestling phase:			
2006	Male	Hemmingsen Creek	Chick fell out of nest while being fed by adult
2005	Male	Rica Canyon	Chick died of non-predatory factors
2005	Female	South Fork Hoh	Chick died of non-predatory factors
2004	Male	Morse Creek	Unknown
2005	Female	Cullite Creek	Unknown
2007	Male	North Fork Sol Duc Cliff	Unknown (suspect grounded while fledging)
2008	Male	North Fork Sol Duc Tree	Unknown

[a] Details on the determination of nest fate are in Appendix 2 and photos of nests are in Appendix 3.

of feathers but did not visibly consume anything (Appendix 2). A second nest (Sombrio) was also visited by a Steller's Jay. The jay visited approximately 17 d after the egg failed to hatch (assuming an incubation period of ~ 30 d) and seven days after the parents ceased incubation. The jay did not touch the egg. The third nest visited by a putative predator was the Boulder Creek nest. Boulder Creek was visited by a Douglas squirrel *Tamiasciuris douglasii* nine days after adults stopped incubation. The squirrel rolled the egg off the limb with its head (Appendix 2). When we returned to remove the camera we found fragments of eggshell on the ground below the nest.

Parental visits

We noted the time of 105 nest visits by 10 parents (five males, five females) to six active nests. This included 39 visits by females and 38 visits by males (28 visits by birds of unknown sex). We did not formally test for differences in visitation rates by sex due to the small sample size.

During the incubation phase, all visits occurred before official sunrise (n = 32 visits between 18 June and 18 July; Fig. 3). Most visits (91 %) occurred during morning civil twilight (Table 2). During the nestling phase (06 June to 11 August), 70 % of 73 parental visits occurred in the morning (within 84 min of sunrise) and 29 % occurred in the evening (within 48 min of sunset), with one unusual mid-day visit that occurred at 13h57 PDT (Fig. 3). On average, morning visits during the nestling phase occurred within 44 min of sunrise (median = 37 min, range 61 min before to 197 min after sunrise). Evening visits occurred within 21 min of sunset on average (median = 17 min, range 36 min before to 48 min after sunset). The two latest evening visits were to the Sunday Creek nest in the Cascade Range and occurred on clear, moonlit nights.

Nest reuse among years

We monitored eight nests for reuse. Two of these eight nests (25 %) were reused for nesting and two were revisited but not reused (25 %). Seven of the eight nests were initially located with radio-tagged murrelets and were then monitored by video (n = 5) or by revisiting (n = 2) in later years. The eighth nest (Heart o' Hills) was initially located incidentally and without radio telemetry.

Among five video-monitored nests, we observed nest visits at two of these nests in later years. The first nest (Lake Mills) was successful in its original attempt in 2004. It was visited once on 18 May 2005 by a radio-tagged murrelet (transmitter battery was presumably dead, but a transmitter was visible on the bird's back) near dawn for approximately 5 min. It is likely that this was the same bird that nested at this site in 2004, although this was impossible to verify. The visiting murrelet appeared to look upward at the camera several times, suggesting that the presence of the camera may have disturbed the bird. We also documented one visit by a murrelet to the Morse Creek nest. This nest was unsuccessful in its original attempt in 2004 and was monitored opportunistically during 2005–2007. A murrelet revisited this nest on 10 June 2006; similar to the Lake Mills site, the visiting murrelet was wearing a radio tag.

For two nests that we revisited (but did not video monitor), one had a fresh, partial fecal ring indicating that it was used by murrelets

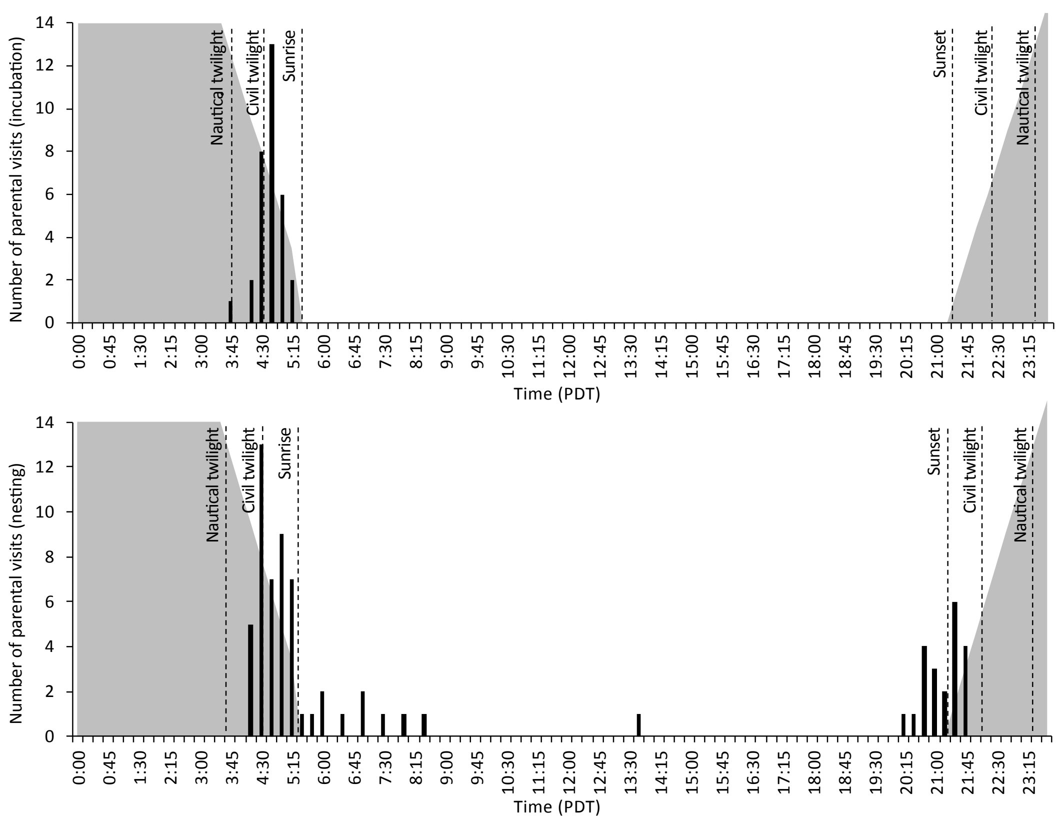

Fig. 3. Number of parental visits to active Marbled Murrelet nests during the incubation phase (top) and nestling phase (bottom) recorded with telemetry data loggers and video cameras for six nests in Washington and British Columbia, from 2004 to 2008 (black bars). Gray shading indicates darkness. Median time of nautical twilight, civil twilight, and sunrise/sunset is indicated with dotted lines.

for two years in a row (but failed in both years). One did not show signs of renesting from a ground viewing location. Finally, the eighth monitored nest (Heart o' Hills) was found incidentally in 2006 and monitored with a video camera in 2007. The nest was used successfully in both 2006 and 2007. We observed fledging of the murrelet chick on 22 June 2007 between 21h46 (29 min after official sunset and 13 min before the end of civil twilight) and 24h54, and 3 h 9 min after the last two visits by parents with food.

DISCUSSION

In our study, among Marbled Murrelet nests with a known cause of failure, we observed no cases of nest predation. This was unexpected because nest predation, particularly by ravens *Corvus corax* and jays, was a leading cause of murrelet nest failure in past studies (Singer *et al*. 1991, Peery *et al*. 2004, Hebert & Golightly 2007; Golightly & Schneider 2011). It is especially surprising because corvids are common in our study area. Artificial nest studies with hundreds of monitored nests in Washington and British Columbia have shown that ~ 33 % to 48 % of artificial murrelet nests are visited or depredated by corvids (Luginbuhl *et al*. 2001, Marzluff & Neatherlin 2006, Malt & Lank 2007, 2009). While artificial nest studies have many biases (e.g., Faaborg 2004, Thompson & Burhans 2004), these studies demonstrate that corvids are common in murrelet nesting habitat in our study area. We also found it remarkable that two of four video-monitored murrelet nests in our study were visited by corvids after nest failure. In these cases, corvids visited inactive nests but did not appear to forage on the dead murrelets or otherwise scavenge them. Additional studies with larger sample sizes of monitored nests are needed to determine if our observations are representative of this region.

Instead of corvid nest predation, known causes of nest failure in our study included one observation of a chick falling from the nest platform and three cases of egg abandonment or failure of the egg to hatch. We suspect that one additional nest failed when the chick became grounded while fledging, and we documented two additional cases of nestlings dying from non-predatory factors. Chicks falling from platforms has previously been documented for Marbled Murrelets (Carter & Sealy 1987, Hamer & Cummins 1991), and nest abandonment is well documented for other alcids when food availability is low and parents cannot obtain enough food to sustain their breeding efforts (e.g., Bertram *et al*. 2001, Sydeman *et al*. 2006). Our study is different from these other alcid studies, however, because in two cases of egg abandonment, parents incubated eggs for sufficiently long incubation periods, thus indicating that lack of food did not directly contribute to nest abandonment. Parent murrelets only abandoned the nest when the egg failed to hatch, indicating problems with the viability of the egg.

Insights may be gained from research on the closely related Kittlitz's Murrelet *Brachyramphus brevirostris* in Alaska. Nest fate is known for > 200 Kittlitz's Murrelet nests monitored during the last 10 years. The Kittlitz's Murrelet has many similar life history traits to the Marbled Murrelet, except that Kittlitz's Murrelets nest exclusively on the ground and do not occur south of Alaska. Among 176 failed Kittlitz's Murrelet nests, nest failure from non-predator factors is common, accounting for 51 % of nest failures that we found in the literature (Appendix 1). During incubation, egg abandonment was the most common non-predatory cause of nest failure. Eggs were abandoned due to problems with egg viability, depredation of a parent, or disturbance to the nest site (see references in Appendix 1). For nestling Kittlitz's Murrelets, major causes of death were exposure, starvation, and saxitoxin poisoning (Appendix 1). One case in our study was strikingly similar to saxitoxin poisoning described for Kittlitz's Murrelets. Our South Fork Hoh nestling was found dead in the nest with one fish on the nest platform and a second fish within the nestling's bill. In Kittlitz's Murrelets, nestlings that tested positive for saxitoxin died within hours of consuming fish (Shearn-Bochsler *et al*. 2014) and were sometimes found with dead fish still in the chick's bill (Knudson *et al*. 2015). Unfortunately, we were not able to test for saxitoxin poisoning in our study because too much time had elapsed between nestling death and necropsy. We are not aware of studies that have tested for saxitoxin in nestling seabirds in this region, although harmful algal blooms (HABs) and dinoflagellum that cause HABs are common in marine areas in Washington (Cox *et al*. 2008, Moore *et al*. 2009, Horner *et al*. 2011) and have caused die-

Table 2
Timing of parental visits to six active Marbled Murrelet nests during the incubation and nestling phase, recorded with telemetry data loggers and video cameras in northwest Washington and southwest British Columbia from 2004 to 2008[a]

	Percent (*n*) of parental visits	Timing of parental arrival[a]
Incubation phase (*n* = 32 visits)		
Nautical twilight (morning)	9 % (3)	Average (range) minutes before sunrise that parent arrived: 58 (44–84)
Civil twilight (morning)	91 % (29)	Average (range) minutes before sunrise that parent arrived: 29 (12–40)
Nestling phase (*n* = 73 visits)		
Nautical twilight (morning)	12 % (9)	Average (range) minutes before sunrise that parent arrived: 52 (42–61)
Civil twilight (morning)	41 % (30)	Average (range) minutes before sunrise that parent arrived: 30 (7–46)
Morning after sunrise	16 % (12)	Average (range) minutes after sunrise that parent arrived: 72 (1–197)
Afternoon	1 % (1)	
Evening before sunset	8 % (6)	Average (range) minutes before sunset that parent arrived: 15 (3–36)
Nautical twilight (evening)	18 % (13)	Average (range) minutes after sunset that parent arrived: 19 (3–38)
Civil twilight (evening)	3 % (2)	Average (range) minutes after sunset that parent arrived: 48 (47–48)

[a] We did not determine the timing of parents' departure from nests or the duration of their visits.

offs in adult seabirds in Washington and British Columbia (Jones *et al*. 2017). In future studies of Marbled Murrelets, researchers should consider testing for these toxins whenever possible.

Nest monitoring of Kittlitz's Murrelets has also documented cases of nest or egg abandonment in which the nest contents were scavenged (Lawonn *et al*. 2011; Knudson *et al*. 2015, 2016; Kissling & Lewis 2016), resulting in an empty nest cup when researchers visited the site. Without cameras, these nests may have mistakenly been classified as depredated. With this in mind, we encourage the use of video cameras, direct observations, necropsies, and other unequivocal methods in studies of Marbled Murrelets that wish to assign nest fate. Additional studies are needed to determine the major threats to murrelet nests. If corvids are less of a threat in our region than toxins (HABs), prey availability, egg viability, parental depredation, or other factors, managers will need to consider different strategies than those that have been implemented in California to address corvid depredation (Peery & Henry 2010, Bensen 2013). At this time, we do not have enough information to confirm causes of nest failure in Marbled Murrelets, but our study indicates that non-predatory factors may be important determinants of nest outcomes in Washington and British Columbia.

It is important to note possible biases caused by radio-tagging murrelets in this study. As discussed by many other authors (e.g., McFarlane Tranquilla 2001, Kissling *et al*. 2015), the radio tags we used may have affected the ability of murrelets to lay viable eggs, or to properly incubate eggs and provision nestlings, and this may have contributed to unusual nest fates. Many studies have looked at the effects of tags on alcids, including several studies that have reported that tags negatively impact nest success and provisioning rates (Kidawa *et al*. 2001, Paredes *et al*. 2005, Whidden *et al*. 2007, Robinson & Jones 2014, Schacter & Jones 2017). For Marbled Murrelets specifically, Peery *et al*. (2006) reported that radio tags affected murrelet survival, and Barbaree *et al*. (2014) suspected lower breeding propensity for radio-tagged female murrelets (compared to untagged females). Northrup *et al*. (2018) reported that larger 5-g satellite transmitters negatively affected Marbled Murrelets, potentially contributing to death. The size of transmitters, as well as the length and angle of transmitter antennae, are known to impact diving birds (Wilson *et al*. 2004, Ropert-Coudert *et al*. 2007). The 1.2-cm^3 tags we used may have contributed to drag underwater, negatively impacting the ability of murrelets to sustain themselves and their young.

It is also important to consider that our activities at nests may have influenced nest fate by disturbing murrelets or affecting predator behavior, although this should not differ from past studies that have used similar nest monitoring methods. Another shortcoming of our study is that we do not know the causes of nest failure for 10 nests in this study. These nests may have been depredated. Thus, although we did not document nest predation, the conclusions derived from this study should be reassessed as new research is conducted and larger numbers of nests are monitored.

One interesting finding from our monitoring of nest reuse was the observation that radio-tagged murrelets visited nests one to two years after being tagged. While it was impossible to verify the identity of these murrelets, it is likely that they were the original breeders at these sites. If so, radio tags attached with the subcutaneous anchor method can be retained on murrelets for up to two years. This conclusion is supported by anecdotal evidence from recaptured murrelets. There were two occasions on which we recaptured a murrelet that had been radio-tagged in a prior year; one of those individuals had shed its transmitter and one had retained its transmitter. Kittlitz's Murrelets have also been captured wearing previous-year transmitters (two of five recaptured murrelets; M. Kissling unpubl. data). Previously, it was assumed that radio tags attached with a subcutaneous anchor fall off within months of deployment. For example, Newman *et al*. (1999) determined that with prong and suture methods, transmitters were retained on Marbled Murrelets for a maximum of 78 d. The presumed short duration of tag attachment has precluded year-round studies of *Brachyramphus murrelet* space use. We encourage researchers to use longer-lasting batteries or programmable transmitters that last for at least one year to track marbled murrelets. Transmitters in the 1–2 g range are currently available that last one year, some of which contain programmable chips that turn transmitters off at user-defined times, allowing use of a lightweight battery that permits an increased study duration. Among a sample of murrelets tagged with the subcutaneous anchor method, some are likely to retain their transmitter for at least one year. Tracking these murrelets for one or two years could shed light on many important information gaps, such as space use among years, breeding site fidelity, and fall and winter space use.

Information on the timing of murrelet nest visits is important for informing inland survey protocols for Marbled Murrelets. In turn, these survey protocols are used to guide land management decisions. This information is also important for wind power risk models, disturbance restrictions, assessing the potential for collisions with power lines, and more. For the six nests we monitored for parental visitation, incubation visits occurred exclusively before dawn, whereas nestling visits were concentrated in the morning around sunrise but also occurred in the evening. These observations align with past studies (Naslund 1993, Nelson & Peck 1995, Manley 1999, Nelson & Wilson 2002). For example, Nelson & Peck (1995) reported that incubation visits at nine nests in Oregon occurred 8–30 min before sunrise. Nestling feeding visits were concentrated in the morning but also occurred within 90 min of sunrise, but rarely occurred during the day. In California, Naslund (1993) found that most incubation visits occurred before dawn, whereas nestling visits occurred around sunrise and sunset, with two mid-day visits. Manley (1999) noted similar behavior in British Columbia; incubation visits occurred 25–28 min before dawn, whereas nestling feeding visits occurred in the evening and morning but were most common at dawn, with one unusual mid-day visit. Other studies using audio-visual surveys, radar, and telemetry have also reported peaks of activity near sunrise and sunset, although these studies cannot distinguish between breeders and non-breeders, or breeders at different stages of the nesting cycle (Burger 2001, Bradley *et al*. 2002, Cooper & Blaha 2002, Hebert & Golightly 2007).

We documented one case of successful nest reuse, one case of unsuccessful reuse, and two cases in which previous-year nests were briefly visited by murrelets. Because of small sample sizes, it is difficult to confidently compare the rates of nest reuse between our study and past studies (Hebert & Golightly 2007, Burger *et al*. 2009, Golightly & Schneider 2011). Hebert & Golightly (2007) reported that 30 % of 10 nests were reused in subsequent years in California. Golightly & Schneider (2011) monitored one nest cup for 10 y with video and found that it was used in 7 of 10 y. Burger *et al*. (2009) consolidated information on nest reuse for British Columbia. Rates of reuse for nest trees ranged from 11 % to 18 % for different studies, and rates of reuse for nest cups averaged 6 % (two of 35 nest cups monitored; Manley 1999). Our rates of nest-cup reuse were higher, at 25 % (two of eight limbs monitored). Burger *et al*. (2009) hypothesized that nest reuse may be higher in areas where suitable habitat has been reduced or fragmented. While we lack sufficient data to test this hypothesis, it is noteworthy that three nests that were revisited or reused in our study occurred in the northern Olympic Peninsula and within 20 km of the city of Port Angeles, Washington, which has substantial agricultural and suburban development. Overall, our results add to the literature that murrelets show fidelity to individual nest sites. They also indicate that rates of nest reuse in Washington may be higher than reported elsewhere.

CONCLUSION

Despite our small sample sizes of monitored nests, our study provides some of the only definitive information on causes of Marbled Murrelet nest failure in Washington and British Columbia. Our findings suggest that nest failure resulted from problems with chick vigor and health (potentially caused by lack of food or disease), parental attentiveness (possibly due to adult mortality, overly long commutes, or poor foraging conditions), egg viability and fertility, and nest platform size. For some of these problems—such as poor egg viability and fertility—we do not have sufficient information about the events that led to nest failure to make management recommendations. Overall, however, we suggest that providing large, contiguous tracks of high-quality, suitable nesting habitat close to sea would almost certainly benefit this species. In our study area, suitable nesting habitat for Marbled Murrelets is often located far inland compared to historic times. While murrelets are capable of successfully nesting as much as 58 km from sea in this region (Lorenz *et al*. 2017), long commutes are more energetically costly than short commutes and could reduce nest success in many ways. To mitigate problems with chicks falling from platforms, we encourage managers to retain trees with the largest platforms. The limb occupied by one fallen chick in our study was 18 cm diameter, with a tree diameter at breast height (DBH) of 128 cm, compared to a mean limb size of 31 cm and a tree DBH of 136 cm for other nests (Appendix 2). Providing large trees with limbs, and platforms larger than 18–21 cm, should be a focus of conservation efforts. Last, we call for additional research studies that monitor larger numbers of Marbled Murrelet nests. Studies are needed that use video-monitoring, necropsy, and similar unambiguous methods to determine causes of Marbled Murrelet nest failure within their threatened range. Currently, managers are forced to make land management decisions based on extremely small sample sizes, which may not be representative of murrelet nest success in this region.

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REFERENCES

BARBAREE, B.A., NELSON, S.K., DUGGER, B.D. ET AL. 2014. Nesting ecology of Marbled Murrelets at a remote mainland fjord in southeast Alaska. *The Condor* 116: 173–184.

BENSEN, K.J. 2013. *Forest and beach corvid monitoring and management, trail and backcountry management plan implementation: 2012 annual progress report*. Orick, CA: Redwood National and State Parks. [Available online at: https://www.wildlife.ca.gov/OSPR/NRDA/Restoration-Monitoring-Reports. Accessed 18 April 2018].

BERTRAM, D.F., DREVER, M.C., McALLISTER, M.K. ET AL. 2015. Estimation of coast-wide population trends of Marbled Murrelets in Canada using a Bayesian hierarchical model. *PLoS One* 10: e0134891.

BERTRAM, D.F., MACKAS, D.L. & McKINNELL, S.M. 2001. The seasonal cycle revisited: interannual variation and ecosystem consequences. *Progress in Oceanography* 49: 238–307.

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, L.W. & BOYD, W. S. 2004. Inferring breeding success through radiotelemetry in the Marbled Murrelet. *Journal of Wildlife Management* 68: 318–331.

BURGER, 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., MANLEY, I.A., SILVERGIETER, M.P. ET AL. 2009. Re-use of nest sites by Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia. *Northwestern Naturalist* 90: 217–226.

CARTER, H.R. & SEALY, S.G. 1987. Inland records of downy young and fledgling marbled murrelets in North America. *Murrelet* 68: 58–63.

COOPER, B.A. & BLAHA, R.J. 2002. Comparison of radar and audio-visual counts of marbled murrelets during inland forest surveys. *Wildlife Society Bulletin* 30: 1182–1194.

COX, A.M., SHULL, D.H. & HORNER, R.A. 2008. Profiles of *Alexandrium catenella* cysts in Puget Sound sediments and the relationship to paralytic shellfish poisoning events. *Harmful Algae* 7: 379–388.

FAABORG, J. 2004. Truly artificial nest studies. *Conservation Biology* 18: 369–370.

FAIR J., PAUL, E. & JONES, J. 2010. *Guidelines to the use of wild birds in research*. Washington, DC: Ornithological Council.

FALXA, G.A., RAPHAEL, M.G., STRONG, C. ET AL. 2016. Status and trend of Marbled Murrelet populations in the Northwest Forest Plan area. In: FALXA, G.A. & RAPHAEL, M.G. (Eds.) *Northwest Forest Plan—the first 20 years (1994–2013): status and trend of Marbled Murrelet populations and nesting habitat*. General Technical Report PNW-GTR-933. Portland, OR: US Department of Agriculture Forest Service, Pacific Northwest Research Station, pp 1–36.

FORD, C. & BROWN, M. 1995. Unusual Marbled Murrelet nest. *Wilson Bulletin* 107: 178–179.

GOLIGHTLY, R.T. & SCHNEIDER, S. 2011. *Years nine and ten of a long-term monitoring effort at a Marbled Murrelet nest in northern California: final report.* Arcata, CA: Department of Wildlife, Humboldt State University.

HAMER, T.E. & CUMMINS, E.B. 1991. *Relationship between forest characteristics and the use of inland sites by Marbled Murrelets in northwestern Washington*. Lynnwood, WA: Nongame Program, Wildlife Management Division, Washington Department of Wildlife.

HAMER, T.E. & NELSON, S.K. 1995. Characteristics of Marbled Murrelet nest trees and nesting stands. In: RALPH, C.J., HUNT, G.L., RAPHAEL, M.G. & PIATT, J.F. (Eds.) *Ecology and conservation of the Marbled Murrelet.* General Technical Report. PSW-GTR-152. Albany, CA: US Department of Agriculture, Forest Service, pp. 69–82.

HEBERT, P.N. & GOLIGHTLY, R.T. 2007. Observations of nest predation by corvids at a Marbled Murrelet nest. *Journal of Field Ornithology* 78: 221–224.

HORNER, R.A., GREENGROVE, C.L., DAVIES-VOLLUM, K.S., ET AL. 2011. Spatial distribution of benthic cysts of *Alexandrium catenella* in surface sediments of Puget Sound, Washington, USA. *Harmful Algae* 11: 96–105.

JONES, T., PARRISH, J.K., PUNT, A.E. ET AL. 2017. Mass mortality of marine birds in the northeast Pacific caused by *Akashiwo sanguinea*. *Marine Ecology Progress Series* 579: 111–127.

KIDAWA, D., JAKUBAS, D., WOJCZULANIS-JAKUBAS, K., ILISZKO, L. & STEMPNIEWICZ, L. 2012. The effects of loggers on the foraging effort and chick-rearing ability of parent little auks. *Polar Biology* 35: 909–917.

KISSLING, M.L. & LEWIS, S.B. 2016. Nesting Activity of Kittlitz's Murrelet in the Kakagrak Hills, Northwestern Alaska. *Arctic* 69: 246–252.

KISSLING, M.L., LUKACS, P.M., GENDE, S.M. & LEWIS, S.B. 2015. Multi-state mark-recapture model to estimate survival of a dispersed-nesting seabird, the Kittlitiz's murrelet. *Journal of Wildlife Management* 79: 20–30.

KNUDSON, T.W., CORCORAN, R.M., LOVVORN, J.R., PIATT, J.F. & PYLE, W.H. 2015. *Breeding ecology and behavior of Kittlitz's Murrelet in Kodiak National Wildlife Refuge, Alaska: 2014 progress report*. Refuge Report 2015.1. Washington, DC: US Fish and Wildlife Service.

KNUDSON, T.W., CORCORAN, R.M., LOVVORN, J.R., PIATT, J.F. & PYLE, W.H. 2016. *Breeding ecology and behavior of Kittlitz's Murrelet in Kodiak National Wildlife Refuge, Alaska: 2015 progress report*. Refuge Report 2016.3. Washington, DC: US Fish and Wildlife Service.

LAWONN, M.J., PIATT, J.F., CORCORAN, R.M. & PYLE, W.H. 2011. *Breeding ecology and behavior of Kittlitz's Murrelet in Kodiak National Wildlife Refuge, Alaska: 2010 progress report*. Washington, DC: US Fish and Wildlife Service.

LORENZ T.J., RAPHAEL, M.G., BLOXTON, T.D. & CUNNINGHAM, P.G. 2017. Low breeding propensity and wide-ranging movements by Marbled Murrelets in Washington. *Journal of Wildlife* Management 81: 306–321.

LUGINBUHL, J.M., MARZLUFF, J.M., BRADLEY, J.E., RAPHAEL, M.G. & VARLAND, D.E. 2001. Corvid survey techniques and the relationship between corvid abundance and nest predation. *Journal of Field Ornithology* 72: 556–572.

MALT, J. & LANK, D. 2007. Temporal dynamics of edge effects on nest predation risk for the Marbled Murrelet. *Biological Conservation* 140: 160–173.

MALT, J. & LANK, D. 2009. Marbled murrelet nest predation risk in managed forest landscapes: dynamic fragmentation effects at multiple scales. *Ecological Applications* 19: 1274–1284.

MANLEY, I.A. 1999. *Behavior and habitat selection of Marbled Murrelets nesting on the sunshine coast*. MSc thesis. Burnaby, BC: Simon Fraser University.

MARZLUFF, J.M. & NEATHERLIN, E. 2006. Corvid response to human settlements and campgrounds: Causes, consequences, and challenges for conservation. *Biological Conservation* 130: 301–314.

MCFARLANE TRANQUILLA, L. 2001. *Using multiple methods to describe breeding, stress response, and disturbance of Marbled Murrelets,* Brachyramphus marmoratus. MSc thesis. Burnaby, Canada: Simon Fraser University.

MCFARLANE TRANQUILLA, L., PARKER, N.R., BRADLEY, R.W. ET AL. 2005. Breeding chronology of Marbled Murrelets varies between coastal and inshore sites in southern British Columbia. *Journal of Field Ornithology* 75: 357–367.

MOORE, S.K., MANTUA, N.J., HICKEY, B.M. & TRAINER, V.L. 2009. Recent trends in paralytic shellfish toxins in Puget Sound, relationships to climate, and capacity for prediction of toxic events. *Harmful Algae* 8: 463–477.

NASLUND, N.L. 1993. *Breeding biology and seasonal activity patterns of Marbled Murrelets (*Brachyramphus marmoratus*) nesting in old-growth forests.* MSc thesis. Santa Cruz, CA: University of California, Santa Cruz.

NASLUND, N.L., KULETZ, K.J., CODY, M.B., & MARKS, D.K. 1995. Tree and habitat characteristics and reproductive success at Marbled Murrelet tree nests in Alaska. *Northwestern Naturalist* 76: 12–25.

NELSON, S.K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). In: POOLE, A. (Ed.) *The Birds of North America Online*. Ithaca, NY: Cornell Lab of Ornithology.[Accessed online at http://bna.birds.cornell.edu/bna/species/276, 25 March 2016.]

NELSON, S.K. & HAMER, T.E. 1995. Nest success and the effects of predation on Marbled Murrelets. In: RALPH, C.J., HUNT, G.L., RAPHAEL, M.G., & PIATT, J.F. (Eds.) *Ecology and conservation of the Marbled Murrelet.* General Technical Report. PSW-GTR-152. Albany, CA: US Department of Agriculture.

NELSON, S.K. & PECK, R.W. 1995. Behavior or Marbled Murrelets at nine nest sites in Oregon. *Northwestern Naturalist* 76: 43–53.

NELSON, S.K. & WILSON, A.K. 2002. *Marbled murrelet habitat characteristics on state lands in western Oregon: unpublished report*. Corvallis, OR: Department of Fisheries and Wildlife, Oregon State University.

NEWMAN, S.H., TAKEKAWA, J.Y., WHITWORTH, D.L. & BURKETT, E.E. 1999. Subcutaneous anchor attachment increases retention of radio transmitters on Xantus' and Marbled Murrelets. *Journal of Field Ornithology* 70: 520–534.

NORTHRUP, J.M., RIVERS, J.W., NELSON, S.K., ROBY, D.D. & BETTS, M.G. 2018. Assessing the utility of satellite transmitters for identifying nest locations and foraging behavior of the threatened Marbled Murrelet *Brachyramphus marmoratus*. *Marine Ornithology* 46: 47–55.

PAREDES, R., JONES, I.L. & BONESS, D.J. 2005. Reduced parental care, compensatory behavior, and reproductive costs of thick-billed murres equipped with data loggers. *Animal Behaviour* 69: 197–208.

PEERY, M.Z., BEISSINGER, S.R., BURKETT, E. & NEWMAN, S.H. 2006. Local survival of Marbled Murrelets in central California: Roles of oceanographic processes, sex, and radiotagging. *Journal of Wildlife Management* 70: 78–88.

PEERY, M.Z., BEISSINGER, S.R., NEWMAN, S.H., BURKETT, E. & WILLIAMS, T.D. 2004. Applying the declining population paradigm: Diagnosing causes of poor reproduction in the Marbled Murrelet. *Conservation Biology* 18: 1088–1098.

PEERY, M.Z. & HENRY, R.W. 2010. Recovering marbled murrelets via corvid management: A population viability approach. *Biological Conservation* 143: 2414–2424.

ROBINSON, J.L. & JONES, I.L. 2014. An experimental study measuring the effects of a tarsus-mounted tracking device on the behavior of a small pursuit-diving seabird. *Behaviour* 151: 1799–1826.

ROPERT-COUDERT, Y., KNOTT, N., CHIARADIA, A. & KATO, A. 2007. How do different data logger sizes and attachment positions affect the diving behavior of little penguins? *Deep-Sea Research Part II* 54: 415–423.

SCHACTER, C.R. & JONES, I.L. 2017. Effects of geolocation tracking devices on behavior, reproductive success, and return rate of Aethia auklets: an evaluation of tag mass guidelines. *Wilson Journal of Ornithology* 129: 459–468.

SHEARN-BOCHSLER, V., LANCE, E.W., CORCORAN, R., ET AL. 2014. Fatal paralytic shellfish poisoning in Kittlitz's Murrelet (*Brachyramphus brevirostris*) nestlings, Alaska, USA. *Journal of Wildlife Diseases* 54: 933–937.

SILVERGIETER, M.P. 2009. *Multi-scale analyses of nest site selection and fledging success by Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia*. MSc thesis. Burnaby, BC: Simon Fraser University.

SINGER, S.W., NASLUND, N.L., SINGER, S.A. & RALPH, C.J. 1991. Discovery and observations of two tree nests of the Marbled Murrelet. *The Condor* 93: 330–339.

SYDEMAN, W.J., BRADLEY, R.W., WARZYBOK, P., ET AL. 2006. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: unusual atmospheric blocking? *Geophysical Research Letters* 33: L22S09.

THOMPSON, F.R. & BURHANS, D.E. 2004. Differences in predators of artificial and real songbird nests: evidence of bias in artificial nest studies. *Conservation Biology* 18: 373–380.

US FISH AND WILDLIFE SERVICE (USFWS). 1997. *Recovery plan for the threatened Marbled Murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California*. Portland, OR: USFWS

WHIDDEN, S.E., WILLIAMS, C.T., BRETON, A.R. & BUCK, C.L. 2007. Effects of transmitters on the reproductive success of tufted puffins. *Journal of Field Ornithology* 78: 206–212.

WILK, R.J., RAPHAEL, M.G. & BLOXTON, T.D. 2016. Nesting habitat characteristics of Marbled Murrelets occurring in near-shore waters of the Olympic Peninsula, Washington. *Journal of Field Ornithology* 87: 162–175.

WILSON, R.P., KREYE, J.M., LUCKE, K. & URQUHART, H. 2004. Antennae on transmitters on penguins: balancing energy budgets on the high wire. *Journal of Experimental Biology* 207: 2649–2662.