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RESEARCH ARTICLE

Nesting ecology of Marbled Murrelets at a remote mainland fjord in southeast Alaska

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ABSTRACT

Studying the ecology of endangered species in portions of their range where the population remains abundant can provide fundamental information for conservation planners. We studied nesting by radio-tagged Marbled Murrelets (*Brachyramphus marmoratus*) during 2007 and 2008 in Port Snettisham, a relatively pristine, remote mainland fjord in southeast Alaska with high at-sea densities of Marbled Murrelets during the breeding season. Of 33 active Marbled Murrelet nest sites located during the study, we found 15 within forested habitat (tree nest sites), 16 in nonforested habitat (ground nest sites), and 2 that could not be determined. Some nests were located farther inland from the coast (range: 1–52 km) and at higher elevations (range: 42–1,100 m) than previously documented in Alaska. Nesting success to $\geq$20 days posthatch (0.20 ± 0.07 [SE]) was less than half of similar estimates in British Columbia and more comparable to estimates from California and Washington. A logistic regression found that nesting success did not differ between years, but nesting success was higher for tree nests than for ground nests. Conservation planners should consider that Marbled Murrelets will use certain nonforest habitat types for nesting in mainland southeast Alaska. Our reported nesting success was likely a maximum, and our results indicate that nesting success can be low even when nesting habitat is seemingly abundant and marine habitat appears excellent.

Keywords: Alaska, alcid, *Brachyramphus marmoratus*, breeding, Marbled Murrelet, telemetry

Ecología de Anidación de *Brachyramphus marmoratus* en un Fiordo Continental Remoto al Sureste de Alaska

RESUMEN

El estudio de la ecología de especies amenazadas en porciones de su distribución geográfica donde sus poblaciones siguen siendo abundantes podría proveer información fundamental para su conservación. Estudiamos la anidación de individuos de la especie *Brachyramphus marmoratus* marcados con transmisores de rardio durante 2007 y 2008 en Port Snettisham, un fiordo continental remoto y relativamente prístino en el sureste de Alaska que alberga altas densidades de *B. marmoratus* en el mar durante la temporada reproductiva. De 33 sitios de anidación localizados durante el estudio, encontramos 15 dentro de hábitat boscoso (sitios arbóreos), 16 en hábitat no boscoso (sitios terrestres) y 2 que no pudieron ser determinados. Algunos nidos se localizaron más hacia el interior y lejos de la costa (rango: 1–52 km) y a mayores elevaciones (rango: 42–1 100 m) de lo previamente documentado en Alaska. El éxito de los nidos a 20 o más días después de la eclosión (0.20 ± 0.07 EE) correspondió a menos de la mitad de estimados similares para Columbia Británica y resultó más comparable con los estimados de California y Washington. Con una regresión logística encontramos que el éxito de anidación fue mayor para los nidos arbóreos que para los terrestres. Los organismos que hacen planeación para la conservación deberían considerar que *B. marmoratus* usa ciertos tipos de hábitat no boscoso para anidar en el sureste continental de Alaska. El éxito de anidación que reportamos probablemente fue un máximo y nuestros resultados indican que el éxito de anidación puede ser bajo aún cuando el hábitat para anidar parece ser abundante y el hábitat marino parece excelente.

Palabras clave: Alaska, Alcidae, *Brachyramphus marmoratus*, reproducción, mérgulo, telemetría

FIGURE 1. An incubating radio-tagged Marbled Murrelet.

INTRODUCTION

The Marbled Murrelet (*Brachyramphus marmoratus*; Figure 1) is a noncolonial seabird (family Alcidae) that inhabits the Pacific coast of North America from the Aleutian Islands to central California. Over the past century, significant population declines have been documented throughout the species' range (McShane et al. 2004, Piatt et al. 2007). Since 1990–1992, the Marbled Murrelet (hereafter "murrelet") has been listed as federally threatened in California, Oregon, Washington, and British Columbia. Although the vast majority of research on the murrelet has been conducted in the southernmost portions of its range (British Columbia to California), up to 90% of murrelets breed in Alaska (McShane et al. 2004, Piatt et al. 2007). Conducting research on a species of conservation concern in regions where abundance is high and habitat quality is considered excellent should help guide management aimed at species restoration and provide context for data from other portions of the species' range.

At-sea densities of murrelets during the breeding season are highest in southeast Alaska (Piatt et al. 2007), presumably because of high reproductive output in the area. For example, the average density of murrelets recorded during at-sea surveys from Washington to California during May–July, 2001–2010, was 1.9–2.7 murrelets km^{-2} (Falxa et al. 2011), whereas the average at-sea density of murrelets at two sites in southeast Alaska was 22 and 111 murrelets km^{-2} (DeGange 1996, Haynes et al. 2011). The high abundance of murrelets in southeast Alaska during the breeding season is likely a result of excellent environmental conditions for nesting, including high densities of prey close to an abundance of nesting habitat.

Murrelets nest in diverse habitats, including moss platforms in older-aged coniferous trees, on the ground, and on cliffs. Tree nesting predominates from California to British Columbia, whereas ground and cliff nesting predominates in the mostly treeless landscape of western Alaska (Aleutian Islands, Alaska Peninsula, Kodiak Island; Nelson 1997, Piatt et al. 2007). In the central part of the range, from south-central Alaska to northern British Columbia, most nesting is thought to occur in trees (Burger 2002, McShane et al. 2004, Piatt et al. 2007), but nests on the ground or on cliffs have been found (e.g., Ford and Brown 1995, Bradley and Cooke 2001, Kuletz 2005, Willson et al. 2010). In southeast Alaska, where ~2 million ha of suitable forested nesting habitat remain, mostly on islands (Albert and Schoen 2006), our understanding of what constitutes nesting habitat is limited to mostly serendipitous discoveries of nests at low elevations near the ocean (reviews in DeGange 1996, Piatt et al. 2007). Only two studies, totaling seven nests, have located nest sites from a randomly marked sample of murrelets in southeast Alaska (Quinlan and Hughes 1990, Whitworth et al. 2000). More records of randomly located nest sites are needed to understand the types of nesting habitat used by murrelets in this portion of their breeding range because large amounts of nonforested habitat are available in mainland southeast Alaska, particularly at higher elevations farther from the coast.

Sustained low recruitment, primarily from low reproductive rates, has been considered the key factor limiting population sizes of murrelets in the southern portion of their breeding range (Cam et al. 2003, Peery et al. 2006, Beissinger and Peery 2007). Suspected causes of low recruitment are mostly related to anthropogenic factors, such as increased rates of nest predation associated with habitat modification (Marzluff et al. 2000, Malt and Lank 2009), and reduced food availability and diet quality, possibly related to fishing practices and climate change (Becker and Beissinger 2006, Becker et al. 2007, Norris et al. 2007, Ronconi and Burger 2008). Information on reproductive rates from southeast Alaska, where the murrelet population is large and human impacts on breeding habitat are comparatively few, is needed to clarify the potential causes of decline.

We studied the nesting ecology of murrelets during 2007–2008 in Port Snettisham, southeast Alaska. This remote mainland fjord has few human impacts on potential nesting habitat, and the marine habitat supports the highest known density of murrelets at sea during the breeding season (111 km^{-2}; Haynes et al. 2011). Our primary objectives were to characterize murrelet nesting habitat and estimate reproductive rates by locating nest sites and monitoring them during incubation and rearing of nestlings. Given that southeast Alaska appears to provide relatively good habitat for nesting murrelets, we predicted that murrelets would nest in trees within forested habitats close to the coast, and that reproductive rates would be higher than in southern portions of the

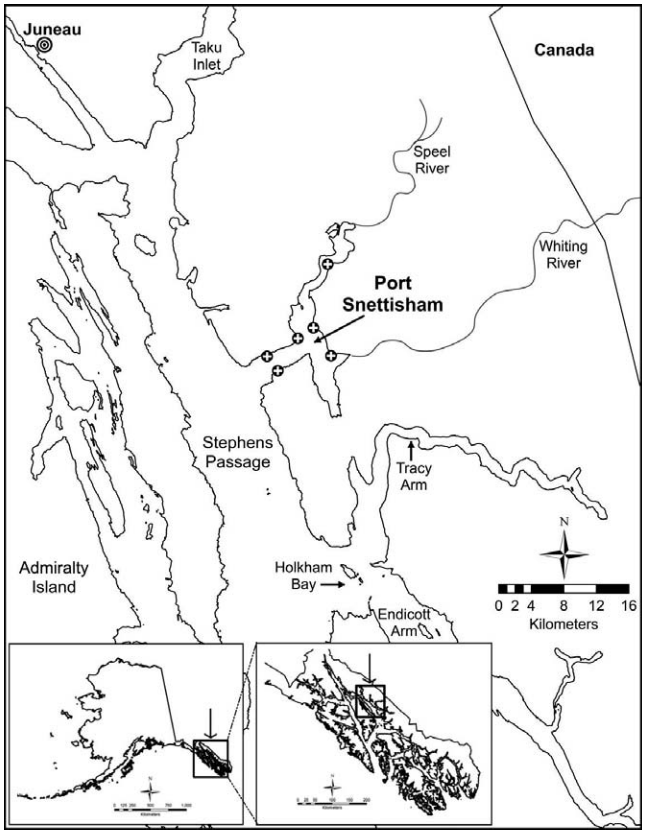

FIGURE 2. Study area near Port Snettisham, southeast Alaska. Encircled white crosses indicate locations of six stationary data logger receivers that monitored presence and directional movements of radio-tagged birds 24 hr day^{-1}.

species' range, where anthropogenic habitat change is considerable.

METHODS

Port Snettisham is a remote mainland fjord ~40 km south of Juneau, Alaska (Figure 2). The study area is protected from the Gulf of Alaska current and weather circulation patterns by Admiralty and Chichagof islands. Tide and wind forcing mix glacially influenced freshwater runoff with seawater in the narrow but deep arms of the fjord. Most land is part of the Tongass National Forest (U.S. Department of Agriculture, Forest Service), with the Tracy Arm-Fords Terror Wilderness Area to the south, the Kootznoowoo Wilderness Area (most of Admiralty Island National Monument) to the west across Stephens Passage, and interior northwestern British Columbia, Canada, 30–35 km inland. Terrestrial habitat at Port Snettisham is characterized by rugged topography; permanent ice, rock cliffs, and alpine habitats dominated most areas above 600 m, and dense forests covered lower elevations. There has been little timber harvest in the Port Snettisham area besides a linear, narrow cut on the path of an electricity transmission line that runs along the northern coast of the fjord. Albert and Schoen (2006) classified most forests in the area as either small (<43 cm quadratic mean diameter [QMD]) or medium (43–53 cm QMD) productive old-growth, with medium-tree forests only at lower elevations of the Whiting and Speel river drainages and along the coast.

We used night-lighting to capture murrelets (Whitworth et al. 1997) near the mouth of Port Snettisham on nights around the new moon that generally coincided with the beginning of their breeding season (May 15–16, 2007, and May 26–28, 2008). VHF radio transmitters that weighed ~2.5 g (~1% of average adult murrelet body mass) were attached to the dorsal surface of each bird using a subcutaneous anchor (Newman et al. 1999). We also scored brood-patch development (after Sealy 1974) and drew a small amount of blood from the medial metatarsal vein to determine sex. Each bird was allowed a recovery period prior to release. Mean (± SD) handling time from capture to release was 55 ± 15 min in 2007 and 38 ± 14 min in 2008.

Aerial-, boat-, and ground-based radio-tracking were used to locate murrelet nest sites, monitor daily nest attendance, and determine at-sea locations of individual murrelets. Data logger receivers were also deployed at strategic locations along the shores of Port Snettisham to record presence–absence data 24 hr day^{-1} (Figure 2). Data loggers recorded date and time for all confirmed radio-transmitter detections, so the presence and directional movements of radio-tagged murrelets were monitored throughout the fjord during the entire study.

Nest sites were located during aerial-telemetry surveys from fixed-wing aircraft by "boxing," whereby the relative signal strength received by antennas on each wing was compared to determine the signal direction and circle an area around the radio-tagged bird. We surveyed all marine areas within the study area prior to flying inland in search of birds not detected at sea. Most aerial telemetry surveys were conducted prior to June 30 each year to maximize the number of survey days during the suspected peak of murrelet nest initiation. A comparison of aerial coordinates and locations of nest sites subsequently visited on the ground ($n = 7$) indicated that nest-site coordinates were recorded with an accuracy of approximately ±100 m. For nest sites visited on the ground, we also confirmed nest site type (tree or ground), recorded elevation (using an altimeter), and estimated characteristics of the nest tree when possible (tree species, diameter, height, percent moss cover on all limbs, location of nest platform in relation to trunk, and distance of nest limb from the ground). For nests not accessible by foot, suspected nest site type was determined from the aircraft as tree, ground, or undetermined, depending on nesting habitats in the nest-site area;

the "undetermined" category was used when habitat composition in the nest-site area was mixed or when the nest site's location was unknown. All nests in nonforested areas were classified as ground nests. Elevation (m) was estimated for nests not accessible by foot, using topographic mapping software. Distance inland (km) was intended to represent the actual distance an individual traveled from the coast to its nest site, based on flight corridors (flyways) determined by watershed topography. Data from our stationary data loggers and direct observations showed that murrelets traveled along river corridors when commuting to their nests, rather than in straight lines from the ocean, because steep topography and low cloud cover prevented direct flights from marine locations to nest sites.

We categorized radio-tagged murrelets as either breeders or nonbreeders. We defined a "breeder" as any bird attempting to nest at least once after capture, regardless of brood-patch condition at the time of capture. Nesting attempts were identified by using radio-tracking to locate active nests or by using telemetry data to identify behavior patterns consistent with active incubation. Murrelets attend nests for 24-hr shifts during incubation, resulting in an "on–off" nest-attendance pattern (Nelson and Hamer 1995b); thus, actively incubating birds were located at the nest site one day and at sea the following day. On the basis of this pattern, we defined a "nest attempt" as when a radio-tagged murrelet exhibited behavior indicating incubation for $\geq$4 consecutive days (on–off–on–off). "Nest initiation date" was defined as the day on which behavior indicating incubation began for each breeder, even though egg laying without incubation or incubation by its mate could have occurred up to a few days earlier. The timing and duration of the murrelet nesting season were quantified using estimated nest initiation dates and previously published information on the average duration of the incubation (30 days) and nestling periods (28 days; Hamer and Nelson 1995). Nesting-season duration was calculated as the period between the first nest initiation date and the extrapolated (potential) fledging date from the latest date a nest was active (Hamer and Nelson 1995, Lougheed et al. 2002).

"Nest initiation rate" was defined as the proportion of radio-tagged murrelets classified as breeders after capture and marking. We could not visit most nests to confirm their fates because they were not accessible by foot. However, because murrelets have distinctly different movement patterns during incubation and the nestling period, we used behavior patterns identified in the telemetry data to infer hatching success and nestling survival to $\sim$20 days posthatch (Bradley et al. 2004). A nest was considered to have successfully hatched a nestling when behavior patterns consistent with incubation lasted for $\geq$28 consecutive days (Nelson 1997) and were followed by behavior patterns consistent with chick provisioning. Hatching rate estimated in this manner was, however, a minimum, because some nestlings may have died soon after hatching and before they were provisioned by parents. Chick provisioning was inferred when shore-based data loggers detected a radio-tagged murrelet leaving the fjord, moving toward its nest, followed by a period of no detection (range: 30–120 min) before the bird was again detected moving through the fjord, away from its nest. Murrelet chicks have been reported to fledge at 27–40 days posthatch (Nelson 1997). Detecting actual fledging dates on the basis of behavior patterns from radio telemetry was difficult because estimated dates of egg laying and hatching might be off by as much as a few days, and chick-provisioning rates can differ considerably during late stages of the nestling period (Nelson and Hamer 1995b, Bradley et al. 2002). Consequently, we adopted the approach of Bradley et al. (2004) to infer the duration of nesting attempts and defined "successful fledging" as adult behavior patterns consistent with chick provisioning for $\geq$20 days. This method of estimating fledging success is biased high because it does not include nests that failed late in the nestling period, but this method was the only viable option for monitoring widely dispersed nests located in inaccessible habitat.

We defined hatching or fledging as "unsuccessful" when behavior patterns consistent with incubation or chick provisioning ceased for 4 consecutive days, which allowed for up to two missed nest visits by the radio-tagged murrelet without assuming nest failure. In addition, we calculated a renesting rate as the proportion of birds (regardless of brood patch condition at the time of capture) that initiated a second nest (identified using the methods above) following a failed first nest attempt and sufficient time for replacement egg formation ($\sim$14 days; Hébert et al. 2003).

Statistical Analyses

We reported the proportion of individual radio-tagged murrelets by year and nest site type that successfully reached three stages of nesting: (1) nest initiation, (2) hatching success, and (3) fledging success. Probability of success at each stage of nesting was contingent on success during the previous stage; thus, only individuals categorized as "breeders" were included in estimates of hatching and fledging success. For our sample of nesting attempts, we used the Kaplan-Meier estimator (Kaplan and Meier 1958) to estimate success across the two intervals of the active nesting cycle (hatching and fledging). We chose this method because it allowed for censoring individuals whose nest fates were unknown (Millspaugh and Marzluff 2001). Nest success was the cumulative probability that an individual egg hatched and the nestling survived to $\geq$20 days posthatch. If both members of the breeding pair were

TABLE 1. Proportions (± SE) and numbers of radio-tagged Marbled Murrelets that reached three consecutive stages of nesting near Port Snettisham, southeast Alaska (2007–2008). Proportions represent probability of success at each stage (1–3) and are contingent upon success in the previous stage. Nesting success is the cumulative probability (Kaplan-Meier estimate) that an individual breeder succeeded at both nesting stages 2 and 3, including the 95% confidence interval (CI). Fledging success and nesting success are based on nestling survival to ∼20 days posthatch (late nestling phase).

	Year		Nest site type		
Stage	2007	2008	Tree	Ground	Overall
(1) Nest initiation	0.50 $n = 36$	0.46 $n = 37$	NA	NA	0.48 $n = 73$
(2) Hatching success	0.63 ± 0.11 $n = 20$	0.32 ± 0.11 $n = 19$	0.59 ± 0.12 $n = 17$	0.39 ± 0.11 $n = 18$	0.47 ± 0.08 $n = 39$
(3) Fledging success	0.38 ± 0.17 $n = 8$	0.50 ± 0.20 $n = 6$	0.67 ± 0.19 $n = 6$	0.14 ± 0.13 $n = 7$	0.43 ± 0.13 $n = 14$
Nesting success 95% CI	0.24 ± 0.12 0.08–0.52 $n = 20$	0.16 ± 0.08 0.05–0.39 $n = 19$	0.39 ± 0.14 0.17–0.67 $n = 17$	0.06 ± 0.05 0.01–0.31 $n = 18$	0.20 ± 0.07 0.10–0.38 $n = 39$

radio-tagged ($n = 3$), we included only one randomly selected individual from each mated pair in our analyses.

We tested for sex and year effects on breeding status using a logistic regression, excluding birds tracked for <10 days ($n = 3$) and birds of unknown sex ($n = 2$). After log-transforming elevation and distance inland for nest sites to normalize both variables, we used two-tailed t-tests to compare nest elevation and distance inland by nest type. Logistic regression models were used to test whether hatching success or nesting success varied by sex, year (2007 or 2008), nest site type (tree or ground), or distance inland of the nest site. Separate models were run to test whether hatching or nesting success varied by sex, and this variable was removed from subsequent analyses. We did not include fledging success as a response variable because the sample size was insufficient. Nest sites with undetermined habitat type ($n = 4$) and nest attempts with unknown fledging and nesting success ($n = 4$) were excluded from the relevant analyses. The significance level for statistical tests was set at $P = 0.10$ to minimize the likelihood of a Type II error as a result of small sample size. Means are reported ± SE for data associated with a statistical analysis, and ± SD otherwise.

RESULTS

We captured and radio-tagged 37 male and 42 female murrelets during 2007 ($n = 39$) and 2008 ($n = 40$), and 76 of 79 murrelets were tracked for ≥10 days (range: 3–88 days). The mean individual tracking period was 61 ± 17 days ($n = 39$) in 2007 and 46 ± 24 days ($n = 40$) in 2008. We conducted 80 aerial surveys, including 22 surveys from May 28 to June 27 in 2007 and 24 surveys from May 30 to June 29 in 2008; the gap between aerial surveys was no more than one day from May 30 to June 16 in 2007 and 2008. Detection rates during aerial surveys were high; prior to the last detection for each individual, radio-tagged murrelets were consistently detected at sea within the study area (96.8% of possible detections in 2007; 95.3% in 2008), except when attending an inland nest site. Data logger stations recorded 69,464 detections of radio-tagged murrelets in 2007 and 65,420 in 2008.

We classified 38 murrelets as breeders after capture, including both members of three breeding pairs in 2007; thus, our minimum nest initiation rate after capture was 0.48 (Table 1). However, fully or partially developed brood patches (score >0) were observed for 32 (82.1%) murrelets radio-tagged in 2007 and 34 (85.0%) of those radio-tagged in 2008. Three of 13 birds with no evidence of a brood patch when captured (score = 0) were classified as breeders. Nest initiation rate did not differ by year ($\chi^2 = 0.280$, df = 71, $P = 0.60$), but the proportion of males that initiated a nest after capture (0.68) was higher than that of females (0.31; $\chi^2 = 10.69$, df = 71, $P = 0.002$). The observed nesting season lasted 113 days, from May 25 to September 16. Mean nest initiation date (including renests) was June 10 ± 2 days (range: May 25–July 19), and mean (potential) hatch date was July 10 ± 2 days (range: June 24–August 18).

We located and described 33 active nest sites (Figure 3). Nest locations were verified by a least two detections of a radio-tagged murrelet at the same inland location during aerial surveys. Telemetry data indicated that two additional radio-tagged murrelets nested, but we were unable to locate their nests during aerial surveys. Nest sites were located either in the Port Snettisham watershed ($n = 28$), on the Snettisham Peninsula ($n = 3$), in the Tracy Arm watershed ($n = 1$), or on the Glass Peninsula of Admiralty Island ($n = 2$). The majority of nests (75.8%) were within the Speel Arm ($n = 17$) and Whiting River ($n = 8$) basins.

We found nest sites in both forested (tree nest sites, $n = 15$) and nonforested habitat (ground nest sites, $n = 16$); habitat type for four nest sites was categorized as undetermined because both forested and nonforested

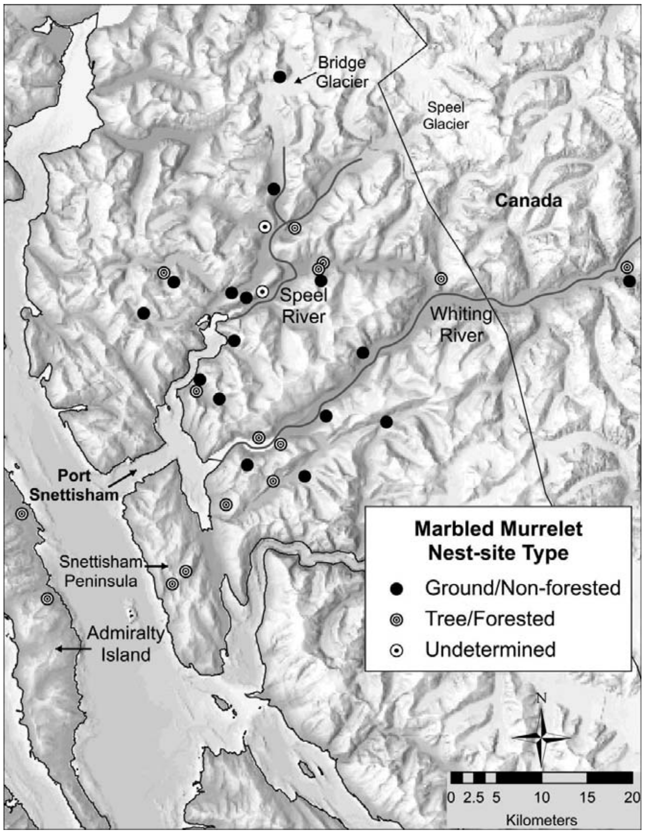

FIGURE 3. Nest site locations ($n = 33$) identified during aerial surveys. Nest site type was characterized from the ground for accessible sites (ground, $n = 1$; tree, $n = 7$) or during aerial surveys for inaccessible sites (ground, $n = 15$; tree, $n = 8$; undetermined, $n = 2$).

habitat were present ($n = 2$) or the nest site's location was unknown ($n = 2$). We visually confirmed nest site type from the ground for seven tree nests and one ground nest. We identified six of seven nest trees to species: Western Hemlock (*Tsuga heterophylla*; $n = 4$), Mountain Hemlock (*T. mertensiana*; $n = 1$), and Sitka Spruce (*Picea sitchensis*; $n = 1$). Characteristics of four nest trees were recorded (mean diameter at breast height = 94 ± 54 cm, range: 58–173 cm; mean height = 46 ± 11 m, range: 40–60 m; mean percent moss = 40 ± 15%). Although we were unable to climb trees in search of the nest platforms, we observed two nest sites in Western Hemlock trees from the ground. These nests were located 1 cm and 90 cm from the trunk on limbs 20 m and 25 m above the ground, respectively. The five accessible tree nests in the Port Snettisham watershed were located within Western Hemlock–Sitka Spruce forests of low species diversity but high vertical complexity. The two nest sites on Admiralty Island were within forests dominated by Western Hemlock, with Western Redcedar (*Thuja plicata*) and Red Alder (*Alnus rubra*) intermixed at lower elevations, and Sitka Spruce and Mountain Hemlock intermixed at higher elevations.

We found ground nests in nonforest habitat types that were characterized by steep, rocky gradients with no tree growth and primarily epiphyte, dwarf shrub, and herbaceous cover (Figure 4). Most ground nest sites were on rock cliff faces ($n = 10$); others were located on steep alpine scree or rocky slopes near or above the tree line ($n = 6$; e.g., Figure 4A). Snow or ice cover commonly surrounded ground nest sites, particularly earlier in the nesting season and at higher elevations. Nest position on rock cliffs ranged from near the talus at the cliff base to >500 m above the base. Presumably, most cliff nests were on ledges; however, one cliff nest likely was located in a crevice or underneath an overhanging rock, because the transmitter signal was detectable only at a horizontal angle during aerial surveys. We located three high-elevation ground nests adjacent to active glaciers on rock cliffs with sparse vegetation and epiphyte cover and >5 km from the nearest tree (e.g., Figure 4B). Only one ground nest was accessible; this 2008 nest site was $\sim$300 m above the base of a 400-m-high cliff face with 15–20% vegetation–epiphyte cover. Several ground nest sites, however, were located in rocky habitat with forested habitat nearby (e.g., Figure 4D).

Median nest-site elevation was 376 m (range: 30–1,100 m), and median distance inland via flyways was 9.6 km (range: 1.0–52.0 km). Ground nests were located at higher elevations, on average, than tree nests ($t_{29} = 2.98$; $P = 0.006$); however, mean distance inland was similar between nest site types ($t_{29} = 0.75$; $P = 0.46$; Figure 5). Sixteen of 33 nest sites (48.5%) were >10 km from the coast via flyways, and four nest sites (12%) were >30 km from the coast via flyways. Two nest sites in the Whiting River basin (one tree nest and one ground nest, 1.5 km apart) were $\sim$52 km from the coast via flyways in interior northwestern British Columbia, Canada (Figure 3).

Hatching success was 0.47 ± 0.08 ($n = 18$ of 39), and fledging success was 0.43 ± 0.13 ($n = 6$ of 14; Table 1). Nest success, or the cumulative probability that a nesting attempt had a chick survive to 20 days posthatch, was 0.20 ± 0.07 ($n = 39$; 95% confidence interval: 0.10–0.38). Neither hatching success nor nesting success differed by sex ($\chi^2 = 0.11$, df = 35, $P = 0.74$, and $\chi^2 = 1.16$, df = 32, $P = 0.28$, respectively). Hatching success did not differ between nest site types ($\chi^2 = 0.94$, df = 33, $P = 0.33$) or by distance inland of the nest site ($\chi^2 = 0.16$, df = 33, $P = 0.28$); there was, however, a trend toward higher hatching success in 2007 than in 2008 ($\chi^2 = 2.44$, df = 33, $P = 0.12$). Nesting success did not differ between years ($\chi^2 = 0.04$, df = 29, $P = 0.84$); there was, however, higher nesting success for tree nests than for ground nests ($\chi^2 = 3.18$, df = 29, $P = 0.07$) and suggestive evidence that nest sites farther inland had higher nesting success ($\chi^2 = 2.74$, df = 29, $P = 0.10$). Failure of three ground nests was attributed to the mortality of the adult during the incubation period, as indicated by the

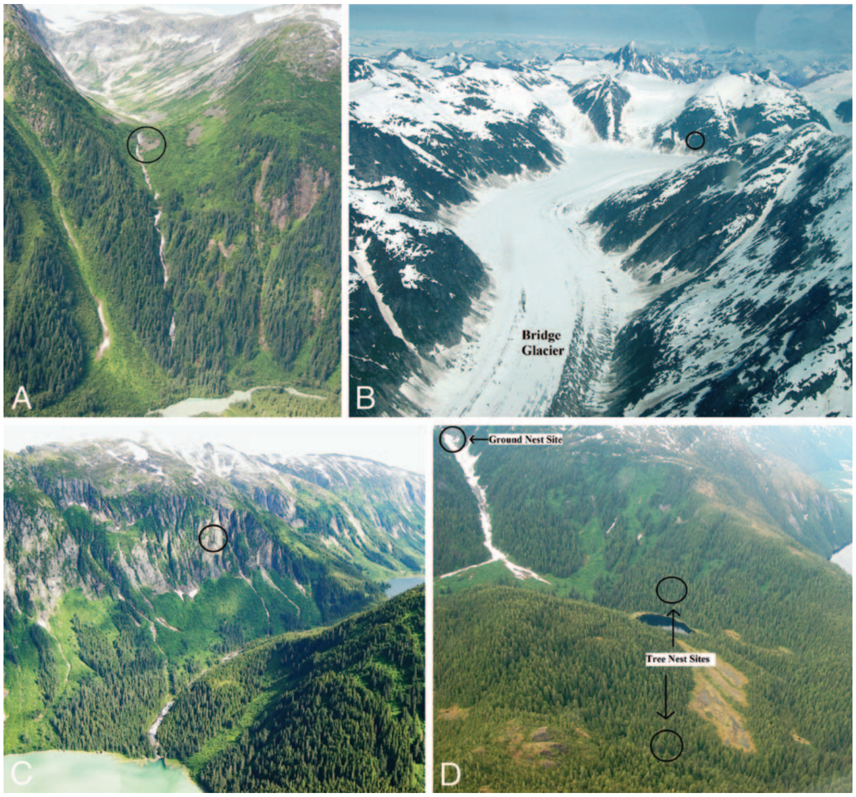

FIGURE 4. Six nest site locations (black circles) for Marbled Murrelets near Port Snettisham, southeast Alaska. (**A**–**C**) Locations for three nest sites in nonforested (ground) habitat. (**D**) Locations for one nest site in nonforested (ground) habitat and two nest sites in forested (tree) habitat.

repeated detection of the radio signal at the same shoreline location during aerial surveys.

Four of 25 murrelets (16%) that failed in their first nest renested, all after June 21. All four murrelets that renested were males with mostly defeathered brood patches (score = 2 or 2+) when captured. No murrelets renested after failure during the nestling period, so of 17 murrelets whose nests failed during incubation, 24% renested. Renesting attempts occurred in the same location and nest site type as the first nesting attempts; however, reuse of the same nest bowl, limb, or tree could not be determined because the nest sites were inaccessible. Detection patterns indicated that renesting murrelets laid the second egg between 11 and 20 days after failure of the first nest.

DISCUSSION

Our study is the first to characterize a large sample of ground and tree nest sites and quantify reproductive success of Marbled Murrelets in southeast Alaska using a random sample of marked birds. Contrary to our prediction, radio-tagged murrelets did not exclusively or even predominantly use trees as nest sites in the Port Snettisham area; they placed nests on cliffs and on the ground as much as in trees. Our conclusion that some murrelets nested on the ground was definite, because transmitter signals from incubating birds were detected in areas without any potential nest trees. However, it is possible that some nests classified as tree nests could have been misclassified if the nest occurred on tree roots or on the ground near ravines covered by forest canopy (Ford and Brown 1995, Willson et al. 2010). Ground nests were located in structurally diverse, nonforested habitats that were mostly inaccessible to humans. Thus, the physical attributes of these nest platforms (e.g., slope, cover type and amount, width of ledge) remain unknown. We suspect that ground nesting by murrelets is less common on islands of southeast Alaska because forested habitat dominates the land cover of most islands in the region; on the mainland, where Port Snettisham is located, the land cover includes older-aged forests in low-elevation areas along the coast and in river valleys, but is dominated by rock and ice, providing a variety of sites for nesting. Ground nesting dominates among alcids and was likely the ancestral trait for murrelets before they evolved to nest in trees (Nelson 1997, Congdon et al. 2000). Ground nesting

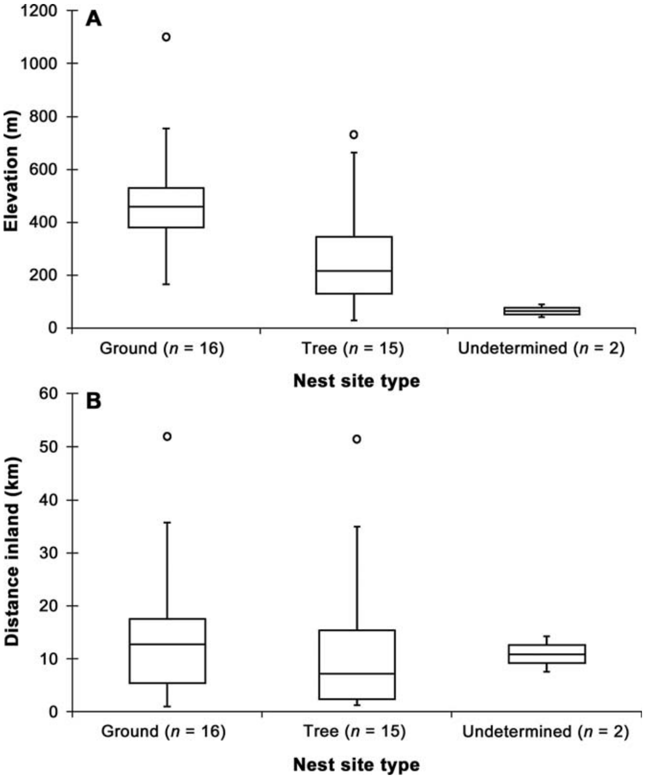

FIGURE 5. Elevation (**A**) and distance to coastline via flyways (**B**) of nest site locations. Boxes represent interquartile values, lines in boxes are median values, and circles are maximum outlier values.

may persist in mainland portions of southeast Alaska because rock cliffs and nonforested slopes remain common, but the use of ground nests may also be related to environmental factors such as differing levels of predation and natal site fidelity.

Our accessible tree nests were located in large, tall trees with abundant moss and in older forests with dense, multilayered canopies, similar to tree nests found elsewhere in Alaska and to the south (e.g., Naslund et al. 1995, Baker et al. 2006). Given the inaccessibility of our nest sites, details on the characteristics of these nest sites and nest platforms were limited. In addition, these characteristics may be biased by our small sample size and the fact that the nest trees were accessible by foot. More data on forest characteristics related to murrelet nest sites are needed to inform habitat management in southeast Alaska; unfortunately, collecting unbiased data on a large sample of nest sites will be difficult because of the rugged and largely inaccessible inland habitat that typifies southeast Alaska.

Just like areas farther south in their breeding range, murrelets in southeast Alaska will select nest sites far inland and at high elevation, even when nesting habitat closer to the coast appears to be readily available. We found that 16 of 33 nest sites were >10 km inland via flyways, including 2 nests that were located ~52 km inland. Of the 13 nest sites in our study that were located at ≥400 m elevation, 10 were placed in nonforested habitat, which suggests that high-elevation nest sites may be common in portions of southeast Alaska where nonforested nesting habitat is widely available. Factors that may favor far inland or high-elevation nest sites include lower nest predation rates and potentially fewer predators (Burger et al. 2000), and lower intraspecific competition for nest sites. Our data on nesting success suggest that nest sites farther inland are more likely to fledge a chick; however, nonforested habitat, which had lower nesting success than forested habitat, predominates in most inland areas of mainland southeast Alaska. More research with a larger sample size of nests is needed to assess the interactive effects of distance inland, elevation, and nest site type on nesting success.

Conservation planners had previously considered only old-growth forested habitat as Marbled Murrelet nesting habitat in southeast Alaska because the extent of ground nesting was unknown (DeGange 1996, Albert and Schoen 2006). Our findings suggest that the definition of what constitutes Marbled Murrelet nesting habitat in southeast Alaska should be expanded to include certain nonforest habitat types, such as rock cliff, subalpine, and other high-elevation areas where snow and ice cover melts early in the year. For example, three ground nests were located on high-elevation rock cliff faces near glaciers, and >5 km from the nearest tree. These high-elevation ground nest sites were previously considered to be used for nesting only by the closely related Kittlitz's Murrelet (*B. brevirostris*; Day et al. 1999). Because terrestrial habitat with extreme topography and minimal vegetation, features prevalent throughout most of southeast Alaska, is apparently available to Marbled Murrelets for nesting, the surface area available for nesting is greater than two-dimensional mapping reveals. The total area of nesting habitat available to Marbled Murrelets in southeast Alaska is therefore larger than was previously believed. However, the amount of forested habitat is being reduced by timber harvest and urban growth, whereas the amount of nonforested habitat may be increasing as ice and snow cover decrease because of climate change. We recommend that all old-growth and older-aged forests, and alpine and rock cliff habitat up to 1,100 m elevation and up to 52 km inland via flyways, be considered potential murrelet nesting habitat in southeast Alaska until more information is available regarding forested and nonforested nesting-habitat suitability. Extensive ground nesting and abundant older-aged-forest nesting habitat help explain how Port Snettisham and other parts of southeast Alaska (e.g., Glacier Bay) can support large populations of murrelets during the breeding season.

The nest initiation rate after capture (0.48) in our study was low in relation to other alcids (DeSanto and Nelson 1995), but similar to the results of previous radio-telemetry studies on murrelets (e.g., Bradley et al. 2004, Peery et al. 2004, Hébert and Golightly 2006). A small portion of our sample that we classified as nonbreeders were likely either subadults that had not reached breeding age or nonbreeding adults that did not lay eggs that year (McShane et al. 2004). In addition, we may have misclassified breeders as nonbreeders if (1) nests failed prior to detection of behavior patterns consistent with incubation, (2) breeding adults were captured after their nests had failed, or (3) breeding adults had a reduced propensity to nest or renest due to effects of capture and handling (for more details, see Bradley et al. 2004). Males had a higher nest initiation rate after capture than females, similar to the results of Bradley et al. (2004), which suggests that at least some females may have been more affected by capture and handling or that production of a relatively large, single egg makes renesting more difficult for some females (Sealy 1974). There was no difference, however, in hatching success or nesting success between males and females, which indicates that if radio-tagged females laid an egg and initiated incubation, nesting behaviors ensued at the same rate as in males. Radio-tagging only males during future research would eliminate the potential bias in nest initiation rate associated with capturing females during egg formation.

Contrary to our prediction, the nesting success of murrelets at Port Snettisham, a relatively pristine watershed, was lower than or similar to that described in studies from more southern parts of the breeding range. Using similar methods, our estimate (0.20) was much lower than estimates of “mid-chick nesting success” reported for Desolation Sound (0.69, $n = 116$; Bradley et al. 2004) and Clayoquot Sound, British Columbia (0.59, $n = 29$; Zharikov et al. 2006). Our estimate was more similar to those for radio-tagged murrelets in northern Washington (0.05; Bloxton and Raphael 2009) and northern California (0.22; Hébert and Golightly 2006), where accessible nest sites allowed confirmation of actual nest fate. Low nesting success is therefore not limited to locations that have undergone widespread loss of forested nesting habitat. Inconspicuous environmental or density-dependent factors may be limiting productivity at Port Snettisham, including overwinter stress, prey quality, predation, disturbance, and cumulative and interactive effects.

Nesting success was higher for nest sites in forested habitat and farther inland, but the causes of individual nest failures at Port Snettisham are unknown. Risk of nest predation was likely a major selective pressure that caused murrelets to evolve a secretive and solitary nesting strategy; nest predation is a common cause of nest failure for murrelets in managed forest landscapes south of Alaska (Nelson and Hamer 1995a, Malt and Lank 2009). Coastal predators and remnant effects of past logging may influence murrelet nest-site selection and nesting success in Port Snettisham. We observed known avian predators of adults and nests near the ocean in our study area, including Bald Eagles (*Haliaeetus leucocephalus*), Common Ravens (*Corvus corax*), and Northwestern Crows (*C. caurinus*), and predator avoidance was considered a key factor causing murrelets to leave interior Port Snettisham at night to use nearby portions of Stevens Passage (Haynes et al. 2010). Known predators of adults and nests were rarely seen during our visits to accessible nest sites. Unfortunately, there are no known studies on predator populations in the Port Snettisham area, and the influence of predation on nesting location and nesting success during our study remains unclear. However, if predators were a key factor causing murrelets to nest farther inland, differences in predator populations and behavior may also have caused the difference in nest success between tree and ground nests, but this idea needs further exploration.

Nest failure could also be linked to marine foraging conditions. Reproductive success of four auklet species (*Aethea* spp.) in the North Pacific was correlated to shifts in the Pacific Decadal Oscillation (PDO) regime (Bond et al. 2011), and a shift in the PDO regime, from a warm to a cold anomaly, was recorded in fall of 2007 (National Oceanic and Atmospheric Administration 2011). Cold-PDO anomalies have been linked to increased freshwater discharge in mainland locations of southeast Alaska (Neal et al. 2002). The bottleneck-like geography of Port Snettisham makes the fjord susceptible to rapid fluctuations in freshwater runoff, and high-runoff events result in turbid water conditions prevailing throughout the fjord, where most birds in our study foraged. In fact, we observed few murrelets in the fjord when turbid conditions prevailed. The cold-PDO anomaly observed in 2008 coincided with larger marine home-range sizes and longer average commuting distances from at-sea locations to nests (Barbaree 2011), which indicates that murrelet foraging behavior and likely daily energy expenditure were influenced by a change in marine conditions between 2007 and 2008. Nesting success was low during both years nonetheless, which suggests that additional factors may be limiting nesting success.

Nearly one-fourth of the murrelets whose nests failed during incubation renested, and the renesting rate at Port Snettisham (0.16) was similar to that at Desolation Sound (0.14; McFarlane Tranquilla et al. 2003), calculated in the same manner. These renesting rates were absolute minimums, because some breeders may have initiated a nest that failed prior to or in relation to capture. Replacement nesting is an important aspect of murrelet nesting ecology, and food availability late in the breeding season may have a considerable effect on productivity. In addition, the four renests during our study were all initiated after June 21; thus, any attempt to measure murrelet productivity in southeast Alaska using estimates of adult:juvenile ratios at sea should consider that a substantial portion of nestlings may fledge in late August and September each year.

Despite seemingly abundant nesting habitat and marine foraging conditions that support a large population of adult murrelets during the breeding season, productivity at nesting sites in Port Snettisham was low during our study. However, the population-level consequences of low nesting success remain unclear without data on survival. Significant population declines have been suspected in portions of Alaska since the early 1990s, including Glacier Bay and Icy Strait in southeast Alaska (Piatt et al. 2007), but no population trend data are available for the Port Snettisham area. If reproduction in southeast Alaska is depressed compared with historical levels, as is suspected for murrelets nesting in California (Peery et al. 2006, Beissinger and Peery 2007) and British Columbia (Cam et al. 2003), investigations into the causes of low reproductive success at Port Snettisham, as well as at other sites in this core breeding region, are needed to further elucidate the mechanisms that are limiting murrelet recruitment.

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