TREE AND HABITAT CHARACTERISTICS AND REPRODUCTIVE SUCCESS AT MARBLED MURRELET TREE NESTS IN ALASKA

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ABSTRACT—In 1991 and 1992, we located 14 tree nests of the marbled murrelet (*Brachyramphus marmoratus*) on Naked, Kodiak, and Afognak islands, Alaska. All nests were in old-growth forests on moss-covered platforms of western hemlock (*Tsuga heterophylla*; $N = 2$), mountain hemlock (*T. mertensiana*; $N = 7$), and Sitka spruce (*Picea sitchensis*; $N = 5$). Most nest trees were located in large tree-size class and volume-class forests (the highest in the region). In addition, 21 trees were recorded where murrelets landed but where nests were not known to occur. The diameters at breast height (dbh) of nest and "landing" trees were 30–104 cm and 35–118 cm, respectively. Naked Island nest and landing trees were similar to each other. They were larger in diameter, had more potential nest platforms, and had greater epiphyte cover than did the 9 closest upper-canopy trees adjacent to each. Nest trees were similar to those at more southern latitudes in that they were old-growth conifers that contained large moss-covered platforms with foliage shielding the nest from above. Sitka spruce possessed qualities that seem to be important to nesting murrelets more frequently than the other 2 conifer species. All 7 nests where reproductive success was known failed due to nest abandonment, predation or unknown causes. Reuse of landing trees, and nesting in a landing tree from the previous year, indicate some degree of site fidelity. The proximity of nest sites on each island suggested clumped or semi-colonial nesting.

Marbled murrelets (*Brachyramphus marmoratus*) are unusual for their family because they nest almost exclusively on large branches of old-growth or mature coniferous trees (Quinlan and Hughes 1990; Singer et al. 1991; Hamer and Nelson 1995a). They are also remarkable because they nest solitarily or in small groups, perhaps as far as 100 km inland (Carter and Morrison 1992; T. E. Hamer, pers. comm.).

Characteristics of murrelet nests and nesting habitat have been difficult to document. In Alaska, most murrelets are distributed offshore of old-growth coniferous forests during the breeding season, and a small percentage are found offshore of treeless areas (Piatt and Ford 1993; Piatt and Naslund, in press). Only 1 tree nest and 5 ground nests were documented in Alaska prior to 1991 (Day et al. 1983, Johnston and Carter 1985, Quinlan and Hughes 1990), although many tree nests have been found in the southern portion of the murrelet's range (Binford et al. 1975, Singer et al. 1991, 1994, Hamer and Nelson 1995a, Jordan and Hughes 1995, Kerns and Miller 1995, Manley and Kelson 1995).

Marbled murrelets were directly and indirectly impacted by the 1989 *Exxon Valdez* oil spill in Prince William Sound, Alaska (Piatt et al. 1990; Kuletz, in press). To assist restoration efforts for the affected murrelet population, murrelet nesting habitat needed to be identified. However, forest characteristics of coastal Alaska differ substantially from more southern regions (Viereck and Little 1972). This makes it difficult to access habitat requirements of murrelets nesting in Alaska. Our objective was to identify nesting habitat in the spill zone by locating nests and quantifying nest-site characteristics. Here we report and discuss our findings, and compare them to what is known about murrelet nesting habitat in the southern portion of the species' range. We also discuss reproductive outcome (success or failure) of the nests we documented.

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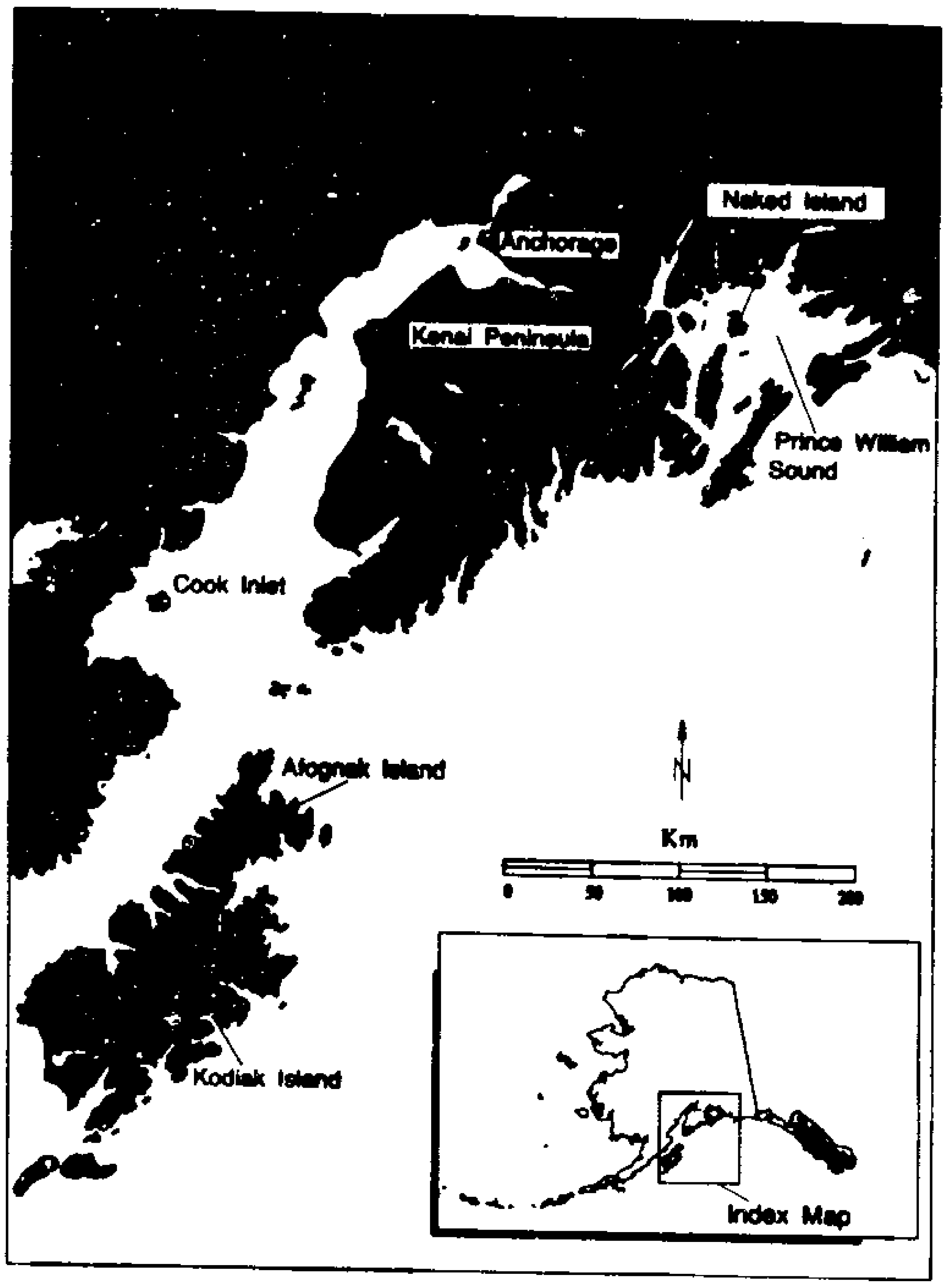

FIGURE 1. Study area showing Naked, Afognak and Kodiak islands, where marbled murrelet tree nests were documented in 1991 and 1992.

METHODS

Study Area

We studied marbled murrelets during the breeding seasons of 1991 and 1992 on Naked Island in Prince William Sound, Alaska, and during 1992 on Kodiak and Afognak islands, off the Alaska Peninsula (Fig. 1). All 3 islands have diverse habitats ranging from old-growth coniferous forests to muskeg meadows. Upland tundra and alpine-like communities occur on Kodiak and Afognak islands. Canopy species on Naked Island are mountain hemlock (*Tsuga mertensiana*), western hemlock (*T. heterophylla*), and Sitka spruce (*Picea sitchensis*). On Kodiak and Afognak islands, forests are comprised solely of Sitka spruce. Blueberry (*Vaccinium alaskensis*), salmonberry (*Rubus spectabilis*), devil's club (*Echinopanax horridus*), and rusty mensiesia (*Menziesia ferruginea*; Naked Island only) dominate the understory of the islands. U.S. Forest Service (1992) and Viereck et al. (1992) described vegetation for this region.

Naked Island is forested to its summit, with peaks up to 400 m. High mountainous peaks of 1300 m are snow-covered year-round on Kodiak Island and peaks reach 760 m on Afognak Island. Areas of Afognak have been heavily logged (primarily clear cut) since the mid-1970's whereas Kodiak Island has been subjected to only small-scale logging (T. P. Gerlach, pers. comm.). Naked Island remains uncut, with the exception of a few trees that were recently cut during a logging feasibility study.

Locating Nests

On Naked Island, we concentrated our search efforts around 5 bays and 2 high-elevation stands (ca. 230–330 m) where murrelets were suspected to nest (Kuletz et al. 1995b; unpubl. data). Nest-search efforts on Kodiak and Afognak islands were done opportunistically in forested and non-forested habitat while conducting other surveys of murrelet activity (M. B. Cody and T. P. Gerlach, unpubl. data).

The primary method used to locate murrelet nests on Naked Island was a ground-based search technique (Singer et al. 1991; Naslund 1993). This technique involves observing murrelet behavior in forests during their pre-dawn activity period. We identified potential nest sites by locating trees where murrelets exhibited flight behaviors (*e.g.*, flights to or from branches, multiple flights by a specific branch) or calls (*e.g.*, incubation exchange calls or short calls made near a branch) associated with nesting. Observers were initially stationed around a group of trees and observations were generally made over several days, while progressively narrowing down areas of activity. This allowed us to pinpoint trees on which murrelets landed. Nest searches began 105–120 min before official sunrise and lasted about 2 hr. Nest searches were occasionally conducted around dusk (beginning about 30 min prior to official sunset). In addition to visual observations of murrelets flying below the forest canopy, we listened for murrelets landing in or leaving trees, or vocalizing from or near branches. During nest searches we recorded the following each time a murrelet(s) came to within 100 m of observers: time, number of murrelets, direction and nearest distance relative to the observer, behaviors, and vocalizations. Nests were confirmed by visual observation from the ground, by viewing the nest from an elevated vantage point in a nearby tree, or by climbing the tree and documenting the nest cup after nesting activity had ceased. A variation of the nest-search technique was used where observers conducting dawn surveys (Paton et al. 1990) of murrelets were trained to distinguish behaviors that indicated nesting (see above). When these behaviors were recorded, the observer visually searched possible nest trees from the ground for signs of nesting.

Nests were also located by climbing and searching potential nest trees in areas where eggshell fragments were found on the forest floor and in areas with high levels of murrelet activity. On Naked Island, we sometimes used night-viewing devices, video cameras, and audio-recording equipment directed at restricted portions of forest stands. Tapes were

evaluated later for signs (flights or calls) of nesting activity.

On Naked Island, most active nests were checked about 1–7 days/wk to ascertain the status of the nest and stage of breeding. In 1992, we periodically (1–8 times) checked 1991 nests and failed 1992 nests for signs of nesting or re-nesting. Nest checks were made from the ground and disturbance was minimized. In 1992, we climbed 1 of the 1991 nest trees to inspect the nest platform for signs of the prior year's nesting effort. We examined murrelet eggshell fragments found in or around nests for evidence of predation, including holes pecked by birds or tooth marks.

Characteristics of Nests and Nesting Habitat

Characteristics of nests, nest trees, and landing trees were collected using previously developed methods with some modifications (Singer et al. 1991, Kuletz et al. 1994). In addition, we quantified cover directly above nests by photographing the view up from nest cups, then determining the percentage of sky visible in each photograph.

In most cases, a circular (50-m radius) 'general vegetation plot' was established around each nest ($N = 10$) or landing ($N = 12$) tree and at forested sites ($N = 11$) where nest searches were conducted but nests were not found. In 2 instances, 2 adjacent landing or nest trees occurred within the same plot. The following data were collected in each plot: (1) tree species, diameter at breast height (dbh), vigor, top condition, number of potential nest platforms, and epiphyte (moss and lichen) cover on branches, for nest and landing trees and the 9 upper-canopy trees nearest them, (2) canopy closure (estimated visually) and canopy height (measured with a clinometer), (3) elevation, slope, and aspect, (4) presence and location of fresh water, and, (5) distance to salt water. Data from (1) were used for analyses of tree characteristics, whereas data from (2) through (5) were used to characterize habitat in the immediate vicinity of documented nest and landing trees. Vigor was classified as live, declining, or dead (Maser and Trappe 1984). Platforms were defined as any flat horizontal surface ≥ 15 cm in diameter (including moss) and > 10 m above the ground. Epiphyte cover was categorized as none, trace ($< 1\%$ cover), low (1–33%), moderate (34–66%), or high ($> 66\%$). Distance from salt water was determined from aerial photos and topographic maps. On Naked Island, we also recorded the presence or absence of epiphyte cover on platforms in 30 general vegetation plots and the degree of epiphyte cover on each platform at 22 plots.

We also collected data in a 'detailed vegetation plot' around each of 8 nest trees on Naked Island and at 1 nesting area on nearby Storey Island. In these plots, we recorded all trees ≥ 10 cm dbh and all snags in a 25-m radius circle (Singer et al. 1991). The approximate area of contiguous forest around each nest on Naked Island (*i.e.*, the area that contained only forest of tree-size and volume classes [m^3/ha] similar to the nest stand) was provided by the U.S. Forest Service (USFS, Anchorage, Alaska, unpubl. data; see Kuletz et al. 1995b).

Data Analyses

Possible differences between nest and landing tree characteristics (dbh, number of platforms, epiphyte cover) were examined. Data from general vegetation plots were used for 4 analyses: (1) to determine differences between trees used by murrelets and upper-canopy trees around them, (2) to examine relationships between tree characteristics, (3) to evaluate differences among tree species, and (4) to examine differences among trees on the 3 islands. For analysis (1), trees were grouped into 4 categories: nest trees, the 9 upper-canopy trees adjacent to nest trees, landing trees, and the 9 upper-canopy trees adjacent to landing trees. This allowed us to examine which tree characteristics murrelets might use as criteria for choosing a specific tree from among a small group of trees within a stand. We also examined each nest tree relative to the trees around it using data from general vegetation plots to further evaluate characteristics murrelets might prefer in a given group of trees. We analyzed data from general vegetation plots around nest and landing trees on Naked Island separately from Kodiak and Afognak islands because the 2 areas were quite different and because sample sizes for Kodiak and Afognak were too small for many analyses.

Data from detailed vegetation plots on Naked Island were used to calculate basal area and frequency of tree species around nest trees. To better understand tree characteristics and how forest stands differed between the 2 areas, we combined all trees in general vegetation plots at 26 forested sites ($N = 260$) on Naked Island and at 12 sites ($N = 117$) on Kodiak and Afognak islands.

To test for differences among means of continuous variables (dbh, number of platforms), we computed an F-statistic to test for equality of variances. We then computed t-statistics when variances were equal and approximate t-statistics when variances were unequal (TTEST, SAS Institute Inc. 1988b). We used Tukey-Kramer's studentized range test to test for differences among means of continuous variables (GLM, SAS Institute Inc. 1988b). To test for relationships between dbh and the number of platforms on a tree, we used Pearson product-moment correlation (CORR, SAS Institute Inc. 1988a). We used Pearson chi-square statistic and Fisher's exact test (when over 50% of cells had expected counts of <5; FREQ, SAS Institute Inc. 1988b) to test for relationships between categorical variables (epiphyte cover, tree species, presence of moss, presence of a platform with mod-

TABLE 1. Status of marbled murrelet tree nests found on Naked (N1–N10), Kodiak (K11–K12), and Afognak (A13–A14) islands, Alaska, in 1991 and 1992.

Nest no.	Date found	Date egg laid	Date chick hatched	Fate
N1	13 June 1991	<13 June 1991		failed during incubation (predation?)
N2	25 June 1991	<25 June 1991		failed during incubation
N3	6 July 1991	ca. 15 June 1991	ca. 15 July 1991	chick died ca. 7/17/91
N4	26 July 1991	<9 July 1991		failed during incubation (abandoned?)
N5[a]	1 July 1991	unknown		unknown
N6	25 May 1992	ca. 25 May 1992		failed during incubation (abandoned?)
N7	20 July 1992	<17 July 1992		abandoned during incubation
N8	5 August 1992	<17 June 1992		failed during incubation
N9[a]	6 August 1992	unknown		unknown
N10[a]	9 June 1991	unknown		unknown
K11	17 August 1992	<5 June 1992	<5 July 1992	chick hatched, fate unknown
K12	17 August 1992	ca. 26 May 1992		unknown
A13[a]	26 July 1992	unknown		unknown
A14	6 August 1992	unknown		unknown

[a] Tree with nest cup only. Pairs of birds were active at these sites but the stage or status of nests was not determined.

erate or heavy moss cover). The number of platforms per tree was square-root transformed for analysis because these data were highly skewed.

RESULTS

Nests and Reproductive Success

We located 14 murrelet tree nests on Naked, Kodiak, and Afognak islands (Table 1). Based on behaviors (see below) observed at 7 nest cups where nesting status was not known and on the similarity of these nest cups to known active nests (Singer et al. 1994, Grenier and Nelson 1995, this study), we considered all nest cups to have been active at some time. We also documented a probable nest area on Storey Island (adjacent to Naked Island) where a male murrelet with a brood patch was killed by a sharp-shinned hawk (*Accipiter striatus;* Marks and Naslund 1994). The Storey Island nest was not found.

All nests were situated on large moss- or moss- and lichen-covered platforms in relatively large (≥ 30 cm dbh) old-growth conifers (Table 2). The 10 nests on Naked Island were located in 5 different stands (Table 2). Two nest trees (2 and 4) were about 10 m apart and 2 others (11 and 12) were within 50 m of each other. Nest cups contained intact or broken eggs or eggshell fragments, droppings, or apparently natural accumulations of debris (pieces of moss and lichen, needles, bark flakes, and decomposing twigs; Table 3). Nests were located throughout the live crowns of trees (Table 2). The only exception was a nest (10), which was located at the top of a broken tree bole where 5 branches had grown upwards, forming a wide platform at their base. Each nest platform supported a moderate-to-heavy growth of epiphyte cover. Nest substrate included *Antitrichia curtipendula, Dicranum* sp., *Sphaerophorus globosus,* and *Ptilidium* sp. *Dicranum fuscescens, Alectoria sarmentosa, Bryoria* sp., *Hypogymnia* sp., *Cladonia* sp., *Lobaria* sp., *Parmelia saxatilis, Peltigera aphthosa,* and *Platismatia norvegica* occurred elsewhere on nest and landing trees. Cover above 8 nests was 81–95% (Table 3).

There was no indication that 1991 nests were reused in 1992, although nest checks were not made frequently enough to exclude the possibility that murrelets nested and failed between visits. Furthermore, there was no evidence of re-nesting at failed 1992 nests. In 1992, there was no sign of a nest cup depression, droppings, or eggshell fragments at nest 3 (that had been active in 1991).

Murrelets were in the incubation stage of nesting at 6 sites when discovered (nests 1, 2, 3, 6, 7, 8; Table 1). One nest (4) was confirmed after it had been abandoned and the egg was still present. At 7 sites, pairs of birds were active, but the stage of nesting was not determined. At 6 of these nests (nests 5, 10, 11, 12, 13, 14), murrelets landed, displayed, or copulated on a branch where a nest cup was later documented. The contents (*e.g.*, eggshell fragments, yolk) of 2 of these nests confirmed nesting activity (Table 3). Murrelets displayed typical flight behaviors associated with nesting in

TABLE 2. Characteristics of marbled murrelet nest trees and branches found on Naked (N1–N10), Kodiak (K11–K12), and Afognak (A13–A14) islands, Alaska, in 1991 and 1992.

	Tree characteristics				Branch characteristics				
Nest no.[a]	Species	dbh (cm)	Height (m)	Condition	Height (m)	Diameter at bole (cm)	Diameter at nest (cm)	Position in crown	Condition
N1(1)	Western hemlock	30	21	declining	9.7	16.2	16.2	lower ⅓	both live, dying ends
N2 (2)	Mountain hemlock	49	20	declining	15.6	10.5	22.3	middle	live, healthy
N3 (1)	Western hemlock	76	22	declining	17.4	14.6	16.6	upper ¼	live, healthy
N4 (2)	Mountain hemlock	71	30	dead	13.3	22.3	20.4	lower ¼	dead
N5 (1)	Mountain hemlock	49	ca. 20	declining	15.4	11.8	11.8	upper ⅓	live, split
N6 (1)	Mountain hemlock	48	16	declining	10.5	27.1	27.1	middle ⅓	mostly live
N7 (3)	Sitka spruce	72	30	healthy	15.0	12.7		lower ¼	live, split
N8 (4)	Mountain hemlock	60	22	declining	14.8	14.3	14.3	middle	live
N9 (5)	Mountain hemlock	45	20	healthy	9.6	19.4	18.8	lower ½	live, healthy
N10 (4)	Mountain hemlock	65	25	declining	13.3			upper ¼	5 live ● broken top
K11 (6)	Sitka spruce	61	27	healthy	12.5	14.6	20.4	middle	live
K12 (6)	Sitka spruce	65	27	healthy	15.4	13.4[b]	28.3	lower ½	live
A13	Sitka spruce	90	26	healthy	13.7			middle	live
A14	Sitka spruce	104	21	declining	12.4	8.9	18.4	middle	live, split

[a] Nests with the same number indicate nests found in the same forest stand.
[b] Includes two branches.

TABLE 3. Characteristics of marbled murrelet nests found on Naked (N1–N10), Kodiak (K11–K12), and Afognak (A13–A14) islands, Alaska, in 1991 and 1992.

Nest no.	Nest characteristics: Distance to bole (cm)	Nest cup dimensions (cm)	Nest cup depth (cm)	Depth of moss: Nest (cm)	Depth of moss: Elsewhere (cm)	Substrate[a] (cm)	Overhead cover at nest (%)	Nest cup contents[b]
N1	14	15 × 15[c]	5[c]	3.3	5.3	moss & lichen	91	feather[e]
N2	32	8 × 9	4	3.5	7.0	moss & lichen	82	feather
N3	135	13 × 7	4	2.0	3.0	moss & lichen	≥68[d]	droppings, eggshell[e]
N4	138	none	none	5.0	4.0	moss	ca. 25	none[e]
N5	74	8 × 8			2.5	moss & lichen	93	none
N6	3	11 × 9	6	3.5	5.0	moss & lichen	89	broken egg
N7	224	9 × 8	7	2.5	1.5–5.0	moss & lichen	95	intact egg
N8	6	14 × 10	4	4.0	10.0	moss & lichen	91	feather[e]
N9	3	9 × 8	2	6.0	3.0	moss & lichen	94	none[e]
N10	0	10 × 10	4	6.0	8.0	moss	81	none
K11	23	9 × 10	4	2.5	5.7	moss & lichen		eggshell, droppings[e]
K12	101	10 × 10	5	3.2	6.0	moss		[e]
A13						moss		none
A14	61		5	5.1	2.5	moss		yolk?[f]

[a] Cover on branch or platform.
[b] Includes only material related to nesting activity.
[c] Approximate because nest cup was partially destroyed prior to taking measurements.
[d] Measurement taken near nest.
[e] Eggshell fragments found on ground nearby.
[f] Droppings and feather on branch below nest.

TABLE 4. Characteristics of nest trees and the 9 closest upper-canopy trees around them (N other), and landing trees and the 9 closest upper-canopy trees around them (L other), on Naked, Kodiak, and Afognak islands, Alaska, in 1992.

Island and tree category	dbh (cm)		No. platforms		Moderate/high cover[a]		Mossy platform[b]	
	$\bar{x} \pm$ SE	*N*	$\bar{x} \pm$ SE	*N*	(%)	*N*	(%)	*N*
Naked								
Nest trees	54 ± 4.5	9	8 ± 1.3*	9	100*	9	100**	6
N other	47 ± 1.9	81	4 ± 0.8*	81	54*	81	41**	54
Landing trees	70 ± 9.5	8	8 ± 1.4**	8	63	8	67	6
L other	49 ± 1.6	72	4 ± 0.5**	72	39	72	48	54
Kodiak & Afognak								
Nest trees	65	1	18	1	100	1		
N other	67 ± 4.4	9	17 ± 2.7	9	89	9		
Landing trees	66 ± 9.7	4	8 ± 1.5	4	75	4		
L other	60 ± 2.7	36	10 ± 1.8	36	56	36		

[a] Moderate/high cover = trees with ≥34% epiphyte cover on branches.
[b] Mossy platform = at least one platform with moderate or heavy epiphyte cover was present.
* $p < 0.05$, ** $p < 0.01$.

the vicinity of 1 nest tree (nest 9), but were not seen on or around the nest branch.

Two nests reached the chick stage. The nestling disappeared when only a few days old at 1 nest and the fate of the other nestling was unknown. All nests where reproductive success was known ($N = 7$) failed (Table 1). Circumstantial evidence (eggshell fragments with holes believed to have been made by Steller's jays [*Cyanocitta stelleri*]) suggest that predation was a factor in nest failure. However, it appeared that in at least 2 cases, Steller's jays may have gained access to eggs after nests had already been abandoned.

Landing Platforms

We documented 21 trees (9, 6, and 6 on Naked, Kodiak, and Afognak islands, respectively) where murrelets landed on branches but where no nests were found. Fifteen of these trees were not climbed, although flight behaviors and calls at some indicated that they may have contained nests. Nests were not found in the other 6. However, 4 of these 6 had potential nest platforms that were impossible to view or trees were not climbed until the year following their discovery, when nest cups may no longer have been visible (see above). All landing trees on Naked Island and 6 on Kodiak Island were located within 200 m of a known nest tree.

Landing platforms were located throughout the live crowns of healthy ($N = 10$) and declining ($N = 9$) trees (no data for 2 trees) and the majority supported moderate or heavy epiphyte cover. The diameters of 3 landing platforms were 14, 24, and 72 cm. At least 4 landing platforms were used repeatedly and in consecutive years, including 1 that was used in 1991 and subsequently supported a nest in 1992 (nest 6). One landing platform contained a slight depression and worn spot in 1992. Murrelets were active on this branch during both 1991 and 1992, and the depression may have indicated a nesting attempt.

Characteristics of Trees Used on Naked Island

Most nest trees were approximately 5–10 m shorter than the surrounding canopy, whereas 3 nest trees were among the tallest trees in the surrounding canopy. Nest and landing trees did not differ with respect to dbh ($t = 1.309$, df $= 11.2$, $p = 0.217$), number of platforms ($t = -0.324$, df $= 16$, $p = 0.750$), epiphyte cover ($\chi^2 = 3.600$, $p = 0.300$), or species ($\chi^2 = 0.693$, $p = 1.000$). Although nest and landing trees tended to be larger in diameter than the other upper-canopy trees around them, differences were not significant ($t = -1.197$, df $= 88$, $p = 0.235$ for nest plots; $t = -2.118$, df $= 7.4$, $p = 0.070$ for landing plots; Table 4). Comparable trends occurred within individual plots. Seven of 9 nest trees and 6 of 8 landing trees were larger in diameter than the mean dbh of the 9 closest upper-canopy trees in each general vegetation plot (Fig. 2). When compared with all trees ≥ 10 cm dbh measured in detailed vegetation plots around nests ($N = 8$), 50%, 75%, and 100% of nest trees had diameters in the upper 5, 10,

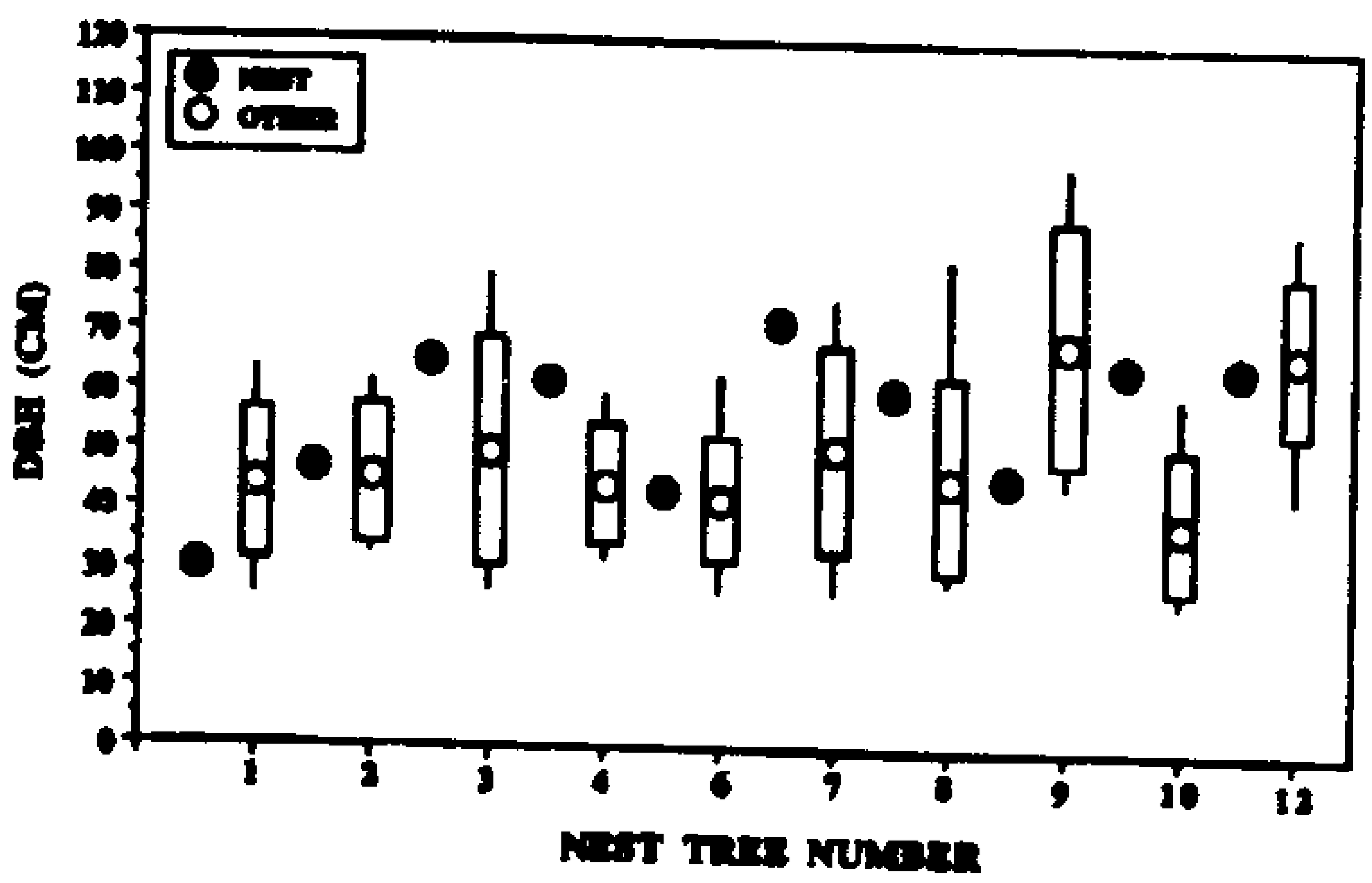

FIGURE 2. Diameter at breast height (dbh) of nest trees relative to the mean dbh of the 9 closest upper-canopy trees (other) around each at general vegetation plots on Naked (nests 1–10) and Kodiak (nest 12) islands. Means (open circles) ± standard deviations (boxes) and ranges (lines) are shown.

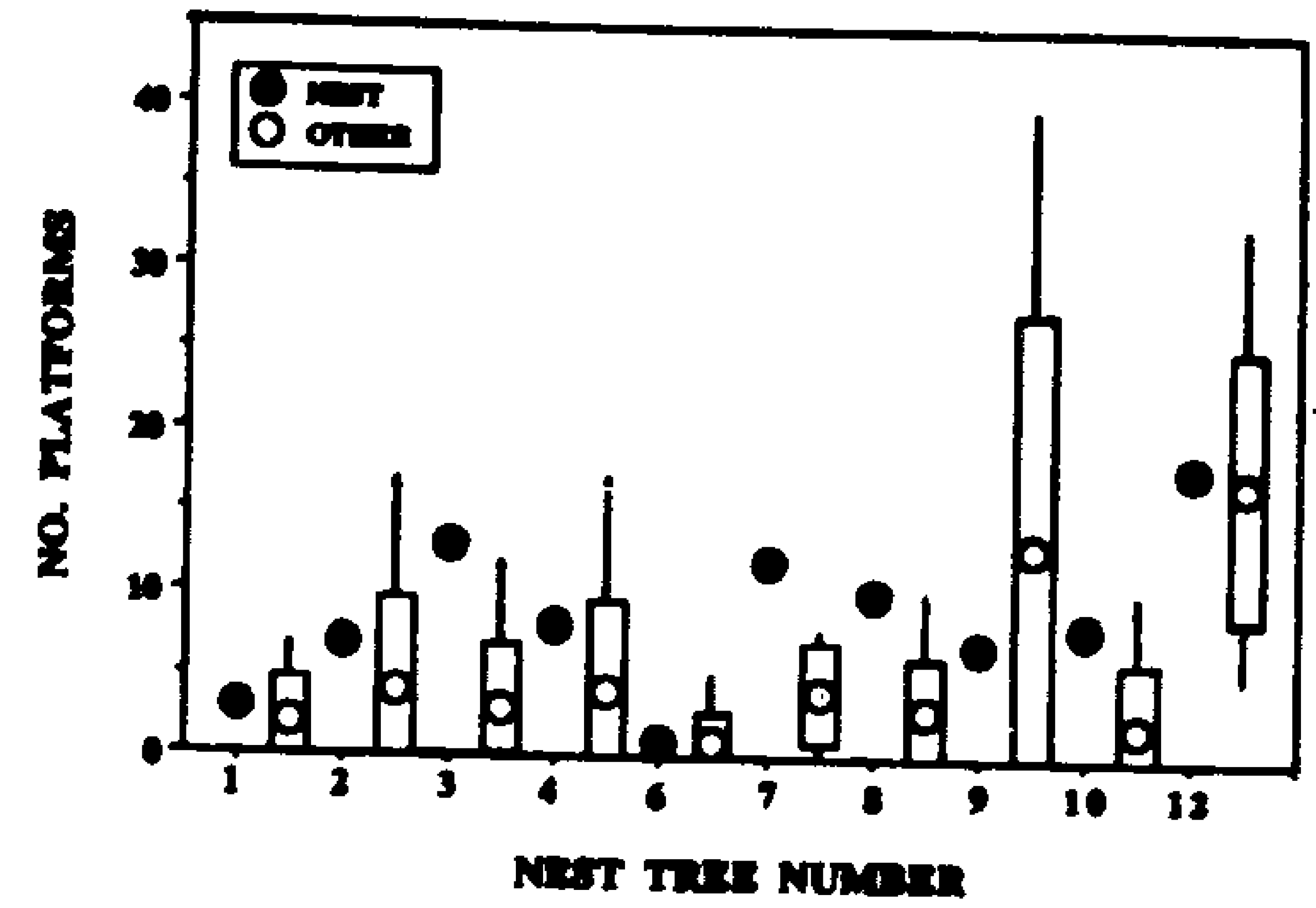

FIGURE 3. Number of platforms on nest trees relative to the number of platforms on the 9 closest upper-canopy trees (other) around each at general vegetation plots on Naked (nests 1–10) and Kodiak (nest 12) islands. Means (open circles) ± standard deviations (boxes) and ranges (lines) are shown.

and 25 percentiles, respectively. Core samples at nests 2 and 4 showed that these nest trees were about 424 and 495 years old, respectively. Core samples from other forested areas on Naked Island indicated that most trees ≥ 30 cm dbh were ≥200 years old (U. S. Forest Service, Anchorage, Alaska, unpubl. data).

Nest and landing trees had more platforms than surrounding trees ($t = -2.219$, df = 88, $p = 0.029$ for nest plots; $t = -2.867$, df = 78, $p = 0.005$ for landing plots; Table 4). Within individual plots, 7 of 9 nest trees and 6 of 8 landing trees had more platforms than the mean value of the 9 closest upper-canopy trees around them (Fig. 3). Nest trees had higher levels of epiphyte cover than the trees around them ($\chi^2 = 7.193$, df = 3, $p = 0.037$; Table 4). High levels of epiphyte cover occurred more frequently and low levels occurred less frequently than expected on nest trees; this accounted for 90% of the chi-square value. Landing trees followed a similar trend but this was not significant ($\chi^2 = 3.048$, df = 3, $p = 0.379$; Table 4). When compared with nearby upper-canopy trees, nest trees were more likely to contain at least 1 platform with moderate or heavy epiphyte cover ($\chi^2 = 7.619$, df = 1, $p = 0.008$; Table 4). This tendency did not hold for landing trees ($\chi^2 = 0.741$, df = 1, $p = 0.671$). Of the 3 conifer species available, mountain hemlocks were most frequently used as nest and landing trees, but this was different only for landing trees ($\chi^2 = 2.703$, $p = 0.345$ for nest trees; $\chi^2 = 9.508$, $p = 0.009$ for landing trees).

Characteristics of Trees Used on Kodiak and Afognak Islands

The surrounding canopy was about 2–6 m taller than 2 of the 4 Kodiak and Afognak island nest trees, but 2 nest trees were among the tallest in the area. Nest trees were relatively large in diameter (Table 2), contained a high number of platforms (range = 8–26), and had moderate or high epiphyte cover ($N = 3$, no data for 1 tree). Similarly, landing trees ($N = 9$) were 22–96 cm dbh, had 5–25 platforms, and 7 trees supported moderate or high epiphyte cover. Landing trees were not different from the trees around them with regards to dbh ($t = -0.551$, df = 38, $p = 0.531$), number of platforms ($t = -0.039$, df = 38, $p = 0.969$), or epiphyte cover ($\chi^2 = 1.310$, df = 3, $p = 0.735$; Table 4). Landing trees used by murrelets were larger than the mean dbh of surrounding trees at all sites where general vegetation plots were conducted ($N = 4$).

Nest trees on Kodiak and Afognak islands were larger ($t = 2.968$, df = 12, $p = 0.012$) and had more platforms ($t = 3.222$, df = 12, $p = 0.007$) than Naked Island nest trees (Table 5). Characteristics of landing trees on the 3 islands exhibited similar differences between island groups, but these differences were not significant (all $p > 0.05$).

Association of Tree Characteristics

The number of platforms on trees was positively correlated with dbh ($r = 0.686$, p =

TABLE 5. Tree characteristics of nest and landing trees, on Naked, Kodiak, and Afognak islands, Alaska, in 1992.

Tree category and island	dbh		No. platforms		Moderate/high cover[a]	
	$\bar{x}$ (cm) ± SE	*N*	$\bar{x}$ ± SE	*N*	(%)	*N*
Nest trees						
Naked	54 ± 4.1*	10	7 ± 1.3**	10	100	10
Kodiak & Afognak	81 ± 10.2*	4	17 ± 3.5**	4	100	3
Landing trees						
Naked	67 ± 8.5	10	7 ± 1.3	10	67	9
Kodiak & Afognak	74 ± 6.9	6	15 ± 2.9	6	100	6

[a] Moderate/high cover = trees with ≥34% epiphyte cover on branches.
* $p < 0.05$, ** $p < 0.01$.

0.0001 for Naked Island; $r = 0.452$, $p = 0.0001$ for Kodiak and Afognak islands; Fig. 4). The minimum dbh associated with a tree having at least 1 platform was 29 to 37 cm, therefore old-growth (see above), depending on island (Fig. 4). On Naked Island, mean dbh of trees with moderate ($\bar{x}$ = 59 cm) and high ($\bar{x}$ = 54 cm) epiphyte cover was higher than trees with low or trace ($\bar{x}$ = 42 cm) and no ($\bar{x}$ = 40 cm) epiphyte cover, but these differences were not significant (df = 254, $p > 0.05$). On Kodiak and Afognak islands, mean dbh of trees with moderate ($\bar{x}$ = 65 cm), low ($\bar{x}$ = 64), and high ($\bar{x}$ = 61 cm) epiphyte cover was higher than trees with trace ($\bar{x}$ = 48 cm) epiphyte cover (df = 113, $p < 0.05$).

Differences Between Tree Species on Naked Island

Tree characteristics varied among species (Table 6). Sitka spruce typically had the highest epiphyte cover ($\chi^2 = 30.894$, df = 6, $p < 0.0001$)

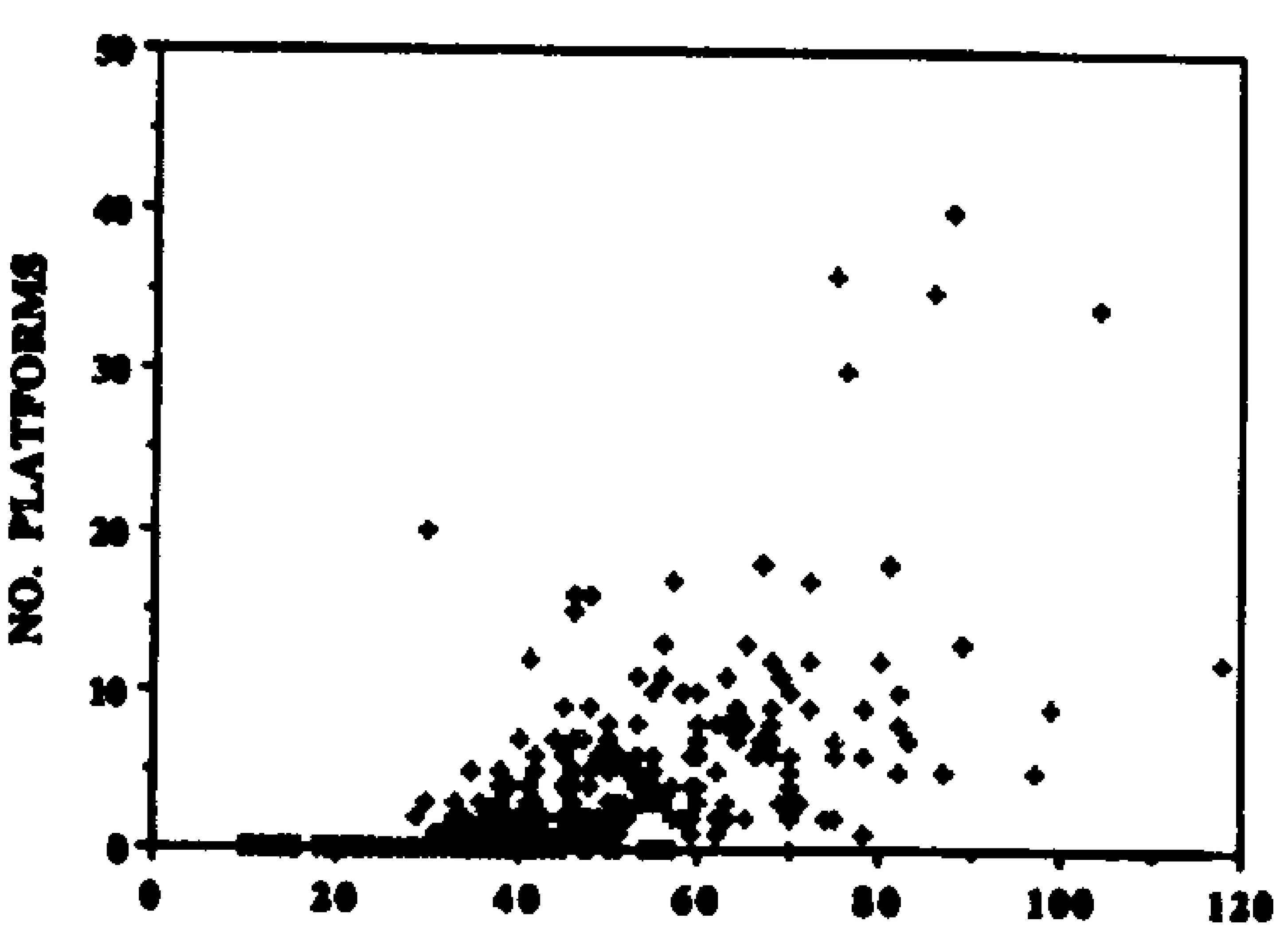

FIGURE 4. Number of platforms versus dbh of 260 trees measured in 26 general vegetation plots on Naked Island, in 1992. Pearson's $r = 0.686$, $p = 0.0001$.

and greatest number of platforms (df = 254, $p < 0.05$), followed by mountain hemlock and western hemlock. Of upper-canopy trees for which the presence or absence of moss on platforms was recorded (N = 197), the mean percent of platforms with moss per tree was 84%, 90%, and 92% for mountain hemlock, western hemlock, and Sitka spruce, respectively. However, of 122 trees for which the degree of epiphyte cover (none, trace, low, moderate, heavy) was recorded for each platform, the presence of 1 or more platforms with moderate or heavy epiphyte cover differed significantly among species ($\chi^2 = 15.419$, df = 2, $p < 0.0001$; Table 6). Sitka spruce had more platforms and western hemlock had fewer platforms with moderate or heavy cover than expected, comprising 98% of the Chi-square value. Mean dbh of trees with or without such a platform did not differ for all species combined ($t = -0.975$, df = 120, $p = 0.332$) or within each species ($t = -1.256$, df = 50, $p = 0.215$ for mountain hemlock, $t = -0.078$, df = 41, $p = 0.938$ for western hemlock, $t = -0.003$, df = 25, $p = 0.998$ for Sitka spruce).

Mean dbh of all upper-canopy trees did not differ significantly among species (df = 254, $p > 0.05$; Table 6). However, when including all trees with dbh ≥ 10 cm (from detailed vegetation plots), Sitka spruce had the largest mean dbh at 4 of 8 nest sites on Naked and Storey islands (Table 7).

Habitat Features of Stands Containing Nest and Landing Trees

All trees used by murrelets on Naked Island were located in large tree-size class (> 28 cm dbh) and high-volume class (1883–5649 m^3/ha) hemlock-spruce forests. Sizes of contiguous

TABLE 6. Tree characteristics of three species of conifers on Naked Island, Alaska, in 1992 (based on trees in general vegetation plots).

Species	Composition		dbh[a]		No. platforms[a]		Moderate/high cover[b]		Mossy platform[c]		dbh with MP		dbh without MP	
	(%)	N	$\bar{x}$ (cm) ± SE	N	$\bar{x}$ ± SE	N	(%)	N	(%)	N	$\bar{x}$ (cm) ± SE	N	$\bar{x}$ (cm) ± SE	N
Western hemlock	40	104	47^{d} ± 1.7	104	3^{e} ± 0.3	104	36	104	47*	43	54 ± 1.5	20	54 ± 1.9	23
Mountain hemlock	40	104	50^{d} ± 1.6	104	4^{e} ± 0.5	104	50	104	58*	52	58 ± 2.0	30	52 ± 1.5	22
Sitka spruce	20	52	51^{d} ± 2.2	52	6^{f} ± 1.1	52	75	52	93*	27	55 ± 2.5	25	55 ± 0.4	2

[a] Tukey-Kramer studentized range test; numbers with same letter not significantly different from each other; $p = 0.05$.
[b] Moderate/high cover = trees with ≥34% epiphyte cover on branches.
[c] Mossy platform (MP) = at least one platform with moderate or heavy epiphyte cover was present.
* $p < 0.0001$.

TABLE 7. Density and basal area of trees ≥10 cm diameter at breast height (dbh) in 25-m radius plots (N = 8) centered on 8 marbled murrelet nest trees on Naked Island, and 1 nest area on Storey Island, Alaska, in 1991 and 1992.

Species	Density (no./ha) $\bar{x}$ ± SE (range)	Basal area (m^2/ha) $\bar{x}$ ± SE (range)	Relative density (%) $\bar{x}$ ± SE (range)	Relative basal area (%) $\bar{x}$ ± SE (range)	Mean dbh (cm) $\bar{x}$ ± SE (range)
Western hemlock	275 ± 80.5 (15–693)	24 ± 5.9 (9–57)	37 ± 6.9 (4–71)	35 ± 5.5 (15–63)	34 ± 5.8 (24–73)
Mountain hemlock	216 ± 26.3 (87–306)	21 ± 3.0 (7–33)	37 ± 5.3 (9–61)	37 ± 5.7 (8–55)	31 ± 2.2 (23–40)
Sitka spruce	88 ± 17.2 (20–138)	10 ± 1.3 (5–15)	14 ± 2.6 (4–29)	16 ± 1.6 (7–22)	36 ± 3.6 (24–53)
Sitka alder	6 ± 3.6 (0–25)	1 ± 1.0 (0–8)	1 ± 0.8 (0–6)	2 ± 1.5 (0–12)	12 ± 1.2 (10–14)
Snag	64 ± 8.8 (20–92)	7 ± 1.0 (1–10)	11 ± 1.8 (5–18)	11 ± 1.1 (4–15)	33 ± 1.9 (27–42)
Total	649 ± 92.1 (391–1070)	62 ± 6.4 (34–89)	100	100	30 ± 1.5 (25–37)

TABLE 8. Habitat characteristics of marbled murrelet nest trees and stands found on Naked (N1–N10), Kodiak (K11–K12), and Afognak (A13–A14) islands, Alaska, in 1991 and 1992.

Nest no.	Tree			Stand						
	Nearest saltwater (m)	Nearest creek (m)	Approx. elev. (m)	Nearest saltwater (m)	Nearest creek (m)	Approx. elev. (m)	Aspect	Slope (%)	Canopy closure (ha)	Contiguous forest area (ha)
N1	375	150	115	200	0[a]	30–180	WNW	65	70	17.5
N2	250	200	100	10	0[a]	1–150	NW	60	75	62.6
N3	375	325	75	200	0[a]	30–180	WNW	70	85	17.5
N4	250	200	100	10	0[a]	1–150	NW	60	75	62.6
N5	510		100	200	0[a]	30–200	W	84	40	62.6
N6	280	5	75	200	0[a]	30–200	WNW	70	70	17.5
N7	105	75	70	0	0[a]	0–100	NW	84	75	60.7
N8	725	2	105	590	0[a]	120–150	WSW	47	60	3.6
N9	1040	10	260	920	0[a]	230–330	SSW	100	60	4.2
N10	620	10	100	590	0[a]	120–150	WSW	47	60	3.6
K11	800	30	65	0	0[a]	65	ENE		40	
K12	800	35	65	0	0[a]	65	N		40	
A13	1200	50	80	0	0[a]	80	WNW			
A14	400	1	30	0	0[a]	30	W			

[a] Creek runs through stand.

forest stands were 3.6–62.6 ha on Naked Island (Table 7). Similar data are not currently available for Kodiak and Afognak islands, though contiguous forest stands tend to be larger on these islands (pers. obs.). All nest stands contained creeks and most were near muskeg ponds (Table 8). Slopes were generally gradual or moderate, but were occasionally steep (0–100%; Table 8). Nest stands were located at heads of bays on slopes with aspects that tended to face towards the west (Table 8). On Naked Island, this distribution coincided with many of the available old-growth stands and much of our effort. However, this was not the case for Kodiak and Afognak islands where effort and old-growth habitat were more evenly distributed.

On Naked and Storey islands, tree coverage in nest stands (basal area) was 34–89 m^2/ha (Table 7). On average, hemlock species had similar high densities and basal areas, with Sitka spruce and snags comprising a smaller component of the landscape (Table 7). However, density and basal area of each conifer species at individual plots were extremely variable (Table 7). Mountain hemlock was the dominant species at 6 sites (nests 2, 4, 6, 7, 9, and nesting area), whereas western hemlock was the dominant species at 3 sites (nests 1, 3, 8). Dominant conifer species sometimes varied around nest trees within the same contiguous forest area (*i.e.,* nests 1, 3, and 6). Stands dominated by western hemlock occurred at low to moderate elevations (30–180 m), and mountain hemlock-dominant stands occurred at a wide range of elevations (0–330 m). Sitka spruce and snags were important components at all sites (relative coverage of 7–22% and 4–15%, respectively; Table 7). Patches of Sitka alder (*Alnus crispa sinuata*) occurred at 3 sites.

On Kodiak and Afognak islands, where all conifers were Sitka spruce, dbh of trees averaged 11 cm greater than those on Naked Island. Similarly, Kodiak and Afognak island trees had almost 3× as many platforms and greater epiphyte cover than trees on Naked Island.

Discussion

The 14 marbled murrelet tree nests on Naked, Kodiak, and Afognak islands comprise most of the tree nests (N = 17) found in Alaska through 1992. Furthermore, the 10 nests on Naked Island represent a relatively large sample of murrelet nests in a small area and approach a meaningful sample size for identification of suitable tree-nesting habitat in southcentral Alaska.

Nest trees on the 3 islands shared several characteristics with nest trees in other regions (Hamer and Nelson 1995a). Trees were relatively large, old conifers that contained broad moss-covered platforms. Furthermore, it ap-

pears that tree structure (*e.g.*, presence of a platform) is of greater importance than the actual size (dbh) of trees, as has been found elsewhere (Hamer 1995, Hamer and Nelson 1995). Nearby branches typically afforded cover above nests, thereby providing some degree of protection from inclement weather. These branches may also help murrelets avoid being detected by aerial predators (see also Nelson and Hamer 1995b). Sitka spruce trees more frequently possess characteristics that are important to nesting murrelets, including high epiphyte cover and many platforms with thick moss. In Washington State, Sitka spruce was also found to be the conifer species most likely to have characteristics suitable for nesting (Hamer 1995). Sitka spruce is the least-common conifer on Naked Island and this may partially account for its apparent rareness as a documented nest tree. Other factors that may be important for nesting (*e.g.*, foliage around the sides of nests) require further investigation.

Old-growth coniferous forests are an important habitat for marbled murrelets nesting in Alaska, as is true elsewhere in the murrelets' range (Ralph et al. 1995a). Nest trees on the 3 islands we studied were similar in size to the 3 other known tree nests in Alaska (120 cm dbh, Baranof Island, Quinlan and Hughes 1990; 74 cm dbh, Prince of Wales Island, M. Brown, pers. comm.; 64 cm dbh, Prince William Sound, D. Youkey, pers. comm.). Yet nest trees in Alaska were generally smaller than trees used in the southern portion of the murrelet's range (*i.e.*, south of Alaska), and basal area in nest stands was noticeably less. For example, nest trees in British Columbia south through California ranged from about 88 to 530 cm dbh, and basal area around nests was 3–9× higher than that found in our study (Singer et al. 1991, 1995; Hamer and Nelson 1995a). However, Naked Island nests were in the highest tree-volume and tree-size class forests in the study area, and among the highest in Prince William Sound (USFS, Anchorage , Alaska, unpubl. data).

Habitat characteristics at murrelet nests in southcentral Alaska corroborate results of other studies examining murrelet habitat use. Kuletz et al. (1995b) found that high levels of murrelet activity and nesting behavior were associated with high tree-size class forests in the Naked Island area. Similarly, high activity levels in western Prince William Sound were associated with forests where trees had more than 1 potential nest platform (Kuletz et al. 1994). In Washington State, characteristics of habitat where murrelets exhibited high levels of activity or nesting behavior included low-elevation (< 1067 m) old-growth forest, with relatively large trees and many potential nest platforms (Hamer 1995). Creeks or streams are common components in nesting habitat, and may serve as important flight corridors to nest sites (Hamer and Nelson 1995a, this study).

In the Pacific Northwest, the average nest-stand size was 206 ha (Hamer and Nelson 1995a). Paton and Ralph (1990) suggested a relationship between murrelet activity and stand size of inland sites in California, with the highest activity levels associated with stands ≥ 250 ha. This is in contrast to the relatively small stands of contiguous forest used by nesting murrelets on Naked Island. Murrelet use probably reflects features of the available habitat. For example, on Naked Island, small patches of high tree-size and volume-class forests are intermixed with areas of open muskeg as well as low tree-size and volume-class forests. Therefore, large contiguous stands are not generally available to murrelets on Naked Island.

Although all nests found in this study were on thick moss, nests on bare branches with layers of accumulated debris have been found elsewhere in the murrelet's range (Hamer and Nelson 1995a). This difference may be due to our limited sample size and that debris may not readily accumulate on platforms in Alaska due to harsh winter weather. Potential nest platforms without moss cover are common components of the forest structure in the study area (unpubl. data). Therefore, the use of moss-covered platforms may reflect a difference in murrelet nesting preferences in southcentral Alaska. In this area, breeding-season weather may include prolonged periods of torrential rain, strong winds (20+ knots), and near-freezing temperatures. Protection from inclement weather may be critical for egg and nestling survival. Nest insulation can be important for maintaining suitable nest temperatures during low ambient temperatures (Zann and Rossetto 1991). Thick moss cover may provide an important microclimate for eggs and nestlings by providing insulation and allowing only minimal accumulation of standing water. This may be particularly important to young nestlings,

which are typically left alone when only a few days old (Naslund 1993, Nelson and Hamer 1995a, Nelson and Peck 1995). Nest stands tended to face westward, thus minimizing exposure to prevailing weather systems, which further suggests that weather influences nest-site selection. Variable placement of murrelet nests within the canopy may also help maximize their protection from inclement weather. Positioning nests within the tree crown to maximize heat retention (in cold weather) or loss (in hot weather), or to minimize exposure to predators has been documented for other species, and may vary with nesting experience (Marzluff 1988; Zann and Rossetto 1991).

Our observations of murrelets using the same trees for landing or nesting in consecutive years suggests that murrelets exhibit some degree of site (or area) fidelity (also see Nelson and Peck 1995; Singer et al. 1995). Many alcids have high nest-site fidelity (Tuck 1960; Kuletz 1983; Murray et al. 1983; Nettleship and Birkhead 1985; Harris and Wanless 1989). The close proximity of landing and nest trees, and the 2 pairs of nests within 50 m of each other (nests 2 and 4, 11 and 12), supports other observations that murrelets may nest in groups within forest stands (Nelson and Peck 1995; T. Hamer, unpubl. data). However, on Naked Island, the timing of 1 nest pair (nests 2 and 4) implies that it may have been a 2nd nesting attempt by the same birds, rather than 2 pairs nesting in adjacent trees.

Marbled murrelets appeared to have low reproductive success on Naked Island, where at least 70% of the nests failed. This may partly reflect small sample size and may be biased because nests that are easiest to find may not be optimal nest sites. For example, a site with less foliage around the nest may be easier for observers to see and may also be more exposed to predators or inclement weather (see Nelson and Hamer 1995b). However, the general vicinities of nests were usually located first by sound, rather than visually, and the view of most nests was at least partially obscured from the ground. Low reproductive success was corroborated by the observation of relatively few juvenile murrelets around Naked Island during 1989–1991 and during mid-August 1992 (Kuletz et al. 1994; Kuletz, in press). This low number of juveniles may have been influenced by the *Exxon Valdez* oil spill or may reflect poor foraging conditions in Prince William Sound (Kuletz, in press; Piatt and Naslund 1995).

Predation appeared to be a factor in the reproductive success of murrelets in southcentral Alaska, as it is in other regions (Singer et al. 1991, Nelson and Hamer 1995b). Our presence around nests may have contributed to nesting failure, although our presence was minimal at 2 failed nests (*i.e.*, 1 visit to the area of nest 4, 3 pre-dawn surveys > 50 m from nest 8 when it was active), and nest 3 failed during a period when personnel were off the island for several days. Abandonment by some pairs on Naked Island suggests that the high failure rate that we observed may reflect poor environmental conditions during 1991 and 1992. Other seabirds, including some alcids, abandon nests during years of adverse environmental conditions (*e.g.*, poor food supply; Ainley and Boekelheide 1990). Evidence indicates a large-scale change in forage fish populations in the Gulf of Alaska that appears to have negatively affected productivity and populations of higher vertebrates that depend on them (Piatt and Anderson, in press; Piatt and Naslund 1995). Furthermore, the *Exxon Valdez* oil spill may have impacted forage fish populations in Prince William Sound (Kuletz, in press).

Components of old-growth forest appear to unite murrelet tree nests throughout the species' range. Forests in southcentral Alaska were generally comprised of trees that are smaller than those at more southern latitudes, yet nest-tree characteristics were similar between the 2 regions. It is evident that tree size alone does not predict the suitability of a nest tree and that a suite of tree characteristics (*e.g.*, age, size, species, presence of platforms, epiphyte cover) and physiographic features (*e.g.*, aspect, exposure) should be considered when evaluating potential nesting habitat for murrelets. Further comparison of nest-tree characteristics between tree species and geographical location may provide additional insight into murrelet habitat requirements. An evaluation of predator populations, habitat characteristics, and their effect on reproductive success will also be important for determining key attributes of murrelet nesting habitat.

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