MARBLED MURRELET ACTIVITY RELATIVE TO FOREST CHARACTERISTICS IN THE NAKED ISLAND AREA, PRINCE WILLIAM SOUND, ALASKA

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ABSTRACT—We studied dawn activity of marbled murrelets (*Brachyramphus marmoratus*) relative to forest characteristics in the Naked Island group in central Prince William Sound, Alaska, in 1991. The forests were old-growth stands of hemlock (*Tsuga mertensiana* and *T. heterophylla*) and Sitka spruce (*Picea sitchensis*). At 72 sites, murrelet activity ≤ 200 m from the observer differed significantly among 4 forest types defined by timber-type coverage on a geographic information system. The lowest detection rates (6.4 /site, SE = 2.4) occurred in forests with ≤ 28 cm diameter trees and < 1882 m^3/ha volume. The 3 forest types with average tree diameter > 28 cm varied in volume from low, moderate and high, and average detection rates in these were 17.6 (SE = 4.7), 24.6 (SE = 4.7), and 14.6 (SE = 4.4), respectively. Subcanopy flight behaviors that indicated nesting comprised 4% of detections, and were observed at 22% of the sites. Subcanopy flight behaviors were most frequent in high tree-size class (larger trees) and moderate-volume forests, and were positively correlated with on-site measurements of the diameter (dbh) of canopy trees. Our results suggest that in forested areas, old-growth forests with mean tree diameter > 46 cm dbh, especially inland of bays, provide important nesting habitat in Prince William Sound. The U.S. Forest Service timber database was a relatively useful tool for identifying potential nesting habitat in Prince William Sound.

The marbled murrelet (*Brachyramphus marmoratus*) is the most abundant seabird in Prince William Sound, Alaska, in summer (Isleib and Kessel 1973, Klosiewski and Laing 1994). Because murrelets were affected by the 1989 *Exxon Valdez* oil spill (Piatt et al. 1990; Ecological Consulting, Inc. 1991; Kuletz, in press), the acquisition of old-growth forests was proposed to aid natural recovery by protecting murrelet nesting habitat. However, old-growth forests had not been established as nesting habitat for murrelets in the spill zone. In southcentral Alaska, only ground and cavity nests had previously been found (Day et al. 1983; Johnston and Carter 1985). Prior to 1990, there had been no systematic inland surveys in southcentral Alaska to determine if murrelets occupied old-growth forests.

In California, Oregon and Washington, the highest murrelet activity levels (audio or visual observations of murrelets flying to or in nesting areas at dawn) have been found in coastal old-growth and mature forests. The features that separated high from low activity sites for a given study were stands > 200 yr in age, with trees averaging > 86 cm in diameter in California (Paton and Ralph 1990, Miller and Ralph 1995), > 100 yr old and > 82 cm diameter in Oregon (Nelson et al. 1992, Hamer and Nelson 1995a) and > 134 cm in Washington (Hamer 1995, Hamer and Nelson 1995a). In British Columbia, the highest activity levels were found in old-growth forests > 140 yr in age with mean tree diameters of 141 cm (Rodway et al. 1992). Subcanopy flight behaviors, indicative of murrelet nesting, occurred in stands with average tree diameters of > 53 cm in Oregon (Grenier and Nelson 1995) and >82 cm in Washington (Hamer 1995). Southcentral Alaska has a low percentage of trees in the size ranges reported in these studies. Prince William Sound is the northern boundary of the north temperate rainforest. Here trees tend to be smaller and are species typically found in poor soils or at high elevations in lower latitudes (Viereck and Little 1972).

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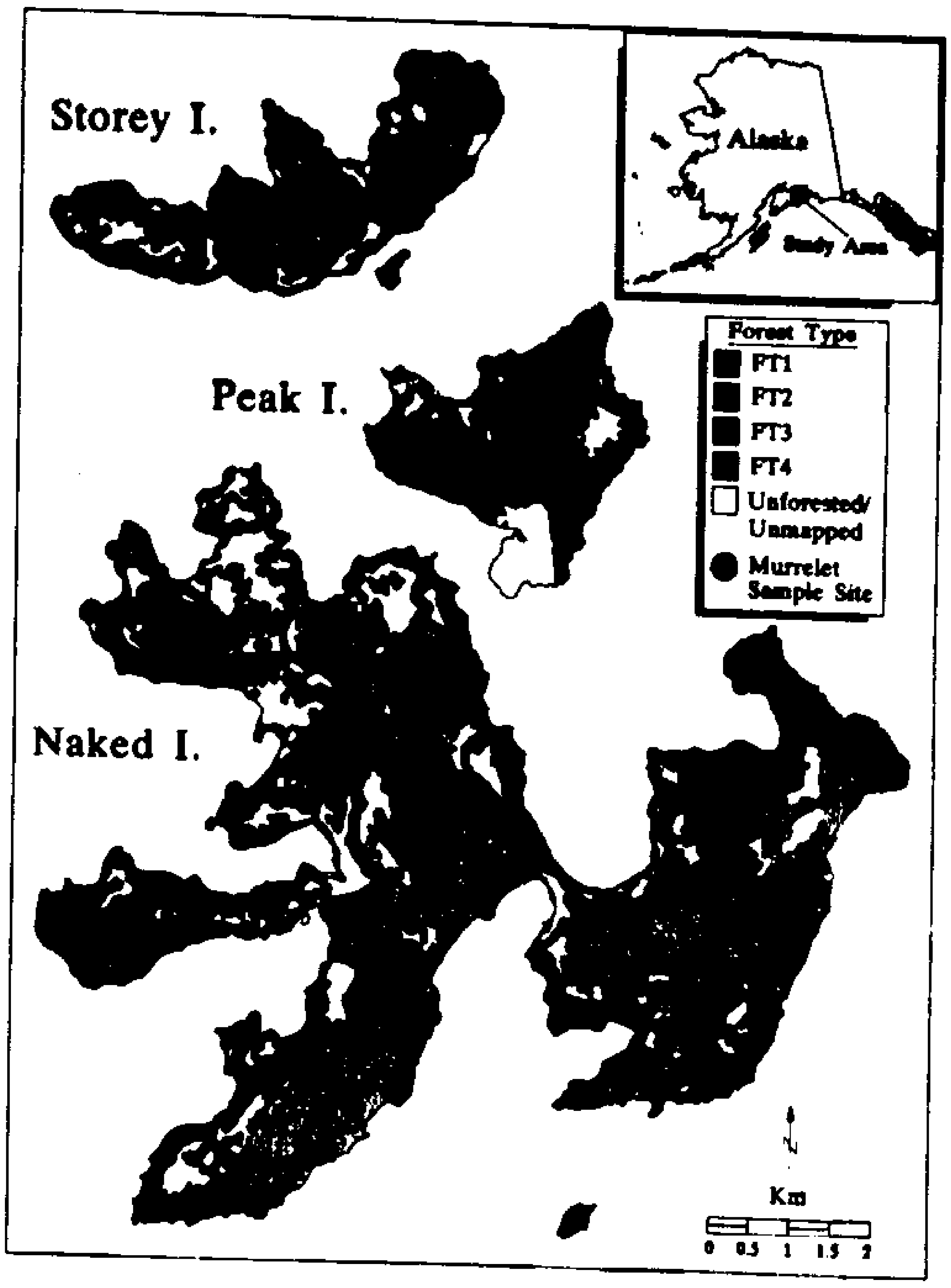

FIGURE 1. The 1991 habitat study areas at Naked, Storey and Peak islands, Prince William Sound, Alaska. Habitat polygons were derived from Chugach National Forest timber data. Forest types (FT1–FT4) are described in Table 1. Murrelet dawn activity was surveyed at 72 randomly selected sites (black circles).

Our goal was to determine if old-growth forests in the spill zone were occupied by marbled murrelets, and to identify forests that had a high probability of providing nesting habitat. This study was our first attempt to test for differences in murrelet activity among forest types in Alaska using existing timber data. Additional work, which included unforested areas, is presented in Marks et al. (1995) and Kuletz et al. (1995a).

METHODS

Study Area

The study area included Naked, Storey and Peak islands in central Prince William Sound, Alaska (Fig. 1). The highest peak is 460 m, and the topography is irregular, producing a variety of forested slopes. No point of land is more than 1.2 km from salt water. The islands are forested to their summits and have never been logged. Forests consist of mountain hemlock (*Tsuga mertensiana*), western hemlock (*T. heterophylla*) and Sitka spruce (*Picea sitchensis*) interspersed with muskeg. The Chugach National Forest timber type database (U. S. Forest Service [USFS], Anchorage, Alaska, ARC/INFO data files) show the islands as 87% forested (at least 10% of area covered by trees), including 27% productive forest (capable of producing harvestable wood). Based on definitions from the timber database, 14% of the stands are primarily saplings < 11.9 cm diameter at breast height (dbh), 24% are 12–28 cm dbh, 2% are > 28 cm and < 150 yr old, and 60% are > 28 cm dbh and > 150 yr old. Tree-core samples taken by the USFS in 1991 showed that dominant canopy trees were 200–495+ yr old (USFS, Anchorage, Alaska, unpubl. data).

TABLE 1. Description of forest types used in the 1991 murrelet nesting habitat study at Naked Island, Prince William Sound, Alaska. The timber type codes and criteria are from the Chugach National Forest Data Dictionary (Anchorage).

Forest type	Timber type codes: Tree size class	Timber type codes: Volume class	Timber type criteria: Tree dbh and age (based on tree class)	Timber type criteria: Net m^3/ha wood (based on volume class)
FT1	1 & 2	1 & 2	≤28 cm <150 yr	0–1882
FT2	3 & 4[a]	1 & 2	>28 cm >150 yr	0–1882
FT3	3 & 4[a]	3	>28 cm >150 yr	1883–3765
FT4	3 & 4[a]	4	>28 cm >150 yr	3766–5648

[a] Tree-size class 3 includes young trees <150 yr old, but due to slow tree growth-rates in the study area, most trees >28 cm dbh were >150 yr old, and were old-growth trees.

Definition and Mapping of Forest Types

USFS timber data on volume and tree-size classes provided an *a priori* description of forest stands of different tree sizes and structure in the study area (the USFS term is 'stand size' class, but to eliminate confusion with area of stand, we use the term 'tree-size' class). Tree-size class categorized the stands by dominant canopy-tree diameter and age. Stand-volume class categorized stands by cubic meters of wood per ha. Both were derived from analysis of aerial photos of stand height and crown closure (Table 1). In general, higher volume indicated greater coverage by large trees, although a few large trees can be in a low-volume forest. We defined 4 forest types (Table 1) based on volume and size classes: (1) low-volume stands of small trees (FT1), (2) low-volume stands of large trees (FT2), (3) moderate-volume stands of large trees (FT3), and (4) high-volume stands of large trees (FT4). We did not sample the muskeg covering the remaining landscape, although it contained small islands of krummholz vegetation with short, open-canopied mountain hemlocks (Wertheim 1991).

The geographic information system (GIS) timber-type map produced by the USFS was derived from interpreted and ground-truthed color aerial photos (1:15,840 scale) taken in the 1970s. Minimum mapping size for forested polygons was 4 ha, and 2 ha for non-forested polygons (U.S. Forest Service 1975). Average polygon size as defined by the forest types was 50 ha (SE = 12). The polygons described by these forest types (Fig. 1) matched vegetation patterns we could discern on aerial photographs and in the field. On site, visual judgement of forest type differed from the timber-type classification at 15 of the 72 sites. However, we found no significant differences in on-site measurements (see below) between questioned and unquestioned sites within a forest type for average tree dbh, canopy height, canopy closure, or percentage of forested area. Therefore, we used the original timber-type classification for all analyses.

Selection of Survey Sites

We sampled the 4 forest types approximately equally, although they were not equally present on the islands. GIS analysis of the 4 timber types on the 3 islands showed coverage of 25% FT1, 37% FT2, 15% FT3, 10% FT4, and 13% unforested (primarily muskeg) or fresh water. We overlaid a 200 × 200 m grid on a habitat map and selected at random 20 sites in each forest type ($N = 80$ sites) (Fig. 1). We were able to survey 72 of these sites before mid-August.

We conducted surveys between 10 June and 11 August 1991. This period encompassed incubation through the nestling stage and avoided the abrupt decline in inland murrelet activity that occurs in mid-August (Kuletz et al. 1994, Naslund et al. 1995). Survey effort was distributed equally among the forest types throughout the season to minimize seasonal effects of murrelet activity level. We conducted 1 survey at each site to maximize sample size in each forest type. The observer located the site on a topographic map and aerial photograph and camped on site the evening before the survey. The location of each site was digitized into a GIS.

Habitat Characteristics of Forest Types

Vegetation was sampled within a 50-m radius of the center of each survey station. We measured dbh of the 10 nearest canopy trees and visually estimated overall canopy height, percentage canopy closure, and percentage of forested area. Slope grade, aspect and elevation were measured on site or taken from topographic maps. Distance from the ocean was measured from aerial photographs. Size of a contiguous stand of the same forest type was obtained using the GIS timber coverage. At 56 sites, we also recorded the presence or absence of moss on tree branches within the plot by visual inspection.

Based on our previous research (Kuletz, unpubl. data), we found that bays had higher levels of murrelet activity than did more exposed coasts, therefore, we classified sites as being near the head of a bay or on a more exposed coast. Bay sites ranged from 25–500 m inland, and were located in the watershed around the bay head. Of the 72 sites surveyed, 21 were categorized as bay heads, 33 as exposed coasts, and 18 sites fell into neither category; the latter were not included in the analysis of bay effects.

Murrelet Activity Levels

Murrelet activity was quantified using the intensive inventory (hereafter referred to as the 'dawn watch') as described in Paton et al. (1990), but modified for Alaska by beginning 105 min before, and lasting until 15 min after, sunrise, or 15 min after the last detection (whichever was later). Sunrise and sunset were obtained from the National Weather Service. The location of the observer during the dawn watch was the 'station'. The station was inside the forest stand, usually < 100 m from an edge, and the observer attempted to center the station under an opening in the canopy to facilitate visual observations. All observers were trained by experienced murrelet surveyors.

The basic unit of measure was the 'detection', defined as "the sighting or hearing of a single bird or a flock of birds" (Paton et al. 1990:2). Detections were recorded as audio, visual or both. Murrelet behavior was noted for each detection. Subcanopy flight behaviors included flying below canopy, emerging from or flying into trees, landing on a branch, or calling from a stationary point in the forest (Paton et al. 1990; 1993 Pacific Seabird Group (PSG) survey protocol, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA, unpubl. rep.). Other behaviors included direct flight above canopy, circling above canopy, flying over water only, and calling from the water only. The latter 2 categories referred to birds that never appeared to pass over land; because many of our sites were < 500 m from salt water, birds could be heard (and sometimes observed) calling from the water, which might be confused with detections of inland flights. Using landmarks for distance estimations, we scored detections as ≤ 200 m or > 200 m from the observer. Observations were recorded on audio tape and later transcribed to data forms and entered into a database.

Data Analysis

We tested for differences among the 4 forest types (FT1–FT4) with respect to continuous variables (distance to salt water, percentage of forested area, canopy closure, canopy height, tree diameter, slope

TABLE 2. Habitat features of the 4 forest types (described in Table 1) surveyed for murrelets in the Naked Island area, Prince William Sound, Alaska, in 1991, based on 72 randomly selected sites.

Forest type	N	Stand size[a] (ha) Mean ± SE	Slope[b] (%) Mean ± SE	Elevation[c] (m) Mean ± SE	Distance to sea (m)[d] Mean ± SE
FT1	18	94 (18)	26 (4)	120 (12)	464 (55)
FT2	18	477 (86)	27 (2)	74 (17)	273 (65)
FT3	17	47 (6)	38 (5)	65 (9)	132 (18)
FT4	19	51 (11)	54 (3)	119 (19)	294 (56)

Forest type	N	Tree dbh[e] (cm) Mean ± SE	N	Canopy height[f] (m) Mean ± SE	Canopy closure[g] (%) Mean ± SE	Forested area[h] of plot (%) Mean ± SE
FT1	18	25.4 (1.7)	15	11 (5)	30 (7)	53 (5)
FT2	18	34.2 (2.4)	16	24 (3)	60 (6)	75 (5)
FT3	17	45.3 (3.0)	15	33 (5)	80 (5)	97 (1)
FT4	19	45.7 (3.2)	16	34 (3)	76 (3)	83 (3)

[a] ANOVA; $F = 21.98$, df = 3,68, $p = 0.0001$. SNK; only FT2 is significantly different.
[b] ANOVA; $F = 8.18$, df = 3,68, $p = 0.0001$. SNK; only FT4 is significantly different.
[c] ANOVA; $F = 3.73$, df = 3,68, $p = 0.0150$. SNK; NS.
[d] ANOVA; $F = 6.46$, df = 3,68, $p = 0.0007$. SNK; only FT1 is significantly different.
[e] ANOVA; $F = 14.02$, df = 3,67, $p = 0.0001$. SNK; FT3 & FT4 not significantly different.
[f] ANOVA; $F = 10.39$, df = 3,59, $p = 0.0001$. SNK; only FT1 is significantly different.
[g] ANOVA; $F = 18.87$, df = 3,59, $p = 0.0001$. SNK; FT3 & FT4 not significantly different.
[h] ANOVA; $F = 20.15$, df = 3,59, $p = 0.0001$. SNK; FT2 & FT4 not significantly different.

grade, and elevation) measured on site, with ANOVA and Student-Newman-Keuls test for comparisons among means. We used Fisher's exact test to test for relationships between forest type and the presence or absence of moss on trees. A t-test was used to compare sites at bay heads and exposed sites for tree diameter, slope, elevation, distance to salt water, and stand size. For all tests, $p \leq 0.05$ was considered significant.

Murrelet activity levels were analyzed by the following categories: (1) total detections, *i.e.*, all detections over land and saltwater, at all distances, (2) circling, *i.e.*, detections of birds circling the area at all distances, (3) over station, *i.e.*, detections over land and ≤ 200 m from observer, and (4) subcanopy flight behaviors ≤ 200 m from observer. Sites were classified as occupied if at least 1 subcanopy flight behavior was recorded. We did not consider circling above canopy as an indicator of occupancy. 'Unknown status' refers to sites where no subcanopy flight behavior was observed, because a single visit was not sufficient to determine if a site was definitely unoccupied (1993 PSG survey protocol).

Murrelet activity levels among the 4 forest types were compared with one-way analysis of variance (ANOVA; procedure GLM, SAS Institute Inc. 1988a). Although the numbers of detections per site were skewed, sample sizes and variances were similar and samples were independent. Under these circumstances, the F-test is robust against departures from normality (Neter et al. 1990:623), so data were not transformed. Comparison among means was done with the Student-Newman-Keuls test. with $p < 0.05$ considered significant.

We tested for correlations between murrelet activity ≤ 200 m from the observer and habitat features measured on site by pooling all sites, regardless of forest type. We used the Kendall *tau-b* correlation to test the relationship between activity levels (detections per survey) and continuous variables (distance to salt water, percentage of forested area, canopy closure, canopy height, tree diameter, slope grade, and elevation). We used Fisher's exact test to analyze the relationship among activity levels and 2 categorical variables: slope aspect (divided into 4 quadrants: NE [0–90°], SE [91–180°], SW [181–225°] or NW [226–359°]) and the presence or absence of moss on tree branches at the site. We used a t-test on continuous habitat variables (or the Cochran and Cox approximation of the t-statistic if variances were unequal [SAS Institute Inc. 1988a]) to compare sites that were occupied to sites of unknown status, and between sites at bay heads and exposed sites.

RESULTS

Habitat Characteristics of Forest Types

All on-site measurements except elevation differed among the 4 forest types (Table 2). Average tree dbh increased from FT1 to FT4 forests, with no difference between FT3 and FT4 forests. Although FT2 forests were also classified as tree size class 3 and 4, the average tree

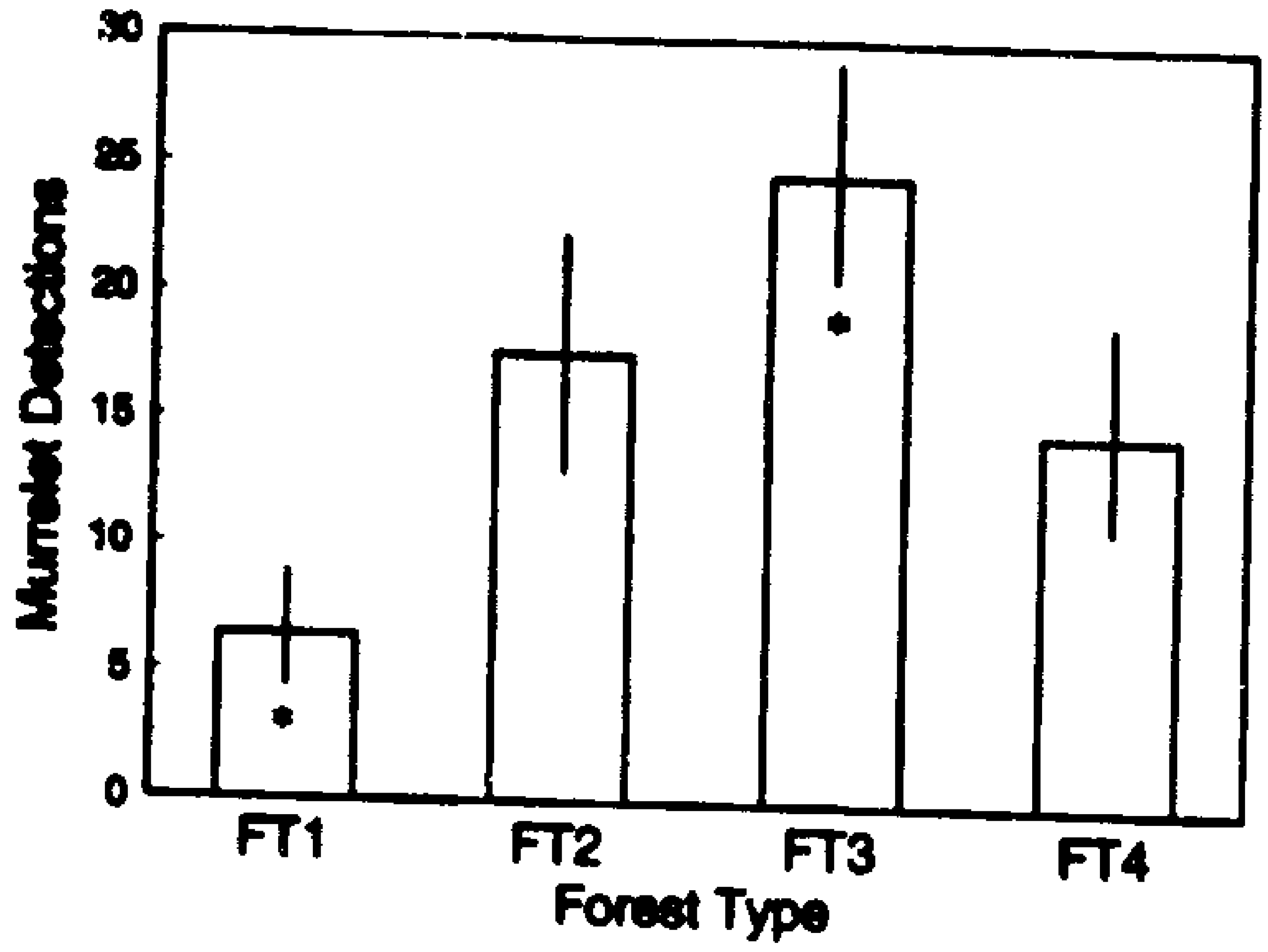

FIGURE 2. Average number of murrelet detections (± SE) ≤ 200 m from station center, among four forest types on Naked, Storey and Peak islands in 1991 (N = 72 sites). Forest types ranged from low volume and tree size (FT1) to high volume and tree size (FT4) (see Table 1). * indicates significant differences (ANOVA; F = 3.19, p = 0.03).

dbh was smaller than dbh in the higher volume FT3 and FT4 forests. FT1 forests had the lowest canopy height, canopy closure, percentage forested area and slope angle, and were farthest from salt water. The largest contiguous stands were FT2 forests. Moss was present on the trees at 11% of the FT1 sites (N = 13), 44% of FT2 sites (N = 13), 88% of FT3 sites (N = 16), and 68% of FT4 sites (N = 14).

We found no association between forest type and location relative to bay heads. The sites in bays did not differ from sites near exposed coasts for any on-site habitat measurement except distance to salt water (t = 2.6, df = 28, p = 0.0147); bay sites tended to be farther inland from salt water than the exposed sites ($\bar{x}$ = 302 m, SE = 49, and $\bar{x}$ = 163 m, SE = 23, respectively).

Murrelet Activity Among Four Forest Types

The number of murrelet detections ≤ 200 m of each station ranged from 0 to 71 ($\bar{x}$ = 15.6, SE = 2.2), and differed among forest types (F = 3.19, df = 3, 68, p = 0.0296; Fig. 2). FT3 forests had the highest and FT1 forests the lowest number of detections ≤ 200 m from the station. The total number of detections (at all distances) per dawn watch ranged from 0 to 140 ($\bar{x}$ = 35.9, SE = 3.7) and did not differ among forest types in audio, visual, or circling detections (Table 3). Fourteen sites (19%) had no detections ≤ 200 m from the station, including 3 sites with no detections at any distance. The number of subcanopy flight behaviors per dawn watch differed among forest types, with the highest observation rate in FT3 forests and the lowest in FT1 forests (Table 3).

Murrelet Activity and Site Characteristics

Among the continuous habitat variables, only the percentage of forested area in the vegetation plot was correlated with the number of detections ≤ 200 m from the station (Kendall's *tau-b* = 0.260, p = 0.0047). There were no significant correlations between the number of circling behaviors or subcanopy flight behaviors and the on-site measurements.

Sites with moss on the trees had higher numbers of detections ≤ 200 m from the station than did sites with no moss ($\bar{x}$ = 21.6, SE = 3.2; $\bar{x}$ = 7.1, SE = 2.1, respectively; t = −3.74, df = 53, p = 0.0009). Sites with moss also had higher numbers of subcanopy flight behaviors (with moss, $\bar{x}$ = 0.71, SE = 0.2; no moss, $\bar{x}$ = 0.17, SE = 0.1; t = −2.49, df = 49, p = 0.0164). Numbers of detections ≤ 200 m from a station and the number of subcanopy flight behaviors were not significantly different among aspect quadrants.

TABLE 3. Mean and SE of the types of murrelet observations made at the 4 forest types surveyed in the Naked Island area in Prince William Sound, Alaska, in 1991. Detections at all distances from the observer were included.

Forest type	N sites	No. subcanopy[a] behaviors/site	No. circling[b] behaviors/site	No. visual[c] detections/site	No. audio[d] detections/site
FT1	18	0.06 (0.06)	5.8 (2.7)	0.51 (0.12)	30.5 (7.3)
FT2	18	0.50 (0.22)	5.6 (1.6)	2.69 (0.63)	24.5 (5.8)
FT3	17	1.00 (0.34)	7.2 (2.1)	0.77 (0.19)	39.8 (6.7)
FT4	19	0.32 (0.22)	8.3 (2.6)	0.93 (0.21)	28.4 (7.7)

[a] ANOVA; F = 2.97, df = 3, 68, p = 0.04. SNK; FT1 and FT3 are significantly different.
[b] ANOVA; F = 0.31, df = 3, 68, p = 0.82. NS.
[c] ANOVA; F = 1.35, df = 3, 68, p = 0.26. NS.
[d] ANOVA; F = 0.84, df = 3, 68, p = 0.48. NS.

TABLE 4. Mean and SE of murrelet detection categories between sites at bay heads and exposed sites. Data are from the randomly selected sites surveyed on Naked, Storey and Peak islands, Prince William Sound, Alaska, in 1991.

	N	No. of subcanopy behaviors	No. of circling detections	No. of detections on land <200 m	No. of total detections
Bay	21	0.33 (0.14)	11.05 (2.8)	22.1 (4.3)	51.8 (6.3)
Exposed	33	0.51 (0.19)	4.5 (1.5)	11.8 (3.2)	26.9 (5.9)
t-test	*t*	= −0.75	2.11	1.96	2.70
	df	= 52	31	52	49
	p	= 0.45	0.043	0.056	0.009

However, mean detection rates were slightly higher in northerly quadrants (NE had 19.1 detections/site, NW had 16.4 detections/site) than in southerly quadrants (SE had 13.3 detections/site, SW had 12.5 detections/site).

Sites near the heads of bays had higher numbers of circling behaviors and total detections than sites near exposed coasts (Table 4). However, there was no significant difference in the number of detections ≤ 200 m from the station or in the number of subcanopy flight behaviors between sites near bay heads and sites near exposed coasts.

Occupied Sites vs. Sites of Unknown Status

Subcanopy flight behaviors comprised 4% of detections ≤ 200 m from the station, and they were observed at 22% (16 of 72) of the sites, including 2 sites where silent subcanopy flight behaviors were observed in the pre-dawn hours before the dawn watch. Occupied sites had higher numbers of detections ($\bar{x}$ = 26, SE = 4.3) than sites of unknown status ($\bar{x}$ = 13, SE = 2.4; $t = -3.18$, df = 70, $p = 0.002$), but did not differ in the numbers of circling behaviors ($\bar{x}$ = 8.6, SE = 2.2 and $\bar{x}$ = 6.2, SE = 1.3, respectively).

Occupied sites had larger trees than sites of unknown status ($t = -2.02$, df = 69, $p = 0.047$; Table 5). Occupied sites did not differ from sites of unknown status with respect to slope grade, percentage of forested area, canopy cover, elevation, distance to salt water, or stand size (Table 5).

Discussion

Murrelet Activity Among Four Forest Types

Our results suggest that forest-stand definitions for Prince William Sound, based on a combination of tree-size and volume classes, could coarsely identify potential murrelet nesting habitat. We observed higher murrelet activity and more subcanopy flight behaviors in the forest type comprised of high tree-size and moderate volume classes (FT3). The forest type of the lowest tree-size and volume class (FT1) had the lowest dawn activity and few indications of nesting birds.

TABLE 5. Mean and SE of habitat characteristics between sites where subcanopy flight behaviors were observed (occupied) and sites where they were not observed (unknown status). Data were from 72 randomly selected sites on Naked, Storey and Peak islands, Prince William Sound, Alaska, in 1991.

Site	N	Slope aspect (no. sites)				Slope grade (%)	Elevation (m)	Distance to sea (m)	Stand size (ha)
		NE	SE	SW	NW				
Occupied	16	6	3	2	5	34 (5)	94 (9)	284 (68)	247 (81)
Unknown status	56	12	16	9	19	38 (3)	96 (16)	296 (32)	144 (31)

Site	N	Average[a] tree dbh (cm)	N	Canopy[b] height (m)	Canopy closure (%)	Forested area of plot (%)
Occupied	16	43.5 (3.3)	15	32 (4)	71 (7)	85 (5)
Unknown status	56	35.8 (1.8)	56	23 (2)	60 (4)	75 (3)

[a] *t*-test; $t = 2.02$, df = 69, $p = 0.047$.
[b] *t*-test; $t = -1.77$, df = 61, $p = 0.081$.

While murrelet activity was definitely lower in the FT1 forests, we obtained mixed results among the forest types with the same tree-size class, but different volume classes (FT2, FT3 and FT4 forests). Our results could have been affected by limitations of the habitat database, as it did not identify stands that had < 4 ha of big trees (> 28 cm dbh) within larger stands of small trees. Our surveys appeared to underestimate murrelet use of FT4 forests, based on nests found in the study area; 4 of 10 murrelet nests found on Naked Island were in FT4 forests, with the remaining in FT3 forests (Naslund et al. 1995).

The lack of a significant difference in murrelet activity between FT2 forests and the higher-volume forests could have been due to a combination of habitat features, or reduced detectability in dense FT3 and FT4 forests. Additionally, because of logistic constraints, we relied on random sampling to maximize our sample size, but 10 visits per site may be required to establish occupancy status (S.K. Nelson, pers. comm.). Nests are sometimes located in areas with relatively few detections (unpubl. data). As weather can affect murrelet activity (Rodway et al. 1991, Kuletz et al. 1994, Naslund and O'Donnell 1995, Nelson and Peck 1995), a single survey is also more subject to bias from environmental conditions.

Birds possibly vocalized more when flying over lower-volume forests and less when close to nest sites. Silent approaches to nest sites were noted in California (Naslund 1993, Singer et al. 1995), Oregon (Nelson and Peck 1995) and Naked Island (Kuletz and Naslund, unpubl. data). Alternatively, our results reflected real use of FT2 forests, although this has not been verified by discovery of nests. The FT2 forests may be essential to murrelets even if not used for nesting; irrespective of nest locations, social activity was high in these forests. Additionally, stands of FT2 forests often abutted the smaller stands of high-volume forests, and may buffer them from avian predators (Bryant 1994, Paton 1994, Nelson and Hamer 1995b), or protect them from windthrow of large trees.

Murrelet Activity and Site Characteristics

Our results agreed with studies at lower latitudes that showed the highest murrelet activity in coastal old-growth forests with large trees (Eisenhawer and Reimchen 1990; Paton and Ralph 1990, Grenier and Nelson 1995, Hamer 1995, Miller and Ralph 1995). In addition to providing nesting substrate, moss also appears to influence murrelet habitat selection (Quinlan and Hughes 1990; Naslund et al. 1995; Hamer, in press). Accumulated moss creates additional potential nesting platforms, and its accumulation is influenced by tree size and species as well as microhabitat features such as moisture, proximity to the ocean or exposure (Burger 1995, Hamer 1995, Naslund et al. 1995). Microhabitat effects may partly explain the low-activity levels in FT1 forests, which were farthest from the ocean, and had the lowest percentage of sites with abundant moss.

Because the 3 forest types of high tree-size classes tended to be closer to the ocean, it was possible that we recorded birds on the water, or that birds circled more near the water and thus increased detection rates. However, there was no significant correlation between distance from water and total detections, or the frequency of circling behavior. Similarly, the high activity levels we observed at bay heads apparently did not result from recording birds on or flying over water, because bay sites tended to be farther inland than exposed sites. Marks et al. (1995) also found higher activity in bays at sites throughout western Prince William Sound. However, we found that the activity at bay heads was only significantly higher when detections at all distances were considered. Thus, generally higher activity at bay heads could influence results at any location in a bay. When testing for a specific habitat preference, analyses should focus on murrelet activity in the immediate vicinity (*i.e.*, < 200 m from the observer) to minimize this bias. Being in a bay may have more influence than slope aspect, as we found no significant differences in murrelet activity relative to aspect.

Occupied Sites vs. Sites of Unknown Status

Our results differed from those of other studies primarily in that murrelets were active and exhibited subcanopy flight behaviors around trees that were smaller than at lower latitudes. South of Alaska, average tree size at occupied sites ranged from 53 to 134 cm dbh, with canopy height up to 100 m (Paton and Ralph 1990, Grenier and Nelson 1995, Hamer 1995). In the Naked Island area, the highest volume and tree-size class forests averaged 46 cm dbh for canopy trees, and average canopy height was 34 m. As tree size decreases with increasing latitude (Viereck and Little 1972), other features of old-growth forests, such as multilayered structure, dense canopy closure, and high epiphyte cover may be particularly important to murrelets in Alaska.

Although occupied sites had higher activity levels than sites of unknown status, activity level alone cannot be used to identify occupied sites, because the frequency of subcanopy flight behaviors was extremely low, and their observation may be statistically dependent on the total number of detections. It is unlikely that we documented every occupied site in our sample with 1 survey per site. These factors, in addition to differences in forest type and latitude, must be considered when extrapolating our findings to other sites in Alaska. Nonetheless, as in other areas of the murrelet's range, sites where subcanopy flight behaviors were observed had larger trees than other sites. We conclude that preservation of old-growth forest stands with the largest trees would benefit murrelets in Prince William Sound.

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