Chapter 15

Inland Habitat Suitability for the Marbled Murrelet in Southcentral Alaska

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Abstract: The majority of Marbled Murrelets (*Brachyramphus marmoratus*) nest in Alaska, where they sometimes nest on the ground, and their nesting habitat requirements are not well understood. The inland activity of murrelets was surveyed, and habitat features measured, between 1991 and 1993, in Prince William Sound, Kenai Fjords National Park and Afognak Island, Alaska (n = 262 sites). We used these data to develop statistical models that explain variation in murrelet activity levels and predict the occurrence of occupied behaviors (indicative of nesting), based on temporal, geographic, topographic, weather, and habitat characteristics. Multiple regression analyses explained 52 percent of the variation in general murrelet activity levels ($P < 0.0001$). The best model included survey date, location relative to the head of a bay, elevation, slope, aspect, percentage of forest cover, tree diameter, and epiphyte cover on tree branches. The highest activity levels were associated with late July surveys at the heads of bays where there was high epiphyte cover on trees. Stepwise logistic regression was used to identify variables that could predict the probability of detecting occupied behaviors at a survey site. The best model included survey method (from a boat, shore, or upland), location relative to the head of a bay, tree diameter, and number of potential nesting platforms on trees. The best predictors for observing occupied behaviors were tree diameter and number of platforms. In a jackknife procedure, the logistic function correctly classified 83 percent of the occupied sites. Overall, the features indicative of murrelet nesting habitat include low elevation locations near the heads of bays, with extensive forest cover of large old-growth trees. Our results were derived from surveys designed to estimate murrelet use of forested habitat and may not accurately reflect use of nonforested habitat. Therefore, caution should be exercised when extrapolating observed trends on a broad scale across the landscape.

The reliance of Marbled Murrelets (*Brachyramphus marmoratus*) on mature and old-growth forest for nesting has been well established in the southern portion of the species' range (see Carter and Morrison 1992; Hamer and Nelson, this volume b). Yet, the majority of Marbled Murrelets breed in Alaska, where nesting habitat requirements are not clearly understood (Mendenhall 1992). Offshore surveys suggest that about 97 percent of the population within Alaska occurs offshore of lands with at least some old-growth forest cover (Piatt and Ford 1993). These forested areas extend from southeast Alaska, north along the Gulf of Alaska, and throughout southcentral Alaska. However, the extent of forested habitat is variable in this region. "Forested" areas include unforested habitat, and tree line may extend only 200 m above sea level and a few kilometers inland.

The choice of nesting habitat for murrelets appears superficially to be broader in Alaska, where murrelets nest both in trees and on the ground, than at lower latitudes. Before the early 1980's, only six Marbled Murrelet ground nests had been found (Day and others 1983). Since then, three tree nests have been documented in southeast Alaska, and one nest was found on a tree root overhanging a cliff (Brown, pers. comm.; Ford and Brown 1994; Quinlan and Hughes 1990). In southcentral Alaska, 15 tree nests and seven additional ground nests were found between 1989 and 1993 (Balogh, pers. comm.; Hughes, pers. comm.; Kuletz and others 1994c; Mickelson, pers. comm.; Naslund and others, in press; Rice, pers. comm.; Youkey, pers. comm.). The apparent importance of ground nesting by murrelets in Alaska is partially an artifact of effort. Ground nests are more easily discovered than tree nests, inflating their relative numbers. Additionally, it is possible that ground nests of the Kittlitz's Murrelet (*B. brevirostris*) can be mistaken for those of Marbled Murrelets (Day and others 1983). Therefore, it was unclear how important ground nesting was to the Marbled Murrelet population.

Following the 1989 *Exxon Valdez* Oil spill, the protection of habitat was identified as a means of restoring injured resources such as the Marbled Murrelet. Our goal was to provide information on murrelet nesting habitat in the spill zone to guide protection and land acquisition decisions. Between 1990 and 1993, we examined aspects of murrelet nesting behavior and habitat use in Prince William Sound and Kenai Fjords National Park (Kuletz and others 1994b, c). Concurrently, in 1992, murrelet surveys were conducted on Afognak Island, north of Kodiak Island (Cody and Gerlach 1993, U.S. Fish and Wildlife Service 1993). Although there were differences in study design among the studies, they provided a substantial data base for relating habitat variables to murrelet activity throughout the spill zone. Data from these four studies were combined to develop a broad-based model of murrelet activity in relation to weather, season, and habitat variables that would apply throughout southcentral Alaska. We also developed a statistical model of site characteristics where occupied behavior, indicative of nesting birds, was observed.

Methods

Study Area

The study area encompasses the Naked Island group in central Prince William Sound, western Prince William Sound, the Kenai Fjords National Park, and two parcels on Afognak Island (*fig. 1*). *Brachyramphus* murrelets comprise a large portion of the avifauna in these areas. The estimated *Brachyramphus* murrelet population for Prince William

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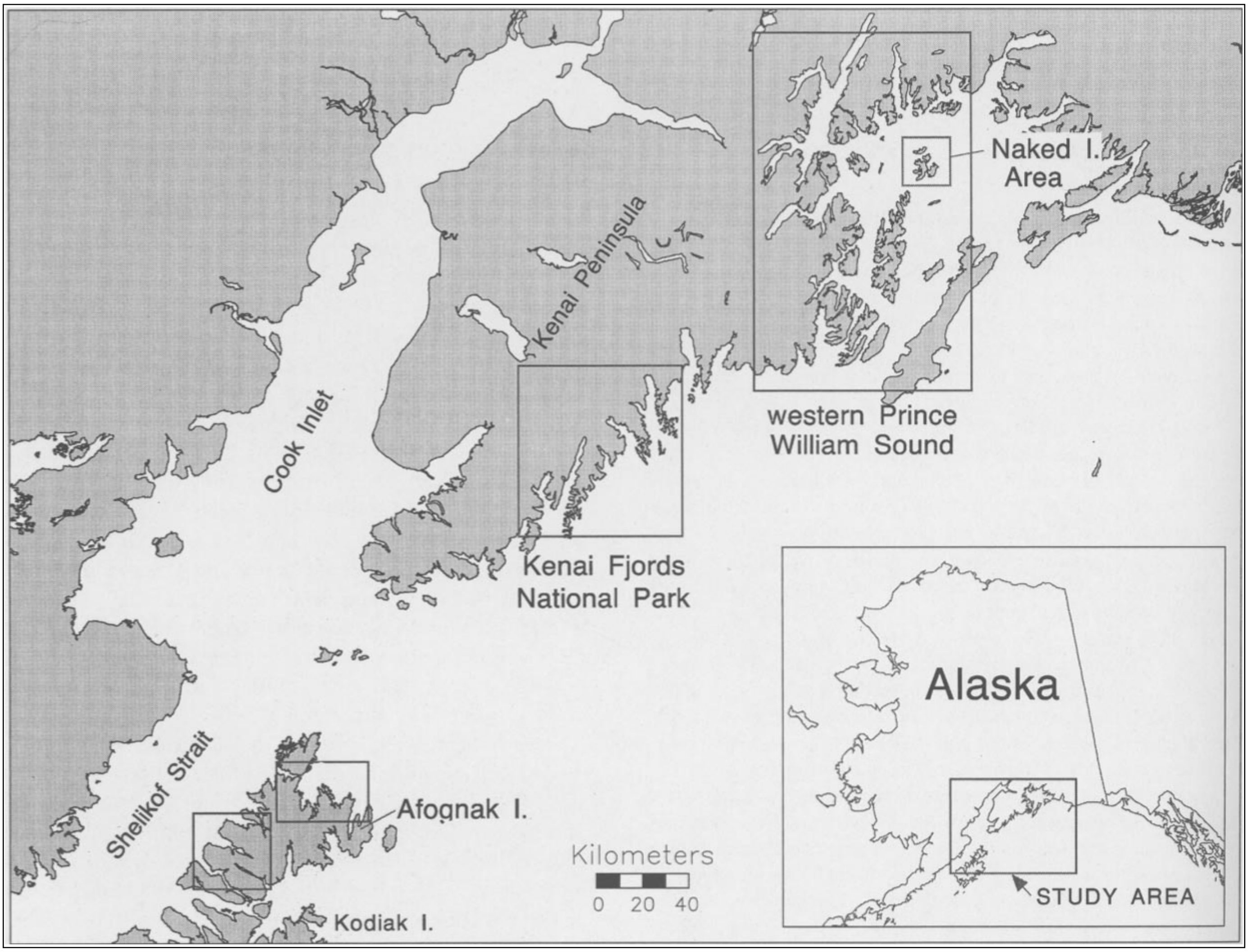

Figure 1—The four study areas of southcentral Alaska surveyed for inland murrelet activity between 1991 and 1993: Naked Island, western Prince William Sound (PWS), Kenai Fjords National Park (KFNP), and Afognak Island (in two parcels).

Sound is approximately 100,000 birds (Klosiewski and Laing 1994). Within 5 km of the Naked Island group (Naked, Peak, and Storey islands), there are an estimated 3,000 Marbled Murrelets (Kuletz and others 1994a). At-sea surveys of Kenai Fjords National Park have been restricted to shoreline surveys (within 200 m of shore) and complete counts in some bays. In 1989 the estimates ranged from 2,000 *Brachyramphus* murrelets in June to 6,500 in August (Tetreau, pers. comm.). At-sea surveys off Afognak Island in summer 1992 produced estimates of 2200 murrelets off the northern section, and 2000 murrelets off the southwest section (Fadely and others 1993). *Brachyramphus* murrelet population estimates include a small percentage of Kittlitz's Murrelets in Prince William Sound (approximately 7 percent; Laing, pers. comm.) and Kenai Fjords National Park (between 7-12 percent; Tetreau, pers. comm.).

General Habitat

Prince William Sound, the northernmost portion of the study area, is characterized by protected waters, numerous islands and bays, and deep-water fjords, including some with tidewater glaciers. Forested areas of mixed hemlock-spruce forests (*Tsuga mertensiana, T. heterophylla,* and *Picea sitchensis*) are interspersed with muskeg meadows, alpine vegetation, and exposed rocks. Tree line ranges from 30 to 600 m (see Isleib and Kessel 1973). Naked Island is in the center of Prince William Sound, and vegetation is a mix of forest and muskeg meadow, but lacks other habitat types (Kuletz and others, in press).

The Kenai Fjords National Park, on the southern Kenai Peninsula, is characterized by steep, rugged coastline and numerous islands on the outer coast. There are protected waters and tidewater glaciers at the heads of fjords, and exposed coasts near fjord mouths bordering the Gulf of Alaska (Bailey 1976). Glaciers cover more than 50 percent of Kenai Fjords National Park (Selkregg 1974). Because of receding glaciers, forested portions of the coast are primarily in the outer, more exposed headlands and islands. Tree line is typically 300 m, and few areas beyond 500 m from shore are forested. Tree species are similar to those in Prince William Sound, and alder is the dominant vegetation in unforested areas.

There were two study sites on Afognak Island. The northern parcel faces north into the Gulf of Alaska and is heavily forested. The southwest parcel faces west into Shelikof Strait and is primarily unforested, except along river valleys and around the heads of bays. There are no glaciers. Tree line ranges from 100 to 300 m and the only conifer is Sitka spruce (*Picea sitchensis*), which tends to be larger than on the mainland.

Data Collection

Dawn Watch Surveys

In Alaska, surveys are limited by logistic considerations due to inaccessibility of coastal habitats, and by the relatively short time available for breeding surveys (mid-May through early August). Therefore, intensive surveys (hereafter referred to as "dawn watches"; Paton and others 1990, Ralph and others 1993) were conducted from land-based ("upland") sites and from boats anchored near shore. The basic unit of measure was the 'detection' which is defined as "the sighting or hearing of a single bird or a flock of birds acting in a similar manner" (Paton and others 1990). We assume that dawn activity (i.e., numbers of detections) is positively related to nesting activity. We recognize, however, that no quantitative relationship between dawn activity and numbers of nesting murrelets has been defined, and conclusions about relative use of different habitats are tentative.

Dawn watches were modified for southcentral Alaska (for more details see Kuletz 1991b, Kuletz and others 1994c). Modifications included: (1) earlier start and finish times relative to sunrise (i.e., usually beginning 105 min before official sunrise and lasting until 15 min after sunrise, or 15 min after the last murrelet detection) to compensate for greater light levels in Alaska; (2) addition of behavior categories not observed further south; and (3) some watches were conducted from boats and shore to allow sampling of shoreline habitat. Using landmarks, we designated each detection as <200 m or >200 m from the observer. When the dawn watch was conducted near the water, a bird passing over land at any time during the observation was designated a land detection.

Behaviors indicative of murrelet nesting are referred to as "occupied behaviors." These included flying below canopy, emerging from or flying into trees, landing on or departing from a branch, or calling from a stationary point in the forest (Paton and others 1990). In unforested areas we considered flights into hillsides or brush or ≤3 m above ground cover to be occupied behaviors. Occupied sites were those with at least one recorded occupied behavior. We considered other sites to be of "unknown status" since a single visit was not sufficient to determine whether a site was unoccupied (Ralph and others 1993).

Habitat Variables

A 50-m vegetation plot was sampled at each dawn watch site. When the dawn watch was conducted from shoreline or from a boat, the vegetation plot center was placed within the habitat most visually representative of the area adjacent to the dawn watch site. Within the plot we measured the diameter at breast height (d.b.h.) of the 10 nearest upper canopy trees, the percentage of epiphyte cover on the branches of each tree, and the number of platforms per tree (horizontal surfaces ≥15 cm diameter and ≥10 m above the ground). Data on epiphyte cover and platforms were not collected for the Naked Island group. We also made visual estimates of overall canopy height, percentage canopy closure, and percentage of forested area. Slope grade, aspect, and elevation were measured on site or from topographic maps. Distance from the ocean was measured from aerial photographs. Each site was classified as either exposed coastline, semi-protected in a bay, or at the head of a bay.

Study Design Sampling and Analyses

The Naked Island group was surveyed between 10 June and 11 August 1991 (n = 69 sites). Sites in western Prince William Sound were surveyed between 15-18 July 1991 (n = 9) and 12 June–3 August 1992 (n = 68). Afognak Island was surveyed from 4 June–5 August 1992 (n = 76). Kenai Fjords National Park was surveyed from 8–29 July 1993 (n = 40). We surveyed Marbled Murrelet activity and recorded weather, survey period, and topographic and vegetation variables at each survey site in the four study areas. Murrelet activity is highly seasonal and generally exhibits a pattern of peak activity during the breeding season (Hamer and Cummins 1991, Nelson 1989, Rodway and others 1993b). Therefore, survey period was categorized as early and late (before or after 10 July, respectively), based on activity patterns previously documented in Prince William Sound (Kuletz and others 1994c). Study designs and survey methods varied among areas (for details see Kuletz and others 1994b, c). At Naked Island, sites were randomly selected equally among four forest types (Kuletz and others, in press), with 69 of the sites having sufficient habitat data to include in this study. In western Prince William Sound, 77 sites were randomly selected from available habitat, although sample sizes among habitat types were not equal. Forty-six surveys were done from an anchored vessel, 23 from shore locations, and eight upland. An additional nine upland sites were surveyed opportunistically in 1991. These sites were located in forested and nonforested habitat, and occurred in areas of western Prince William Sound not previously surveyed. Sampling at Kenai Fjords National Park was randomly stratified by forested versus unforested and bay head versus not bay head. The 38 survey sites were equally distributed among the strata; 21

sites were surveyed from shore, eight from boats, and nine from upland sites. At Afognak Island, 76 dawn watch sites were arbitrarily selected with efforts to sample equally throughout the north and southwest parcels. Two sites were surveyed from shore and 74 upland.

Sites were not randomly located within the entire spill zone. Therefore, our statistical results apply directly only to the sampled sites, and caution should be used when making inferences about other areas. Application of results to the entire area is based on the assumption (supported by our observations) that the study sites were representative of habitat types throughout the spill zone.

Because epiphyte cover and platforms were not recorded at Naked Island, we used Naked Island data for preliminary analyses, but not for the final multivariate analyses. For analyses, we used detections over land <200 m from the observer because it produced stronger relationships with predictor variables in preliminary analysis of portions of the data set. Data from boat- and shore-based surveys were combined with upland survey data because these data are highly correlated (Marks and others, in press). Data from all areas were grouped because preliminary analyses indicated that within-site trends were similar to trends exhibited for all sites combined.

Multiple Regression Analyses of Murrelet Activity Levels

We used multiple regression analyses to examine the continuum of murrelet activity levels relative to independent variables, to examine the interactive effects of those variables, and to describe the amount of variation explained by the model. Although season and weather affect inland activity level, we incorporated all these variables into the model rather than attempting to develop standardization factors. Our initial set of 19 predictor variables were factors known or suspected to be associated with high levels of activity or nesting of Marbled Murrelets, based on previously conducted analyses (Kuletz and others, in press; Marks and others, in press; Naslund and others, in press), and on univariate statistics across the four study areas. We used Kruskal-Wallis nonparametric analysis of variance to test categorical variables for significant effects on the number of detections. We calculated Pearson correlation coefficients between continuous variables and the number of detections, and between each pair of continuous variables. To control for colinearity, only one of a pair of variables with $r > 0.80$, whichever had the strongest correlation with the number of detections, was included in the same regression analysis.

Because categorical and continuous variables were included in the multiple regression model, we used a General Linear Model procedure (SAS Institute 1988) to examine variation in murrelet activity levels. We transformed the number of detections by using natural logarithms and the percent data (canopy cover, forest cover, alder cover, and slope) by using square roots to stabilize residuals. We ran our initial regression model with all sites, and included all significant ($P < 0.05$) categorical variables and those continuous variables which were measured across all four study areas. We ran a second regression model for the three areas for which variables more directly related to Marbled Murrelet nest site selection (epiphyte cover and platforms per tree) were estimated. For this model we included all variables in the initial regression and epiphyte cover, which was highly correlated with platforms per tree. We reduced the model to include *t* probabilities for parameter estimates where $P < 0.25$ in the original model. This criterion was selected because our objective was to include all variables that explained variation in murrelet activity. Standardized parameters (parameter estimates divided by their standard error) were used to determine the relative importance of variables included in the models.

Discriminant Analyses of Murrelet Occupancy

We used univariate tests and stepwise logistic regression to identify variables that could predict the probability of detecting occupied behavior at a survey site. This analysis included a test of how well the logistic model performed in classifying individual observations. For all four areas combined, we tested frequencies of classes of categorical variables for differences between occupied sites and sites of unknown status by using chi-square; and for differences in rank sums of continuous variables between occupied and unknown status sites by using the Wilcoxon 2-Sample Test (procedure NPAR1WAY; SAS Institute 1988). Significant variables ($P < 0.05$) in these tests were entered into a stepwise logistic regression model (procedure LOGISTIC; SAS Institute 1990; Naked Island group excluded). Inclusion and retention of variables in the stepwise logistic analysis were allowed at $P < 0.10$. We included platforms per tree in the model because it performed marginally better than one including epiphyte cover. Standardized parameter estimates were estimated by dividing the parameter estimate by the ratio of the standard deviation of the underlying distribution to the sample standard deviation of the explanatory variable (SAS Institute 1990), and were used to determine the relative importance of variables in the model. The classification error rate was calculated using a jackknife approach to reduce the bias of classifying the same data from which the classification criterion was derived (SAS Institute 1990).

Results

Marbled Murrelet Activity Levels

Activity of Marbled Murrelets differed by study area ($P = 0.018$), with the greatest level of activity occurring at Afognak Island, the least at Naked Island, and intermediate levels in western Prince William Sound and Kenai Fjords National Park (*table 1*). Activity was greater during late summer than during spring and early summer (*table 1*). Activity was greater when the cloud ceiling was low than when there was a high ceiling or clear conditions (*table 1*). Activity was also greater at survey sites located at the heads

Table 1—The number of detections for categorical variables considered for inclusion in multiple regression analyses relating activity of Marbled Murrelets to survey period, weather, topographic, and vegetation variables. A Kruskal-Wallis nonparametric analysis of variance tested the null hypotheses that murrelet activity did not differ between (or among) classes of each variable

Variable regression	Classes (*n*)	Number of detections		Chi-square	df	*P*
		Mean	(*s.e.*)			
Area	Naked Island (69)	15.8	(2.27)	10.12	3	0.0175
	Prince William Sound (77)	23.8	(3.11)			
	Kenai Fjords (38)	29.9	(5.78)			
	Afognak Island (76)	38.4	(5.27)			
Survey period	Early (May 1-Jul 10)(113)	18.1	(2.84)	11.03	1	0.0009
	Late (Jul 11-Aug 31)(147)	33.6	(2.96)			
Survey method	Boat (54)	28.0	(3.62)	2.48	2	0.2890
	Shore (67)	23.6	(4.32)			
	Upland (139)	28.0	(3.10)			
Cloud ceiling	None (26)	15.4	(4.05)	6.44	2	0.0398
	Above ridge (103)	35.1	(4.09)			
	Below ridge (68)	18.6	(2.90)			
Windspeed	0 km/h (123)	31.1	(3.51)	6.51	3	0.0893
	1-8 km/h (103)	23.6	(2.86)			
	9-16 km/h (15)	11.5	(4.14)			
	>16 km/h (18)	28.6	(8.86)			
Headbay	Exposed shore (59)	16.6	(3.45)	27.75	2	0.0001
	Bay (106)	21.1	(2.62)			
	Headbay (95)	39.6	(4.28)			

of bays than elsewhere in bays or on exposed shorelines (*table 1*). Windspeed did not significantly affect murrelet activity and activity did not vary significantly among survey methods (by boat, from shore or upland; *table 1*).

Correlation coefficients between Marbled Murrelet activity and continuous weather, topographic, and vegetation variables measured in all four areas varied from -0.16 for alder cover to 0.39 for d.b.h. (*table 2*). The largest correlation coefficients were between murrelet activity and variables directly related to nest site selection (epiphyte cover; platforms per tree; *table 2*).

Our reduced model explained 52 percent of the total variation in murrelet activity (*table 3*). Parameters for survey period, location relative to the head of a bay, and epiphyte cover were highly significant. Based on ratios of parameters to their standard errors (*table 3*), epiphyte cover, survey period, and location relative to the head of a bay were the most important predictors of murrelet activity.

Across all four study areas combined, tree d.b.h. (χ^2 = 7.58, df = 2, P = 0.02), number of potential nesting platforms (χ^2 = 7.08, df = 2, P = 0.03), and percent epiphyte cover (χ^2

Table 2—Pearson correlation coefficients between continuous variables considered for inclusion in multiple regression model and murrelet activity (Overland detections <200 m from observer)

Variable	Units	Pearson correlation coefficent
Cloud cover	Percent	0.14
Elevation	Meters	–0.14
Slope	Percent	0.08
Degrees from north	Degrees	–0.03
Degrees from east	Degrees	–0.03
Forest	Percent	0.24
Canopy cover	Percent	0.12
Canopy height	Meters	0.24
Diameter at breast height	Centimeters	0.39
Alder cover	Percent	–0.16
Epiphyte cover[1]	Percent	0.48
Platforms[1] per tree	Number	0.43

[1] Not estimated at Naked Island

Table 3—Multiple regression model relating activity of Marbled Murrelets[1] to survey period, weather, topographic, and vegetation variables at three study areas: western Prince William Sound, Kenai Fjords National Park, and Afognak Island. Categorical variables were entered into the regression as dummy variables

Model	Variable	Levels of categorical variables	Estimate (*s.e.*)	Parameter t^2	Parameter P	Standardized estimate
F = 15.21	Intercept		2.326 (0.421)	5.53	0.0001	
df = 10,140						
R^2 = 0.52	Period	0 (Early)	-0.851 (0.19)	–4.38	0.0001	4.39
		1 (Late)				
P = 0.0001	Headbay	0 (Exposed)	-1.028 (0.281)	–3.66	0.0004	3.66
		1 (Bay)	-0.820 (0.200)	–4.10	0.0001	4.10
		2 (Headbay)				
	Elevation		-0.005 (0.002)	–3.03	0.0029	2.50
	Slope[3]		0.131 (0.053)	2.47	0.0148	2.47
	Degrees from north		-0.003 (0.002)	–1.86	0.0648	1.50
	Forest cover[3]		0.121 (0.070)	1.72	0.0700	1.73
	Canopy cover[3]		-0.120 (0.072)	–1.67	0.0964	1.70
	D.b.h.		0.010 (0.006)	1.73	0.0863	1.67
	Epiphyte cover		0.018 (0.004)	4.73	0.0001	4.50

[1] Variable was natural log transformed
[2] Tested null hypothesis that coefficient estimate = 0
[3] Variable was square root transformed

= 6.73, df = 2, P = 0.03) were greater at sites located at heads of bays, than at more exposed sites.

Identification of Occupied Sites

The probability of observing occupied behavior was greater: (1) at Afognak Island than at other areas; (2) during upland surveys than during boat or shore surveys; (3) during days with a high percentage of clouds than during clear days; and (4) at bays (especially at heads of bays) than at exposed sites (*table 4*). The probability of observing occupied behaviors did not vary with survey period or windspeed. Occupied sites had greater levels of cloud cover, forest cover, canopy cover, canopy height, d.b.h., epiphyte cover, and platforms per tree, than other sites (*table 5*). Alder cover was greater at other sites than at occupied sites.

Tree size (d.b.h.) and location relative to the head of a bay entered the model at the $P < 0.10$ level; survey method and platforms per tree were also included. Standardized parameter estimates (*table 6*) indicated that d.b.h. and platforms per tree were the most important predictors of occupied sites. The logistic function correctly classified 78.9 percent of observations in a jackknife procedure; 82.7 percent of occupied sites, and 74.6 percent of sites of unknown status were correctly classified.

Discussion

Habitat Predictors Of Murrelet Use

Murrelet Activity Levels

Several variables were consistent predictors of high murrelet activity. Allowing for survey period, activity was highest at the heads of bays, at low elevations, and in areas with a high percentage of forest cover and large diameter trees. The most important habitat variables across all study areas were location relative to heads of bays, tree size (d.b.h.), and epiphyte cover on trees (excluding the Naked Island group for which there was no data on epiphyte cover). The number of platforms per tree was also important because it is highly correlated with epiphyte cover.

The importance of tree size and the number of platforms per tree was consistent with results from other studies and with attributes of nest trees found in southcentral Alaska (Hamer and Cummins 1991; Hamer, this volume; Naslund and others, in press). The importance of location relative to heads of bays was noted in earlier analyses of Prince William Sound data (Kuletz and others, in press; Marks and others, in press) but has not been reported elsewhere. Further, the trend for a bay effect in Kenai Fjords National Park was not significant in prior analyses (Kuletz and others 1994b). It is

Table 4—Univariate tests for differences in frequencies of classes of categorical variables between occupied sites (where behaviors indicating nesting were observed) and other sites (where behaviors indicating nesting were not observed

Variable	Class (*n*)	Proportion of occupied sites	Chi-square	df	*P*
Area	Naked Island (69)	0.22	42.08	3	0.0001
	Prince William Sound (77)	0.22			
	Kenai Fjords (38)	0.32			
	Afognak Island (76)	0.66			
Survey period	Early (May 1-Jul 10) (113)	0.34	0.23	1	0.629
	Late (Jul 11-Aug 11) (147)	0.37			
Survey method	Boat (54)	0.24	14.56	2	0.001
	Shore (67)	0.24			
	Upland (139)	0.47			
Cloud ceiling	None (68)	0.23	7.74	2	0.021
	Above Ridge (103)	0.44			
	Below Ridge (63)	0.41			
Windspeed	0 Km/h (123)	0.37	1.704	3	0.636
	1-8 Km/h (103)	0.38			
	9-16 Km/h (15)	0.33			
	>16 Km/h (18)	0.22			
Headbay	Exposed shore (59)	0.22	9.42	2	0.009
	Bay (106)	0.35			
	Headbay (95)	0.46			

Table 5—Means, standard errors, and univariate tests for differences in rank sums of continuous variables between sites where one or more occupied behaviors (behaviors indicating nesting of marbled murrelets) were observed (occupied sites) and sites where no behaviors indicating nesting of Marbled Murrelets were observed (other sites)

Variable	Occupied sites			Other sites			Z^1	*P*
	n	Mean	(*s.e.*)	*n*	Mean	(*s.e.*)		
Cloud cover	94	80.85	(3.76)	166	68.75	(3.33)	2.06	0.04
Elevation	87	51.65	(4.61)	140	71.70	(6.81)	–0.62	0.53
Slope	88	21.25	(18.52)	140	22.15	(12.89)	–1.30	0.19
Degrees from north	88	91.25	(5.53)	140	91.29	(4.51)	–0.05	0.96
Degrees from east	88	99.77	(6.00)	140	99.14	(4.61)	0.12	0.90
Forest cover	88	74.64	(2.64)	136	60.34	(3.00)	2.69	0.008
Canopy cover	88	63.26	(2.46)	134	49.69	(2.86)	2.54	0.01
Canopy height	88	26.71	(1.25)	135	17.31	(1.19)	7.94	0.0001
D.b.h.	87	57.11	(1.98)	140	33.70	(1.77)	7.94	0.0001
Alder cover	86	3.03	(0.70)	132	10.90	(1.86)	–3.08	0.002
Epiphyte cover	72	54.57	(3.88)	82	16.78	(2.18)	7.06	0.0001
Platforms per tree	72	7.36	(0.67)	82	2.06	(0.38)	6.95	0.0001

[1]Wilcoxon 2-Sample Test

Table 6—Logistic regression model to predict probability of occupied sites of Marbled Murrelets (sites where one or more behaviors indicating nesting were observed) for the three study sites: western Prince William Sound (1992), Kenai Fjords National Park (1993) and Afognak Island (1992), Alaska (n = 152 sites total)

–2 Log L Chi-square	df	*P*	Variable	Parameter Estimate (*s.e.*)	Parameter Chi-square	Parameter *P*	Parameter Standardized estimate
73.513	4	0.0001	Intercept	4.918 (0.903)	29.633	0.0001	
			Method	–0.679 (0.257)	6.970	0.0083	0.31
			Headbay	–0.559 (0.306)	3.331	0.0680	–0.26
			D.b.h.	–0.040 (0.012)	11.320	0.0008	–0.56
			Platforms	–0.138 (0.057)	5.776	0.0162	–0.41

possible that high detection rates result from murrelets funneling through bay heads and using them as flyways. However, the consistency of high activity at bay heads for the study areas overall, combined with the high proportion of occupied sites at bay heads, suggests otherwise.

Marks and others (in press) found that murrelet activity was positively correlated with stand size in western Prince William Sound. High activity at bay heads may be a result of larger contiguous forests at bay heads, although stand size relative to landform has not been investigated in these areas. Microclimate and minimal exposure to weather at bay heads may foster characteristics associated with known murrelet nesting habitat, including large tree size and mossy platforms on trees. This may explain the larger tree d.b.h., greater number of potential nesting platforms, and higher percentage of epiphyte cover at sites located at heads of bays relative to more exposed sites. However, these trends were not evident at Kenai Fjords National Park in earlier analyses (Kuletz and others 1994b). This is likely due to the recent deglaciation of many of the bay heads.

The importance of tree size and elevation in predicting murrelet activity has been suggested by other studies. Murrelets typically nest in old-growth stands where trees tend to be relatively large (see Hamer and Nelson, this volume b). Hamer and Cummins (1991) and Rodway and others (1991) found that murrelet activity was highest in low elevation forests in Washington and British Columbia. In northern latitudes, larger trees are found at lower elevations (Viereck and Little 1972). Kuletz and others (in press) found a significant negative correlation between tree d.b.h. and elevation on the Naked Island group, even though the highest elevation was <460 m. Thus, the contribution of elevation to the model is likely due to its effect on patterns of vegetation growth.

Conversely, it is also possible that murrelets are detected more frequently at low elevations, as they move from marine to terrestrial areas, because low elevation habitat tends to be closer to shore. Murrelets must pass over the shoreline to reach sites further inland. However, in some areas, murrelets leave the water and rapidly gain altitude before flying to distant inland sites (Van Vliet, pers. comm.), and would not be detected along the shoreline.

Responses of murrelet activity to variation in slope, aspect, and canopy cover were not consistent, and may have been influenced by local geography. Activity was positively related to northerly aspect in preliminary regression models, similar to findings of earlier analyses for Naked Island data. At Naked Island, there was a non-significant positive trend of higher murrelet activity on northerly slopes, possibly due to more high-volume forests on these slopes or the prevalence of southeast winds, that murrelets may seek to avoid (Kuletz and others, in press).

Occurrence of Occupied Behaviors

The influence of habitat features on the occurrence of occupied behaviors was similar to their influence on murrelet activity levels. In particular, the size of trees and the number of potential nest platforms were good predictors of murrelet occupied behavior. This is consistent with Alaskan tree nests that have been documented; most were located on large moss-covered platforms, often on the largest trees in an area (Naslund and others, in press). However, our results could be biased in that occupied behaviors in non-forested habitats have not been adequately defined.

Epiphyte cover, number of potential nest platforms, and tree size were clearly related. The importance of these habitat features to nesting murrelets may vary geographically. For example, epiphyte cover may be more important in Alaska than in other areas; moss was not the primary nest substrate of some nests at lower latitudes (Hamer and Nelson, this volume b; Singer and others 1991). Naslund and others (in press) suggested that moss is more important as insulation in Alaska's severe climatic conditions. Additionally, moss increases platform size, which could be important where small trees predominate.

Nesting clearly occurs in non-forested areas (Day and others 1983). However, the extremely low levels of general activity and of occupied behaviors at non-forested sites suggest that nesting activity in non-forested areas is less common than in forested areas. We believe that our results indicate that murrelet nesting density is low in sparsely forested or non-forest areas and that such habitat is of less importance to the population. However, it is possible that differences in murrelet activity levels and behaviors in non-forested and forested habitats may not reflect actual differences in murrelet abundance. For example, murrelets may be more vulnerable to predation in open areas and therefore less active around ground nests.

Effects of Survey Methods

Levels of murrelet activity did not vary among survey methods. However, significantly more occupied behaviors were observed when surveys were done from upland sites rather than from the shoreline or a boat. Occupied behaviors may be hard to detect during surveys conducted from a boat because the observer is often 50-100 m from forest habitat. However, occupied behaviors were equally low in frequency when surveys were done from the shoreline. Thus, our results may reflect real differences in habitat use. Although murrelets sometimes nest within a few hundred meters of the shore (Cody, unpubl. data; Kuletz, unpubl. data; Marks, unpubl. data; Naslund and others, in press), they may use areas along the shoreline less frequently than those further inland (Hamer, this volume). The effect of survey method was confounded with effect of survey area, because boat and shore-based surveys predominated at Prince William Sound and Kenai Fjords National Park, whereas upland surveys predominated at Naked Island and Afognak Island. The latter had very high activity levels, large trees and high epiphyte cover (Naslund and others, in press), and the high occupied status rate could have been due to truly higher nesting densities.

Sources of Unexplained Variation

Our best multiple regression model explained 52 percent of the variation in murrelet activity. There were many potential sources of unexplained variation. Because sites were surveyed only once, day-to-day variation within the same area could have contributed to incorrect estimation of general activity level of a given site. We did not account for observer variability, which can introduce additional bias to murrelet surveys (Kuletz and others 1994c; Ralph, pers. comm.). Because each area was generally surveyed by different observers, area effects could be due partially to observer variability. In addition, differences in sampling design may have contributed to area effects or other variation. For example, all forest was treated equally in our analyses, yet forest characteristics (e.g., age structure, volume, tree species) are quite variable. The Naked Island group was the only area for which specific forest types were stratified and sampled.

Prevailing winds, local topography and vegetation patterns varied throughout the study area. Therefore, the geographic range of study sites likely contributed to the variation in murrelet activity we observed. In addition, murrelet nesting distribution may vary with availability of suitable habitat. For example, murrelets may be more dispersed in Prince William Sound if prime nesting habitat is abundant and widespread, whereas nesting density may be higher in good habitat on the Kenai Peninsula if suitable habitat is sparse. Thus, the lower activity levels in Prince William Sound, relative to the Kenai Peninsula, may reflect differences in habitat availability, rather than habitat suitability, between the two areas.

An important factor not considered in our models was the adjacent marine environment and the availability of foraging habitat. These factors must ultimately determine the use of suitable nesting habitat. Thus, the apparent increase in murrelet activity from Prince William Sound to Afognak Island may also reflect large-scale differences in prey availability.

Conclusions

These models primarily serve as descriptive tools until they can be tested with independent data. However, we were able to explain 52 percent of the total variation in Marbled Murrelet activity levels based on temporal, topographic, and habitat characteristics. Further, our results suggest an 83 percent success rate of classifying murrelet nesting habitat in the areas examined on the basis of occupied behavior. The features indicative of murrelet nesting habitat include low elevation locations near the heads of bays, with extensive forest cover of large old-growth trees. In some areas, such as the Kenai Fjords, location relative to bay heads may be less important. The best predictors of nesting habitat in forested areas are high epiphyte cover and large numbers of potential nesting platforms on trees.

Our results were derived from surveys designed to estimate murrelet use of forested habitat. Potential variation in murrelet behavior associated with habitat type (i.e., forest or non-forest) has not been adequately examined and could influence accurate interpretation of survey results. Therefore, caution should be exercised when extrapolating observed trends on a broad scale across the landscape.

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