

Chapter 19

Marbled Murrelet Habitat Associations in Oregon

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Abstract: We described habitat associations of Marbled Murrelet (*Brachyramphus marmoratus*) nesting ($n = 10$) and occupied ($n = 184$) sites in Oregon. We compared habitat characteristics of 177 occupied sites to a random sample of 9,625 sites ($n = 531$) of unknown murrelet status. In addition, we briefly described the characteristics of 22 nests and compared 10 of the nest sites to adjacent sites. In general, occupied sites were older, had larger midstory trees, and had larger and greater densities of dominant (or remnant) trees than random sites. In addition, dominant tree height and density, midstory and understory tree diameter and percent cover, and percent canopy closure were important habitat components for predicting murrelet occupancy. All nests were in old-growth Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and Sitka spruce (*Picea sitchensis*) trees > 127 cm in diameter and > 36 m tall. Murrelet nest sites had fewer trees/ha and less canopy closure compared to adjacent sites. Our results support previous studies that concluded murrelets use stands with old-growth characteristics and that stand structure is more important than stand age. Knowledge of habitat associations does not imply habitat quality, which should be quantified through studies on reproductive success in relation to habitat and landscape characteristics.

Marbled Murrelets (*Brachyramphus marmoratus*) use old-growth and mature forests, or forests with old growth components, nearly year-round (Naslund 1993b, Nelson 1990b, Paton and Ralph 1990, Rodway and others 1991). Characteristics of these forests have been analyzed at the stand, landscape, nest, and nest-site levels (Burger, this volume a; Hamer, this volume; Hamer and Nelson, this volume b; Naslund and others, in press; Nelson and Hamer 1992; Rodway and others 1991; Singer and others 1991, in press). From these studies we know that murrelets nest in large diameter trees and may be selecting stands based on number of potential nest platforms, and density and diameter of dominant trees.

Data on the distribution and habitat associations of Marbled Murrelets have been collected in Oregon since 1988. This paper provides a synthesis of murrelet habitat associations by using existing data on occupied stands and nest sites, and summarizes new stand-level habitat data from state and federal agencies. Our objectives were to: (1) summarize habitat characteristics of occupied sites, (2) determine habitat associations by comparing occupied sites to other sites, and (3) identify the key habitat components of murrelet habitat. Knowledge of Marbled Murrelet habitat associations may assist in designing and implementing successful habitat management plans for this species.

Study area

Study sites were located in the Coast Range and Klamath Mountain (Siskiyou Mountains) Provinces in Oregon (Franklin and Dyrness 1973). These areas consisted of rugged, mountainous terrain, with steep slopes and deeply cut river and creek drainages. Elevations ranged from 50 m along the coast of Oregon, to more than 1200 m in the central mountains. The climate consists of cool, wet winters and warm, dry summers. Mean temperatures range from 0° C in winter to 24° C in summer, and annual precipitation varies from 150 to 300 cm (Franklin and Dyrness 1973).

These areas are primarily forested, although they have been intensively managed for timber since the early 1900s, and many stands are <200 years old. In addition, natural and man-caused fires have altered many stands. Relatively small, isolated patches of mature and old-growth tree species remain. Douglas-fir (*Pseudotsuga menziesii*) was the dominant tree species in the north and mixed-evergreen species, including Douglas-fir and tanoak (*Lithocarpus densiflorus*), were dominant in the south.

Methods

Between 1990 and 1993, murrelets were surveyed on state and federal lands throughout the Coast Range and Siskiyou Mountains, primarily within 50 km of the coast. Surveys included intensive research surveys, and intensive and general surveys for agency monitoring projects. Forest stands were surveyed to existing protocols (Paton and others 1990, Ralph and Nelson 1992, Ralph and others 1993) and were classified as occupied (birds exhibiting nesting or below canopy activity), with murrelets present (presence), or without murrelets (undetected), based on murrelet behavior patterns. In addition, we searched for nests using three methods: watching murrelets land in trees, searching for eggshells on the forest floor, and climbing trees to examine branches for nest cups.

Characteristics of Occupied Sites

Four databases were examined. The characteristics of occupied sites were summarized using one state lands database from Oregon Department of Forestry (Reagan, pers. comm.), two U.S. Forest Service databases from the Siuslaw National Forest (McCain, pers. comm.; Wettstein, pers. comm.), and one research database from Oregon State University. Habitat variables differed among databases. Similar habitat variables were used in the analyses where possible. We used Spies and Franklin's (1991) definition for stand age (i.e., young stands = 40–80 years, mature = 80–200 years, and old-growth = 200+ years). Remnant trees were defined as those

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that survived recent fires and were ≥ 66 cm d.b.h., except in one Forest Service database where remnant trees were classified as ≥ 100 cm d.b.h..

State Lands Database

Data were compiled from Oregon Department of Forestry's (ODF) OSCUR Inventory System (Ownership, Soils, forest Cover, land Use, and operation Rating). The OSCUR database was comprised of habitat variables collected between the mid-1970s and 1993 (*appendix 1*). ODF delineated and described habitat characteristics in forest sites through one of the following: (1) photographic interpretation; (2) stand examinations (fixed plot cruising, variable plot inventory, or timber sale appraisal); and (3) reconnaissance (walk-through) (ODF 1991). The OSCUR database included data from 6,409 sites. A site was defined as a uniform, homogeneous tree community that usually was a portion of a larger, contiguous, heterogeneous stand. Sites were characterized by approximately 160 habitat and geographic variables. In addition, comments from original data sheets were included to supplement data for some sites.

We selected 34 key habitat variables (*appendix 2*) and forest sites ≥ 40 years old for analyses. Sites of this age were chosen because the youngest occupied site on state lands was classified as 42 years old (although the site included remnant old-growth trees). In addition, we were interested in examining differences of habitat characteristics between occupied and random sites within a sample universe of only suitable habitat i.e., sites containing large trees with adequate branch sizes and moss coverage to accommodate nesting (Grenier and Nelson 1994). Using maps and databases, we found that 72 occupied sites existed on ODF lands (Allen, pers. comm.; Goggans, pers. comm.; Nelson 1990b; Nelson and Shaughnessy 1992; Platt and Goggans 1992; Shaughnessy and Nelson 1991). Characteristics of these 72 occupied sites were compared to a random sample of 216 sites of unknown murrelet status.

National Forest Land Databases

Vegetation Resource and Structure Examination Databases (VSE)—Older-aged forests or those with multiple canopy layers were monitored on the Siuslaw National Forest in 1990. These study sites were located in areas proposed for timber harvest and in Northern Spotted Owl (*Strix occidentalis*) Habitat Areas. In addition, Vegetation Resource Examinations (VRE) were conducted in 1991 and 1992 to ground truth satellite imagery of old-growth and mature forests with multi-layered canopies. Overlapping data from the two databases (1209 VRE and 1210 VSE plots) were used for analyses. Forty-seven habitat variables were common to both databases (*appendix 2*). Data from 120 sites (Wettstein, pers. comm.), 30 occupied sites and 90 other sites of unknown murrelet status, were used for analyses.

Ecological Habitat Sampling—Ecologists at the Siuslaw National Forest collected habitat data in intensive and

reconnaissance plots throughout the forest from 1981 to 1984 (Hemstrom and Logan 1986; USDA 1983, 1985). The database provided to us included 974 forested sites and 162 habitat variables (McCain, pers. comm.). We used ArcView (1992) to determine that 75 occupied sites overlapped with plots in this database. We selected 13 of the 162 habitat variables for our analyses (*appendix 3*). To be consistent with the ODF database, we used data from sites ≥ 40 years old. The characteristics of the 75 occupied sites were compared with a random sample of 225 sites of unknown murrelet status.

Research Database

In 1992, 40 small (≤ 12 ha), isolated, mature and old-growth stands were selected (Nelson and Hardin 1993a). Using protocol surveys, we determined that 10 of these stands were occupied. Habitat characteristics were measured in two 25-m-radius circular plots randomly located within each of these stands. Variables included number of trees and snags by species, tree and snag diameter at breast height (d.b.h.), heights (m) of five dominant conifers (measured by triangulation with a Suunto optical clinometer), height (m) and decay class of snags (Cline and others 1980), forest zone (Franklin and Dyrness 1973), ecozone (average precipitation levels), plant associations (Hemstrom and Logan 1986), number of canopy layers, canopy cover (visual estimate of percent crown closure), ground cover (percent and species composition), abundance of moss and dwarf-mistletoe (*Arceuthobium* sp.), number of suitable nest platforms (> 18 cm d.b.h., > 15 m height), slope (percent), aspect (degrees), position on slope (canyon bottom, lower 1/3, middle 1/3, upper 1/3, ridgetop), distance to water (m), and distance to opening (m; opening defined as road, river, clearcut, or vegetation type without trees but not forest gap). Calculations made from these data included density (number/ha) of trees (≥ 46 and ≤ 80 cm d.b.h.) and dominant trees (≥ 81 cm d.b.h.), mean diameter (d.b.h., cm) of all trees and dominant trees, mean dominant tree height (m), and tree species composition. Percent cover of epiphytes (moss and lichens) were recorded in four categories: (1) trace, (2) 1-33 percent, (3) 34-66 percent, (4) 67-100 percent. Average mistletoe infestation was calculated for each plot using an index of 0 to 6 developed by Hawksworth (1977). Distance inland (km), latitude, elevation (m), and stand size (ha) were determined from topographic maps (1:250,000) and aerial photos (1:1,000).

Nest Site Characteristics

Nests were located using ground-based and tree climbing techniques, most (15 of 22) in areas where likelihood of finding nests was considered to be high. Ground-based methods consisted of observing the flight of individual birds during dawn and dusk activity periods, and searching for eggshell fragments on the forest floor. Flight behaviors suggesting the presence of nesting birds (e.g., landing in or departing from trees and flying silently below the canopy) were identified at survey stations established in areas where

potential nest trees were located or where general activity levels were high, and at previously unsurveyed sites. Eggshell searches were conducted around all trees where birds were observed landing or taking off, and around numerous other trees that had potential nest platforms (platforms ≥ 18 cm in diameter and ≥ 15 m above ground). When potential nest trees were found, surveys were conducted on 1 to 3 successive mornings to confirm the presence of an active nest and identify its location.

Nests located by tree climbing were found during an intensive tree climbing study at a single site or while re-climbing trees previously known to support nests (Nelson and others 1994a). The tree climbing study consisted of climbing all trees (Perry 1978) within a 40-m-radius plot and examining all platforms for nests. In addition, seven trees containing nests found between 1990 and 1992 were climbed in 1993 to determine if the nests had changed over time and to determine if nests or nest trees were reused.

Characteristics of nests and nest trees were measured at the 22 nest sites. Nest tree measurements included diameter at breast height (d.b.h., cm), height (m), diameter at nest limb (cm), and nest branch height (m), diameter at the trunk and at the nest (cm), branch length (m), and position in crown (percent tree height). Nest measurements included distance from the trunk (cm) and cup dimensions (cm). In addition, the moss depth adjacent to the nest (cm), nest platform dimensions (cm), and canopy closure above the nest (percent) were measured.

Micro-site habitat features of nest sites and 2 to 3 adjacent sites were measured at ten of the nests in 0.2-ha (25-m radius) plots (as described previously). Plots for nest sites were centered on the nest tree. Adjacent plots, centered around a dominant canopy-forming tree, were a minimum of 75 m from nest trees, and were located the same distance from forest edges as nest trees to minimize any edge biases. Micro-site habitat characteristics were compared between nest sites and adjacent sites within the same stand to determine if the location of nests was associated with specific micro-site characteristics.

Data Analyses

Occupied Sites and Habitat Associations

We used the two-sample Kruskal-Wallis test (Zar 1984:138) to compare habitat characteristics of occupied sites to a random sample of other sites (with unknown murrelet status). The number of random sites selected equalled three times the number of occupied sites (Breslow and Day 1980:27; Ramsey, pers. comm.; Schafer, pers. comm.). The Chi-square goodness-of-fit test (Zar 1984) and Bonferroni Z-statistic (Byers and others 1984, Neu and others 1974) were used for categorical data.

Logistic regression was used to determine key habitat components of occupied and random sites for each database (Manly and others 1993, Ramsey and others 1994). The following two steps were used in our analyses: (1) habitat variables (continuous and categorical) were divided into

groups of related variables that described one or two biological aspects of the site. Logistic regression was used to test statistical significance of each variable within the group. (2) habitat variables that were statistically significant within the groups ($P < 0.05$) were then used in the stepwise procedure to determine the final model. Variables were excluded if $P > 0.05$.

Logistic regression helps select a set of key habitat variables that represent the probability of site occupancy. We chose to use logistic regression as a tool to identify key components of murrelet habitat, rather than determining the predictive probabilities of the occupancy rates of murrelets. This was due to: (1) the use of retrospective sampling (Ramsey and others 1994); (2) the limitations of the databases (i.e., data were collected over many years so sampling methods and data collectors may have changed yearly and the data were not collected with the murrelet in mind); and (3) the murrelet status of random sites was unknown.

Nest Sites

Habitat characteristics within nest plots were compared to average values for adjacent plots using a Wilcoxon test (paired-sample signed-rank; Snedecor and Cochran 1980:140). Each nest site was treated as a block, and the overall test statistic was based upon the cumulative differences among plots. A Chi-square test using a Bonferroni Z-statistic was used to compare snag decay class.

Results

Occupied Site Characteristics

State Lands Database

Tree Species—Douglas-fir was the dominant tree species (SPECIES1) in 67 percent of occupied sites ($n = 72$) and 83 percent of random sites ($n = 216$). The codominant trees (SPECIES2) were generally a combination of Douglas-fir, western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and red alder (*Alnus oregona*) in occupied and random sites.

Age, Tree Diameter, and Tree Density—Twenty-two percent (16 of 72) of occupied sites were ≤ 80 years of age (AGE1993) whereas 60 percent (130 of 216) of random sites were ≤ 80 years old. Ninety four percent (15 of 16) of these young occupied sites had remnant trees (TPH66, ≥ 66 cm d.b.h.), averaging 19.5 trees/ha (range: 2.5-75.0 trees/ha; s.e. = 5.0), and 15 of these sites contained mature trees (TPH46, ≥ 46 cm d.b.h.; $\bar{x} = 73.0$; s.e. = 11.6; range = 12.3-140.8). Random sites ≤ 80 years of age averaged only 10 remnant trees/ha (s.e. = 1.4; range = 2.5-59.3) (table 1, appendix 1). All occupied sites ≥ 81 years old had remnant trees, averaging 46.9 trees/ha (range = 2.5-116.1 trees/ha; s.e. = 2.8). Similarly, 97 percent (83 of 86) of random sites ≥ 81 years old had remnants averaging 45.9 trees/ha (range = 2.4-79.0 trees/ha; s.e. = 2.3).

Mistletoe, Platforms, and Moss Abundance—Variables in the database did not include information on nest platforms.

Table 1—Habitat characteristics of 72 Marbled Murrelet occupied sites and 216 random sites on State Lands, Oregon. Data are from Oregon Department of Forestry's OSCUR database, 1993. See appendix 1 for variable definitions

Variable	Occupied			Random			P-value ¹
	$\bar{x}$	(s.e.) Range	n	$\bar{x}$	(s.e.) Range	n	
DBH1	60.7	(3.10) 23-142	72	44.7	(1.30) 18-130	203	0.0001
BA1	35.8	(1.95) 9-91	72	33.3	(0.99) 4-84	200	0.3163
MBFAC1	237.7	(15.56) 52-734	72	173.1	(7.23) 6-548	200	0.0001
DBH2	59.2	(4.65) 18-178	62	40.4	(1.63) 15-122	153	0.0001
BA2	10.2	(1.04) 0-38	62	8.3	(0.46) 0-35	153	0.0554
MBFAC2	65.8	(7.05) 6-274	59	37.9	(2.04) 6-122	147	0.0002
DBH3	48.0	(2.59) 23-97	46	46.7	(2.06) 15-104	82	0.0448
BA3	6.0	(0.76) 1-24	46	5.8	(0.54) 0-22	82	0.6478
MBFZC3	29.7	(3.73) 6-99	45	26.8	(2.68) 6-99	67	0.3677
DBH4	38.6	(2.34) 23-84	30	35.1	(1.78) 15-64	42	0.0351
BA4	7.7	(1.21) 1-21	30	6.4	(1.08) 0-30	42	0.1695
MBFAC4	38.5	(6.29) 6-128	28	26.2	(5.42) 6-157	36	0.0980
TPH15	89.0	(15.47) 17-410	29	134.4	(9.88) 12-645	116	0.0260
TPH20	50.7	(5.73) 12-153	39	112.7	(6.52) 5-432	141	0.0001
TPH25	44.0	(5.76) 7-131	35	68.4	(4.55) 7-334	158	0.0044
TPH30	37.8	(4.13) 5-138	52	53.3	(3.56) 5-247	164	0.0067
TPH36	48.9	(5.76) 2-220	62	67.0	(3.53) 2-230	177	0.0018
TPH46	56.1	(5.04) 2-183	70	48.4	(2.84) 2-277	174	0.2189
TPH66	41.0	(2.79) 2-116	71	30.1	(1.93) 2-79	114	0.0010
AGE1993	105.1	(3.83) 42-213	72	75.9	(1.72) 40-140	216	0.0001
CDBH	55.1	(2.01) 25-112	72	44.2	(1.09) 20-112	210	0.0001
HDBH	37.6	(1.37) 18-58	46	33.8	(0.71) 15-61	125	0.0005
CTPH	248.3	(21.79) 12-961	72	313.1	(16.09) 10-1260	210	0.0616
HTPH	99.3	(12.31) 7-366	46	163.6	(14.08) 5-783	125	0.0208
CBA	45.7	(2.25) 12-100	72	35.6	(1.08) 1-92	210	0.0002
HBA	9.5	(1.01) 1-24	46	11.6	(0.79) 0-54	125	0.3464
CMBFAC	297.2	(16.96) 58-752	72	188.2	(7.87) 6-594	196	0.0001
HMBFAC	46.6	(5.36) 6-128	44	46.6	(3.03) 6-157	113	0.9120

¹Significant difference between occupied and random sites ($P < 0.05$, Kruskal-Wallis test)

However, data concerning tree damage or abnormalities were collected and may indicate presence of nesting platforms. Sixty-three percent (45 of 72) of the occupied sites had tree damage or abnormalities, 33 percent (15 of 45) of which included mistletoe infestations. Damage or abnormalities observed in random sites was similar (59 percent; 128 of 216 trees), however mistletoe infestation was less common in random sites (12 percent; 15 of 128 trees).

National Forest Land Databases

Vegetation Resources and Structure Examination Databases—Douglas-fir was the most common dominant tree in occupied and random sites. However, western red cedar (RC_DBH3, *Thuja plicata*), which occurred in approximately 33 percent of occupied sites, had the largest mean diameter ($\bar{x}$ = 114.3 cm, *s.e.* = 6.65, *n* = 10). Occupied sites had an average of 13.4 remnant trees/ha (REM, trees $\geq$ 100 cm d.b.h.), and 63.7 percent canopy closure (table 2, appendix 2).

Ecology Databases—Occupied sites were mid-seral stage stands with large tall conifer trees (table 3, appendix 3). Most (75 percent) occupied sites were located in western hemlock climax forest types. The most common (17 percent; 13 of 75) plant association in occupied sites was western hemlock/Oregon oxalis (*Oxalis oregana*). This plant association only occurred in 5 percent (11 of 225) of random sites, and the frequency of occurrence was significantly less than in occupied sites (χ^2 = 30.2, *df* = 9, *P* = 0.0004). The most frequently occurring plant association in random sites was western hemlock/vine maple (*Acer circinatum*)/western swordfern (*Polystichum munitum*) (12 percent; 27 of 225). The western hemlock/Oregon oxalis sites occur on moist, shaded upper slopes and benches or alluvial terraces and have high conifer basal area (79.7 m²/ha, *s.e.* = 4.6, *n* = 9 compared to 71.0 m²/ha average for 22 plant associations, *s.e.* = 2.0, *n* = 178; Hemstrom and Logan 1986).

Research Database

Ten occupied sites from this study were located in the western hemlock (*n* = 6) and Sitka spruce (*n* = 4) Zones (Franklin and Dyrness 1973), and included one or more of the following plant associations: vine maple (*n* = 4), salal (*Gaultheria shallon*) (*n* = 3), sword fern (*n* = 5), salmonberry (*Rubus spectabilis*) (*n* = 2), Pacific rhododendron (*Rhododendron macrophyllum*) (*n* = 1), and Oregon grape (*Berberis aquifolium*) (*n* = 2). All sites had two or more canopy layers ($\bar{x}$ = 2.2, *s.e.* = 0.1), were located between middle of the slope and the ridgetop, had > 25 percent moss ($\bar{x}$ index = 3.8, *s.e.* = 0.2), contained some mistletoe or witches brooms ($\bar{x}$ index = 2.2, *s.e.* = 0.3), and had platforms for nesting ($\bar{x}$ = 1.3 per plot, *s.e.* = 0.3) (table 4). The number of suitable platforms was correlated with the number of canopy layers (*r* = 0.39, *P* = 0.02, *n* = 34) and with mistletoe abundance (*r* = 0.43, *P* = 0.01, *n* = 34).

Habitat Associations

State Lands

Twenty-one of 34 habitat variables were significantly different between occupied (*n* = 72) and random (*n* = 216) sites (*P* < 0.05) (table 1). In general, occupied sites were older (AGE1993), contained larger diameter conifers (DBH1-4, CDBH, CBA) and hardwoods (HDBH), had more large remnant trees/ha (TPH66), and had fewer small/medium-sized trees (TPH15-36) and hardwoods/ha (HTPH) than random sites (table 1, appendix 1).

Stepwise logistic regression suggested a model with only large remnant tree density (TPH66) as a significant predictor of murrelet habitat (*P* = 0.0164; *n* = 46 occupied and 80 random sites). It was estimated that the odds of use were 4.9 percent higher for each unit increase in large remnant tree density (95 percent Confidence Interval [CI] = 0.8 percent to 9.1 percent; *s.e.* = 0.02).

National Forest Land Databases

Vegetation Resources and Structure Examinations—Seven variables differed (*P* < 0.05) between occupied (*n* = 30) and random (*n* = 90) sites. Occupied sites had less slope, less canopy closure (CC), more large Douglas-fir/ha (DF_TPH3), larger midstory western hemlocks (WH_DBH1) and western redcedars (RC_DBH1, RC_DBH2), and fewer shade tolerant trees/ha $\geq$ 41 cm (STH_40) than random sites (table 2, appendix 2).

Stepwise logistic regression suggested a model with larger diameters of midstory western redcedar (RC_DBH1) and less canopy closure (CC) as significant predictors of murrelet habitat. It was estimated that the odds of use were 48.3 percent higher for each unit increase in diameter of midstory western red cedar (95 percent CI = 9.1 percent to 100 percent; *s.e.* = 0.1565, *n* = 12 occupied and 28 random sites). Also, it was estimated that the odds of use were 16.5 percent higher for each unit decrease in canopy closure when comparing occupied to random sites (95 percent CI = 2.8 percent to 32.1 percent; *s.e.* = 0.064).

Ecology—Four habitat variables were significantly different (*P* < 0.05) between occupied (*n* = 75) and random sites (*n* = 225). Occupied sites were in later seral stage classes (SERAL), and had taller (HT), older (AGE), and larger diameter trees (DIA) than random sites (table 3, appendix 3).

Stepwise logistic regression suggested a model with tree height (HT) and percent cover of understory trees (TREER) as significant predictors of murrelet habitat. It estimated that the odds of use were 2.3 percent higher for every unit increase in tree height (95 percent CI = 0.8 percent to 3.7 percent; *s.e.* = 0.0022; *n* = 34 occupied and 86 random). Also the odds of use were 4.3 percent higher for every unit increase in percent cover of understory trees (95 percent CI = 0.3 percent to 8.5 percent; *s.e.* = 0.0202).

Table 2—Habitat characteristics of 30 Marbled Murrelet occupied sites and 90 random sites on the Siuslaw National Forest, Oregon, 1990-1992. Data are from forest stand inventories (Vegetation Structure and Vegetation Resource Examination). See appendix 2 for variable definitions

Variable	Occupied			Random			P-value ¹
	$\bar{x}$	(s.e.) Range	n	$\bar{x}$	(s.e.) Range	n	
SLOPE	35.0	(3.63) 7-80	30	47.2	(2.39) 5-90	90	0.0053
ELEV	255.0	(18.68) 122-488	30	268.5	(15.79) 91-823	89	0.9606
REM	13.4	(3.87) 1-64	16	10.4	(2.42) 1-58	29	0.2626
CC	63.7	(3.20) 16-83	30	76.1	(1.16) 36-94	90	0.0004
C_HT	55.4	(1.53) 37-69	30	55.7	(0.85) 35-72	90	0.9999
DF_DBH3	88.4	(3.12) 41-122	29	94.7	(2.18) 64-160	84	0.3472
DF_DBH2	57.7	(3.63) 33-99	23	58.2	(4.17) 25-185	49	0.4253
DF_DBH1	27.9	(2.46) 17-46	10	30.7	(4.01) 13-137	31	0.6054
DF_TPH3	66.0	(8.70) 11-224	29	45.0	(3.34) 2-128	84	0.0267
DF_TPH2	17.8	(4.08) 1-69	23	16.8	(1.66) 0-43	49	0.4249
DF_TPH1	22.2	(10.28) 5-114	10	16.3	(2.30) 2-56	31	0.8021
WH_DBH3	74.9	(2.95) 61-90	14	76.2	(1.93) 51-107	53	0.7991
WH_DBH2	52.6	(4.09) 26-94	19	45.0	(1.52) 25-94	55	0.1090
WH_DBH1	31.5	(3.25) 19-61	15	23.4	(1.14) 13-56	53	0.0021
WH_TPH3	37.8	(11.19) 2-115	14	44.0	(5.14) 2-162	53	0.3468
WH_TPH2	25.0	(4.94) 2-79	19	39.0	(4.25) 3-136	56	0.1038
WH_TPH1	42.7	(9.29) 4-130	15	52.4	(6.25) 3-185	53	0.5483
RC_DBH3	114.3	(6.65) 82-150	10	105.2	(7.62) 5-211	34	0.2263
RC_DBH2	72.6	(3.99) 58-105	12	59.7	(4.80) 8-156	32	0.0081
RC_DBH1	39.9	(4.01) 23-71	13	26.7	(1.80) 3-56	29	0.0031
RC_TPH3	3.5	(1.38) 0-15	10	5.4	(1.26) 1-28	23	0.1265
RC_TPH2	10.6	(1.85) 2-27	12	17.3	(1.16) 2-69	32	0.2626
RC_TPH1	27.4	(7.41) 2-94	13	25.0	(3.83) 4-113	31	0.9384
DF_81	27.9	(2.82) 3-57	30	23.0	(1.70) 1-66	82	0.1046
STH_40	47.4	(8.10) 1-149	26	67.5	(5.14) 1-194	69	0.0270

¹ Significant difference between occupied and random sites ($P < 0.05$, Kruskal-Wallis test)

Table 3—Habitat characteristics of 75 Marbled Murrelet occupied sites and 225 random sites on the Siuslaw National Forest, Oregon, 1981-1984. Data are from the Ecology Program Intensive and Reconnaissance Plots database, 1993. See appendix 3 for variable definitions

Variable	Occupied			Random			P-value ¹
	$\bar{x}$	(s.e.) Range	n	$\bar{x}$	(s.e.) Range	n	
ELEV	248.3	(15.25) 9-604	75	293.2	(11.26) 6-1067	225	0.0650
ASPECT	198.4	(12.06) 6-358	75	194.1	(6.86) 0-361	225	0.6602
SLOPE	42.5	(2.52) 3-85	73	45.8	(1.58) 2-92	224	0.2788
TREER	9.5	(2.37) 1-75	50	4.7	(0.60) 1-35	126	0.1737
SHRUBH	44.2	(3.58) 1-95	75	52.5	(2.07) 1-99	220	0.0518
HERB	52.8	(4.02) 3-99	60	45.7	(2.28) 1-98	181	0.0972
MOSS	22.2	(2.86) 2-95	63	19.8	(1.67) 1-90	185	0.1121
SERAL	2.9	(0.07) 2-4	75	2.7	(0.04) 2-5	218	0.0414
TBAL	72.6	(3.93) 9-156	57	68.3	(2.07) 14-134	169	0.3299
TBAD	17.8	(1.69) 9-46	34	17.3	(1.10) 0-64	103	0.5677
DIA	117.2	(4.75) 58-208	57	101.1	(2.37) 30-216	172	0.0046
HT	57.5	(1.17) 34-79	56	52.4	(0.85) 18-79	172	0.0049
AGE	147.7	(12.81) 58-486	57	112.5	(4.23) 40-400	172	0.0035

¹ Significant difference between occupied and random sites ($P < 0.05$, Kruskal-Wallis test)

Nest Sites

Twenty-two nests were found between 1990 and 1993. Ten nests were located by observing adult Marbled Murrelets landing in or departing from a nest tree, three were found after finding eggshell fragments on the forest floor, six were located during the intensive tree climbing study, and three were found while reascending known nest trees. Overall, nine nests were confirmed active when discovered (Nelson and Peck, in press). Of these, four were in the egg stage and five were in the nestling stage. Nestlings were thought to have fledged from three of these nests (see Nelson and Hamer, this volume a; Nelson and Peck, in press).

Nest and Nest Tree Characteristics

All nests were located in trees ≥ 127 cm in d.b.h. ($\bar{x} = 187.9$, s.e. = 9.4) and ≥ 36 m tall ($\bar{x} = 65.5$, s.e. = 2.4; table 5). Twenty nests were found in Douglas-fir, one was found in a Sitka spruce, and one was found in a western hemlock. Nests generally consisted of depressions in a moss mat

(average moss depth = 5.3 cm), but compacted duff (needles, lichen, debris) substrates were also used. Nest cups averaged 12.0 x 11.1 cm (length x width) and were located on platforms considerably larger than the nest ($\bar{x} = 42.2 \times 31.7$ cm, s.e. = 4.2 and 2.9, respectively). The placement of nests on nest branches was variable, ranging from 1 to 762 cm from the trunk of the tree ($\bar{x} = 101.3$, s.e. = 35.7). The nest in the Sitka spruce was furthest from the tree trunk (at 762 cm); all other nests were located ≤ 230 cm from the trunk. Nest height ranged from 18 to 73 m above the ground ($\bar{x} = 50.3$, s.e. = 2.4; table 5).

Nest Stand Characteristics

Nest stands generally consisted of 2 to 3 canopy layers ($\bar{x} = 2.2$, s.e. = 0.09, $n = 10$). Trees ≤ 45 cm d.b.h. were most numerous (94.3 trees/ha), followed by trees ≥ 81 cm d.b.h., and trees 46-80 cm d.b.h. (64.3 and 39.7 trees/ha) (table 6). There were 7.1 (s.e. = 1.7) standing snags/ha in nest stands, with a mean height of 15.5 m (s.e. = 2.1) and mean d.b.h. of

Table 4—Overall habitat characteristics of occupied stands, Oregon Coast Range, 1992

Characteristics	$\bar{x}$	s.e.	Range	n
Stand size (ha)	6.5	1.1	2.0-12.1	10
Elevation (m)	298.8	56.6	61-610	10
Distance inland (km)	15.9	3.5	2.3-33.0	10
Distance to stream (m)	310.0	98.3	0-1000	10
Aspect (°)	194.3	15.7	65-328	20
Slope (pct)	53.7	7.0	3-126	20
Position on slope ¹	3.9	0.2	2-5	20
Canopy closure (pct)	48.9	4.3	13-83	20
Canopy height (m)	56.9	3.4	32-88	20
Canopy layers (no.)	2.2	0.1	2-3	20
Number of platforms	1.3	0.3	0-5	20
Moss index ²	3.8	0.2	3-5	20
Mistletoe index ³	2.2	0.3	1-5	20
Tree d.b.h. (cm)	43.8	0.9	10-206	1374
Tree d.b.h. ≥46 cm	80.6	1.3	46-206	518
Tree d.b.h. ≥81 cm	109.3	1.7	81-206	208
Tree density (no./ha)	349.8	24.1	208.8-565.2	20
Tree density ≥46 cm (no./ha)	131.9	15.0	10.2-269.9	20
Tree density ≥81 cm (no./ha)	55.7	6.8	15.3-127.3	19
Snag d.b.h. (cm)	57.8	2.7	10.5-187.0	212
Snag density (no./ha)	54.0	9.3	5.1-142.6	20
Tree basal area (m ² /ha)	56.3	5.2	12.6-86.3	20
Tree basal area ≥46 cm (m ² /ha)	69.9	5.9	4.6-111.5	20
Tree basal area ≥81 cm (m ² /ha)	53.1	7.0	8.0-101.1	19
Snag basal area (m ² /ha)	16.8	4.3	0.5-66.8	20

¹ Position on Slope: 1 = canyon bottom, 2 = lower 1/3, 3 = middle 1/3, 4 = upper 1/3, 5 = ridge top.

² Moss Index: 0 = none, 1 = trace, 2 = 1-24 percent, 3 = 25-49 percent, 4 = 50-100 percent.

³ Mistletoe Abundance: Divide tree into thirds. Rate each section; 0 for no mistletoe, 1 if less than 1/3 of branches are infected, and 2 if more than 1/3 are infected. Score range is 0-6.

81.4 cm (s.e. = 7.4). Mistletoe and witches brooms were found on dominant trees in most stands. Nests were located between 1.6 and 40 km from the ocean.

Three habitat variables at 10 nest sites differed from adjacent plots (*table 6*). The density of live trees in the largest size class (d.b.h. ≥81 cm) was greater in adjacent plots than in nest plots (64.3 versus 43.3 trees/ha; $P = 0.03$). Snag height was greater and snags were less decayed in adjacent plots compared with nest plots (15.5 versus 7.5 m; $P = 0.03$; 3.3 versus 3.7; $P < 0.001$, respectively). In addition, canopy closure was marginally greater in adjacent plots than nest plots (61.3 percent versus 41.2 percent, $P = 0.06$).

Discussion

Occupied Sites

In Oregon, sites occupied by Marbled Murrelets were characterized by large diameter conifers and hardwoods, tall trees, high densities of dominant trees, and low densities for small diameter trees (conifers and hardwoods combined). In addition, these sites were older, located on gentler slopes, and had less percent canopy cover than random sites. Important habitat components for predicting occupancy were height and density of dominant trees, diameter and percent cover of midstory and understory conifers, and canopy cover.

Table 5—Summary of nest and nest tree characteristics from 22 nests found in Oregon between 1990 and 1993

Characteristic	$\bar{x}$	s.e.	Range	n^1
Nest tree				
D.b.h. (cm)	187.9	9.4	127-279	19
Diameter at nest limb (cm)	80.1	6.2	36-122	15
Height (m)	65.5	2.4	36-85	19
Nest branch				
Height (m)	50.3	2.4	18-73	21
Diameter at trunk (cm)	31.1	2.6	15-56	19
Diameter at nest (cm)	29.4	2.7	10-50	20
Position in crown (pct.) (nest ht/tree ht)	74.7	2.6	50-9221	
Length (m)	5.1	0.7	1-12	17
Distance from trunk to nest				
	101.3 (68.2) ²	35.7 (14.2)	1-762 (1-230)	21 (20)
Nest cup				
Length (cm)	12.0	1.0	6.0-26.0	19
Width (cm)	11.1	0.7	7.0-17.8	19
Depth of cup (cm)	3.1	0.3	0.5-5.1	17
Depth of moss on branch (cm)	5.2	0.6	0.6-12.0	18
Nest platform				
Length (cm)	42.2	4.2	11-66	14
Width (cm)	31.7	2.9	10-51	21
Canopy closure above nest (pct.)	78.6	3.5	40-100	18

¹ Characteristics were not measured at some nests.

² Excludes a nest in a Sitka spruce 7.6 m from the trunk. This nest was 3.3 times farther than the next most distant nest and 11.2 times farther than the mean.

Tree species composition of occupied sites was consistent with composition across the landscape. The western hemlock/Oregon oxalis plant association, within the western hemlock zone, was especially important. These sites are very fertile and moist and may produce larger trees (Hemstrom and Logan 1986). In addition, moisture in these sites may decrease the likelihood of intense fires, thereby allowing higher densities of remnant trees.

Historically, extensive, and sometimes catastrophic, fires occurred in the Oregon Coast Range (Agee 1994). These fires created diverse forests with attributes of older-aged forests that are not found in intensively managed plantations. For example, natural stands generally have more tree species, less uniform tree sizes, more random spacing of trees, and larger remnant overstory trees, as compared to even-aged stands of the same age (Spies and Franklin 1991). Many of the occupied sites in Oregon were created naturally, and many have not been managed (i.e., thinned or partially harvested). Thus, these sites were uneven-aged forests and they included a variety of tree sizes and ages. Spacing of the dominant trees was not uniform, allowing midstory and understory trees to fill in the gaps in the canopy. The structure of these forests, in most cases, was similar to old-growth

forests, although tree density was lower and average tree size smaller than “classic” old-growth (as defined in Franklin and others 1986). It is the structure of these stands, the large trees with nesting platforms, hiding cover (vertical canopy cover), and variable canopy cover, that are important to murrelets. Mean tree age alone and low canopy closure do not indicate the quality of the habitat. For example, some sites on state lands were typed as young (≤ 80 years old), yet all of these sites had remnant trees (≥ 66 cm d.b.h.), except one, and all had other older forest structures that survived or were created by fire (snags, woody debris). The single young site without remnant trees was located adjacent to and contiguous with a stand that contained 42.0 remnant trees per ha. In addition, while low canopy closure may allow murrelets access to nests, most (70 percent) nests near openings or edges have been unsuccessful (Nelson and Hamer, this volume b). Therefore, suitable murrelet habitat likely includes complex structure, high densities of large trees, large nesting platforms, and hiding cover.

The key components of occupied sites in this study were similar to occupied sites throughout the Pacific Northwest and California, and to other studies in Oregon (Nelson 1989, 1990a). Most sites used by murrelets have

Table 6—Comparison¹ of vegetation characteristics between 25-meter plots around nest trees and within three plots² adjacent to 10 nest trees found in Oregon between 1990 and 1992

Characteristic	Nest plots		Adjacent plots		P-value
	$\bar{x}$	(s.e.) Range	$\bar{x}$	(s.e.) Range	
Canopy closure (pct.)	41.2	(9.2) 12-99	61.3	(6.6) 22-91	0.06
Tree density (no./ha)					
d.b.h. < 45 cm	87.6	(12.3) 25.5-147.7	94.3	(12.7) 5.0-134.1	0.42
d.b.h. = 46-80 cm	44.8	(9.2) 10.2-91.6	39.7	(3.0) 28.9-56.0	0.65
d.b.h. > 81 cm	43.3	(7.1) 15.3-91.6	64.3	(7.5) 20.4-88.3	0.03
Nest platforms (no./tree)	6.7	(1.0) 0.0-11.0	4.7	(0.8) 0.3-8.3	0.10
Mistletoe abundance	2.2	(0.4) 0.0-4.0	2.3	(0.5) 1.0-5.0	0.61
Snag density (no./ha)	5.4	(0.9) 2.0-11.0	7.1	(1.7) 1.3-18.7	0.29
Snag height (m)	7.5	(2.0) 2.0-21.2	15.5	(2.1) 4.9-24.8	0.03
Snag d.b.h. (cm)	75.4	(9.0) 30.8-108.3	81.4	(7.4) 33.2-113.0	0.76
Snag decay class	3.7	(0.2) 1-5	3.3	(0.1) 1-5	<0.001

¹ Comparisons based upon a Wilcoxon paired-sample test for all characteristics except decay class of snags which is compared using a Chi-square test and a Bonferroni Z-statistic (Neu and others 1974) for the distribution of observations within five decay-class categories.

² Characteristics measured within two adjacent plots at one nest site.

been in older-aged forests, with high densities of dominant trees (Burger, this volume a; Hamer, this volume; Miller and Ralph, this volume; Nelson 1989, 1990a; Paton and Ralph 1990). In addition, in British Columbia, the presence of murrelets was correlated with the presence of Sitka spruce and western hemlock, low elevations, and large trees which had platforms for nesting (Burger 1994, this volume a; Manley and others 1992; Rodway and others 1991). In Washington, number of platforms and moss abundance were the most important variables for predicting murrelet occupancy (Hamer, this volume). Elevation (low) and canopy closure (moderate) were also key characteristics of occupied sites (Hamer, this volume).

Nest Sites

Murrelets used mature or old-growth forests and large diameter Douglas-fir, Sitka spruce, and western hemlock trees

for nesting. Nests ($n = 22$) were on large limbs ($\bar{x} = 29.4$ cm) usually 18 m or more above ground level, and were located in trees > 127 cm ($\bar{x} = 187.9$) in diameter. Other structures at the nest were also important, including high vertical canopy cover above the nest cup ($\bar{x} = 78.9$ percent). In addition, all nests were located in forests with multi-layered canopies (2-3) with a wide range of both tree densities (121.0-718.8 ha) and canopy cover (12-99 percent).

In general, the forest immediately around the nest trees was open, with fewer dominant trees. The density of dominant trees at nest sites was lower than at adjacent sites. However, occupied sites had a higher density of dominant trees than random sites. Apparently, it is important for murrelets to have numerous dominant trees throughout a stand to provide nesting opportunities, but at the nest site, a lower density of dominant trees may facilitate access to the nest tree for a bird with limited flying maneuverability.

However, nests may have been easier to find by observers in situations where tree densities were low. In addition, very low canopy cover may allow higher predation rates (see Nelson and Hamer, this volume b). Conclusions about appropriate canopy cover levels for nesting murrelets cannot be made without further research on nesting success and with larger sample sizes.

The characteristics of nests in Oregon were similar to those described by others in Alaska, British Columbia, Washington, and California (Hamer and Nelson, this volume b; Jordan and Hughes, in press; Manley and Kelson, in press; Naslund 1993b; Naslund and others, in press; Nelson and Hamer 1992; Singer and others 1991, in press). Excluding Alaska, all nests have been located in trees > 88 cm in diameter and > 18 m in height ($n = 47$) (Hamer and Nelson, this volume b).

Conclusions

Our results support previous studies and observations that murrelets use older forests or forests with old-growth characteristics. Key habitat characteristics of occupied sites were tree height, density of dominant (or remnant) trees, diameter and percent cover of midstory and understory trees, and canopy cover. Nests were located in large trees with large platforms and high vertical canopy cover.

Additional detailed information on the characteristics (platform availability, abundance of mistletoe and moss) of Marbled Murrelet habitat are needed to refine the definition of suitable habitat in Oregon. Studies designed to collect habitat data specific to murrelets from plots in the forest (including the key variables listed above) are needed. In addition, further investigations into plant associations are recommended.

There are limitations to describing murrelet habitat on the basis of occupancy, presence, or abundance. We can describe the general features of habitat used by this species; however use of these measures as a means for determining habitat quality, suitability, or preference may not be valid, especially in patchy habitats (Fretwell and Lucas 1969, Hanski 1982, Van Horne 1983). Models developed to measure habitat quality and suitability have included components of density, reproductive rates, genetic contribution of adults to the next generation, and survival of adults and juveniles (Fretwell and Lucas 1969, Van Horne 1983). A more adequate means of evaluating habitat suitability will be to explore the relationship between reproductive success, and habitat and

landscape characteristics. This should be an emphasis of future research projects.

In addition, caution is advised in using our description of occupied sites from the state and federal databases. These data were not collected to describe murrelet habitat, and our analysis was retrospective. Occupied sites also were not selected randomly. Therefore, occupied site characteristics may be an artifact of how stands were chosen for timber harvesting and thus murrelet surveying, and which habitat variables were measured. Future research should include collecting data specific to biology of murrelets, e.g., availability of platforms, moss, and mistletoe.

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Appendix 1—Variables used to describe Marbled Murrelet occupied sites using data from Oregon's Department of Forestry OSCUR database. Note that the 1, 2, and 3 assigned to DBH are reversed compared to federal lands database

DBH1	-----	Average diameter (centimeters) at breast height (1.4 m) for the dominant species
BA1	-----	Basal area (m ² /hectare) for dominant species
MBFAC1	-----	Cubic meters per hectare of dominant species ¹
DBH2	-----	Average diameter (centimeters) at breast height (1.4 m) for the codominant species
BA2	-----	Basal area (m ² /hectare) for codominant species
MBFAC2	-----	Cubic meters per hectare of codominant species
DBH3	-----	Average diameter (centimeters) at breast height (1.4 m) for other species (midstory)
BA3	-----	Basal area (m ² /hectare) for other species
MBFAC3	-----	Cubic meters per hectare of other species
DBH4	-----	Average diameter (centimeters) at breast height (1.4 m) for other species (understory)
BA4	-----	Basal area (m ² /hectare) for other species
MBFAC4	-----	Cubic meters per hectare of other species
TPH15	-----	Trees per hectare in the 15.2-20.3 cm d.b.h. class
TPH20	-----	Trees per hectare in the 20.3-25.4 cm d.b.h. class
TPH25	-----	Trees per hectare in the 25.4-30.5 cm d.b.h. class
TPH30	-----	Trees per hectare in the 30.5-35.6 cm d.b.h. class
TPH36	-----	Trees per hectare in the 35.6-45.7 cm d.b.h. class
TPH46	-----	Trees per hectare in the 45.7-66.0 cm d.b.h. class
TPH66	-----	Trees per hectare in the 66.0+ cm d.b.h. class
AGE1993	-----	Age of the tree type calculated from 1993; age was estimated from several large trees in each plot.
CDBH	-----	Average diameter (centimeters) at breast height (1.4 m) for conifers
HDBH	-----	Average diameter (centimeters) at breast height (1.4 m) for hardwoods
CTPH	-----	Trees per hectare for conifers
HTPH	-----	Trees per hectare for hardwoods
CBA	-----	Basal area (m ² /hectare) for conifers
HBA	-----	Basal area (m ² /hectare) for hardwoods
CMBFAC	-----	Cubic meters per hectare of conifers
HMBFAC	-----	Cubic meters per hectare of hardwoods

¹ 1,000 board feet = 5.83 m³/hectare (ha)

Appendix 2—Variables used to describe stands of mature and old-growth forests on the Siuslaw National Forest, Corvallis, Oregon. Data were collected using Vegetation Resource and Structure Examination methods, 1990-1993. Note that the 1, 2, and 3 assigned to DBH are reversed compared to state lands database.

SLOPE	-----	Slope of the plot
ELEV	-----	Elevation of the plot (meters)
REM	-----	Number of remnant trees (≥ 100 cm d.b.h.)
CC	-----	Canopy closure as a percentage
C_HT	-----	Canopy height (meters)
DF_DBH3	-----	Average diameter (centimeters) at breast height for dominant (canopy) Douglas-fir
DF_DBH2	-----	Average diameter (centimeters) at breast height for codominant Douglas-fir
DF_DBH1	-----	Average diameter (centimeters) at breast height for early-seral (midstory) Douglas-fir
DF_TPH3	-----	Number of dominant Douglas-fir per hectare
DF_TPH2	-----	Number of codominant Douglas-fir per hectare
DF_TPH1	-----	Number of early-seral (midstory) Douglas-fir per hectare
WH_DBH3	-----	Average diameter (centimeters) at breast height for dominant western hemlock
WH_DBH2	-----	Average diameter (centimeters) at breast height for codominant western hemlock
WH_DBH1	-----	Average diameter (centimeters) at breast height for early-seral (midstory) western hemlock
WH_TPH3	-----	Number of dominant western hemlock per hectare
WH_TPH2	-----	Number of codominant western hemlock per hectare
WH_TPH1	-----	Number of early-seral (midstory) western hemlock per hectare
RC_DBH3	-----	Average diameter (centimeters) at breast height for dominant red cedar
RC_DBH2	-----	Average diameter (centimeters) at breast height for codominant red cedar
RC_DBH1	-----	Average diameter (centimeters) at breast height for early-seral (midstory) red cedar
RC_TPH3	-----	Number of dominant red cedar per hectare
RC_TPH2	-----	Number of codominant red cedar per hectare
RC_TPH1	-----	Number of early-seral (midstory) red cedar per hectare
DF_81	-----	Number of Douglas-fir per hectare with an average diameter ≥ 81.3 cm at breast height
STH_40	-----	Number of shade tolerant trees per hectare with an average diameter ≥ 40.6 cm at breast height (midstory)

Appendix 3—Variables used to describe forest stands >75 years old on the Siuslaw National Forest. Data were collected by the Ecology Program (USDA 1983, USDA 1985), Siuslaw National Forest, Corvallis, Oregon, 1982-1986

ELEV -----	The elevation of the plot (meters)
ASPECT -----	The aspect toward which the plot faces recorded as degrees azimuth
SLOPE -----	The slope of the plot in percent
TREER -----	The percent cover of understory trees (<3.7 meters in height)
SHRUBH -----	The percent cover of high woody perennial plants greater than 0.9 meters in height
HERB -----	The percent cover of herbaceous plants
MOSS -----	The percentage of the ground area which is covered by moss or lichens
SERAL -----	The seral stage of the site [1 = very early, pioneer (1 to 30 years) brush and small trees; 2 = early seral (30 to 100 years) young stand; 3 = mid-seral (100 to 00 years) mature stand; 4 = late seral, highly stable (200 until late seral species are gone) old growth; 5 = climatic, topographic, or edaphic climax (seral dominants gone)]
TBAL -----	The total basal area in m ² /hectare of living trees
TBAD -----	The total basal area in m ² /hectare of standing dead trees, including snags in all stages of decay greater than 3.7 meters in height
DIA -----	The diameter of the site dominant trees to the nearest centimeter
HT -----	The total height measured on the site dominant trees
AGE -----	The breast height age of the site dominant trees from bore count
