

LOGISTIC REGRESSION ACCURACY ACROSS DIFFERENT SPATIAL AND TEMPORAL SCALES FOR A WIDE-RANGING SPECIES, THE MARBLED MURRELET

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Abstract: The scale at which habitat variables are measured affects the accuracy of resource selection functions in predicting animal use of sites. We used logistic regression models for a wide-ranging species, the marbled murrelet, (*Brachyramphus marmoratus*) in a large region in California to address how much changing the spatial or temporal scale of variables changes accuracy in predicting sites occupied by murrelets (sites believed to be used for nesting). This seabird forages in the ocean and nests inland in large, old trees. Classification accuracy of independent plots, assessed at 4 spatial scales (patch, landscape, subregional, and regional) and 2 time periods (present and previous decade), was highest (by 10%) for the model that incorporated all scales. Of the individual spatial scales, landscape was most accurate probably because it contained the most limiting factors for the murrelet, which were old-growth forest fragmentation and isolation. For temporal scale, there was a time lag before birds showed a negative response to fragmentation, as they still occupied plots in the 1990s that were recently (after 1985) fragmented. Adding the time lag improved accuracy by 4%. When absence data from plot locations beyond the apparent geographic nesting range (delineated by presence of frequent fog) were removed from models, prediction accuracy improved within the nesting range, mostly due to improved optimal classification cutoffs. We more rigorously evaluated our multi-scale model by assessing accuracy within geographic subsections of the nesting range and found it was still high to very high (86-100%), as most studies rarely exceed 85% accuracy. The results confirm that logistic regression can be very useful for predicting animal use when variables are measured at multiple spatial and temporal scales.

Key words: *Brachyramphus marmoratus*, California, habitat, logistic regression, marbled murrelet, prediction accuracy, spatial scale, temporal scale

Addressing resource selection at multiple spatial and temporal scales has become a major topic in ecology (Wiens 1989a, Wiens et al. 1993, Naugle et al. 1999, Thompson and McGarigal 2002). In the past, resource selection functions have often had poor prediction accuracy because habitat was sampled at an inappropriate scale (Wiens 1989b, May 1994, Orrock et al. 2000). With the increasing availability of regional-scale data on species distribution and habitat attributes, researchers are broadening their scale of analysis, and accuracy is improving (Rahbek and Graves 2001, Fletcher and Koford 2002). For example, Welsh and Lind (2002) achieved higher prediction accuracy (85%) of sites occupied by larval amphibians when habitat variables in their model were measured at landscape scales. In contrast, their local habitat models had lower accuracy (75%).

For wide-ranging species which have large ecological neighborhoods (Addicott et al. 1987), variables should be measured at 3 or more distinct spatial scales (extents) that are functionally relevant to the species (Wiens 1989b, Thompson and McGarigal 2002). These scales could include (1) the individual patch (defined as a contiguous area of one habitat type) that the animal uses for some or all life requirements, (2) the landscape (defined as a mosaic of patches), where configuration of patches might be important, and (3) the region, where broad vegetation, climatic, or elevation zones affect habitat use or define the limits of the species' geographic range. A resource selection function that combines variables measured at all of these scales, rather than each scale separately, may be the most appropriate and accurate because it incorporates interactions across spatial scales (Wiens 1989b, Cushman and McGarigal 2002, Fuhlendorf et al. 2002). An alternative viewpoint is that variables measured at the patch scale (e.g., local elevation of patch, mean diameter at breast height [dbh] of trees) may partially or fully substitute for variables measured at larger scales (regional elevation zone, vegetation zone). Such redundancy reduces the need to measure variables at multiple spatial scales (Cushman and McGarigal 2002). Also, if variables at one scale strongly limit a species, other variables at other scales may be of minor importance for predicting habitat use.

Some species may show a time lag in response to habitat modification, and thus, measures of more than one temporal scale might be needed. For example, historical and/or current habitat conditions may be more predictive than just current conditions at the time of the animal surveys (Wiens 1989a, Fuhlendorf et al. 2002). Alternatively, the magnitude of the effects of historical habitat changes may be minor compared to existing conditions for many species.

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The objective of this study was to quantify how much spatial and temporal scaling matters when developing resource selection functions for animals. Does scale affect model accuracy, and if so, by how much? We used a seabird, the marbled murrelet, to address this question because the spatial scale effect is likely to be most pronounced in species with large home ranges or that use more than one habitat, and the temporal effect may be most important in species that show site fidelity or philopatry. The murrelet meets these requirements because it forages in the nearshore ocean but nests in forest patches with large trees (typically old-growth forests) that can be over 100 km inland (Hull et al. 2001). Meyer et al. (2002) observed a time lag in murrelet response to fragmentation of old-growth forest, which suggests that murrelets are loyal to nest sites and delay abandonment of the fragments. Overall, loss of nesting habitat is believed to be the major cause of the decline of murrelets, which resulted in their status as a threatened species in our study area (Miller et al. 1997). However, fragmentation, which could decrease the quality of nest habitat, may be increasing the rate of decline (e.g., by increasing nest predation, Paton 1994).

Our approach was to compare the accuracy of resource selection functions for the marbled murrelet measured at different spatial and temporal scales, and all scales combined. In a previous study, we tested hypotheses about murrelet habitat selection in relation to forest fragmentation and proximity to high quality marine habitat using a multi-scale model approach (Meyer et al. 2002). We found murrelets occupied old-growth forests in low elevation areas with frequent fog. The birds not only showed an adverse response to forest fragmentation after a time lag but also occupied forests closer to areas of high marine productivity. The focus of this current study is not to support the significance of such habitat requirements established in that study but to evaluate whether a multi-scale model is more predictive than single scale models, and to determine which single scale is most predictive for the murrelet. For our across-scale comparisons, we used the logistic regression model, a popular resource selection function used in ecological studies (Manel et al. 2001, Manly et al. 2002). It can estimate the probability of occupancy and thus predict whether a site is occupied (used) or unoccupied (not used) by a species. If a site has a probability above a certain percentage (the cutoff), the site is considered occupied. The accuracy of the prediction can be tested on the observed results in the original data set used to develop the model (referred to as the training data set) or, more ideally, on an independent data set (Harrell 2001). Because prediction success measured in this way is affected by the prevalence of the species (see below), some studies use accuracy measures unaffected by prevalence, such as Somers' d (Harrell 2001). We used both methods (cutoffs and Somers' d). Surprisingly, many studies do not use any method to evaluate the performance of presence-absence models (Manel et al. 2001).

A second approach for evaluating scaling effects is to compare the accuracy of predictions at different scales using studies of many species. However, this is difficult because prevalence of the species varies from study to study, which affects the reported prediction success (which are usually based on cutoffs). Occupied sites are predicted more effectively as species prevalence increases and unoccupied sites as prevalence decreases (Manel et al. 2001). In models with unequal sample sizes of used and unused sites (which indicate the species' prevalence), accuracy of >50% can easily be obtained at random or just by assigning all plots the status of the group with the larger sample size (e.g., just a constant in the model, Fig. 1). Thus, for studies having different levels of species prevalence, percent accuracy beyond what is possible with random classification should be compared. Our review of a small sample of studies shows that accuracy beyond the random level can be poor at any scale, but highest accuracy was associated with studies conducted at regional or multiple scales (Table 1). However, differences in methods (use of independent vs. training data sets, use of random instead of non-use sites), habitat specialization, and home range size of a species limit our ability to compare the performance of models created at various scales across different species and is the reason we focus on our own data set for one species, the marbled murrelet.

Lastly, our extensive surveys identified large areas within the study area that had no observations of birds, areas apparently outside the geographic nesting range of the murrelet. Therefore, in addition to evaluating scaling effects, we also assessed the effect on model accuracy of including absence data beyond the nesting range.

METHODS

The study area extended from the northern California border to Monterey Bay, California, USA and from offshore up to 56 km inland (Fig. 2). The area represents the southernmost portion of the murrelet's geographic range. Elevation ranged from sea level to 1750 m. The forests were classified into vegetation zones influenced by fog (dominated by *Sequoia sempervirens*) and relatively uninfluenced by fog (dominated by *Pseudotsuga menziesii*).

The methods used to survey murrelets and measure habitat variables are detailed in Meyer (1999) and Meyer et al. (2002). We obtained a geographic information system (GIS) vegetation database derived from Landsat Thematic Mapper imagery for northern California (from Point Reyes to northern border, CTF 1993). We used a minimum mapping unit of 4 ha, as that resolution best represented the anthropogenic fragmentation of forests on the landscape (compared to 0.06 ha, see Meyer 1999). In a subset of the area, this map was 94% accurate for tree size and 84% accurate for canopy cover. For central California, we used a map based on aerial photography (Redwood Mapping

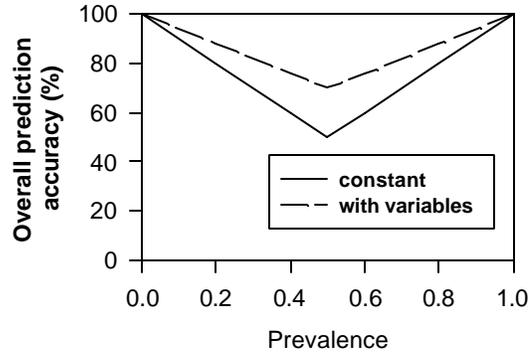


Fig. 1. Example of overall prediction accuracy of logistic regression models in relation to prevalence of occupied sites. The solid line represents best results using a model with no variables, just the constant (= % correct by chance given prevalence). The dashed line approximates a fitted line to data from models presented in Manel et al. (2001) for 34 families of aquatic invertebrates in 180 streams. The difference between the two lines divided by the total increase possible (distance from solid line to 100%) represents the percent increase in accuracy above a random (chance) level for the invertebrate models.

Table 1. The accuracy of logistic regressions in predicting animal use for a select set of species across different spatial scales. Percent correct by chance (from random classifications) is shown and accounts for prevalence of occupied sites. The last column shows the increase in accuracy above the random or chance level, which is the figure that should be compared across studies. Specificity = % unoccupied correct, sensitivity = % occupied correct. Bold = best %.

	Overall Accuracy (%)	Lowest specificity or sensitivity (%)	% correct by chance	% increase above random given prevalence
<i>Patch</i>				
Marbled murrelet (<i>Brachyramphus marmoratus</i>) (Hamer 1995)	74	67	58	38
Booted eagle (<i>Hieraaetus pennatus</i>) (Suarez et al. 2000) ^a	80		50	60
Yellowhammer (<i>Emberiza citinella</i>) (Bradbury et al. 2000)	81	51	74	27
Plumbeous redstart (<i>Rhyacornis fuliginosus</i>) (Manel et al. 1999)	82	74 ^b	64	50
<i>Landscape</i>				
Spotted owl (<i>Strix occidentalis</i>) (Meyer et al. 1998) ^a	76	76	50	52
Spotted owl (Thome et al. 1999) ^a	64		50	28
Red squirrel (<i>Sciurus vulgaris</i>) (Rodriguez and Andren 1999)	70	33	65	14
Eurasian lynx (<i>Lynx lynx</i>) (Schadt et al. 2002)	73	56	50	46
Booted eagle (Suarez et al. 2000) ^a	75		50	50
<i>Regional</i>				
Blackburnian warbler (<i>Dendroica fusca</i>) (Venier et al. 1999)	73	73	64	25
Gray wolf (<i>Canis lupus</i>) (Mladenoff et al. 1995)	89	86 ^c	50	78
<i>Multiple Spatial Scales</i>				
Fisher (<i>Martes pennanti</i>) (Carroll et al. 1999, all scales)	79 ^b	65 ^b	74	19 ^b
Marbled murrelet (Kuletz et al. 1995, patch, subregional)	79 ^b	75 ^b	53	55 ^b
Marbled murrelet (Meyer 1999, Meyer et al. 2002, 3 scales)	93 ^b	90 ^b	65	80^b
Grizzly bear (<i>Ursus arctos horribilis</i>) (Mace et al. 1998, landscape and regional scales) ^a	68	60	50	36

^aAnalysis was on used vs. random sites rather than used vs. unused sites.

^bUsed independent data, which can include jackknifed data sets.

^cIndependent wolf areas = 78% accurate, but accuracy of independent unused areas is unknown (Mladenoff et al. 1999).

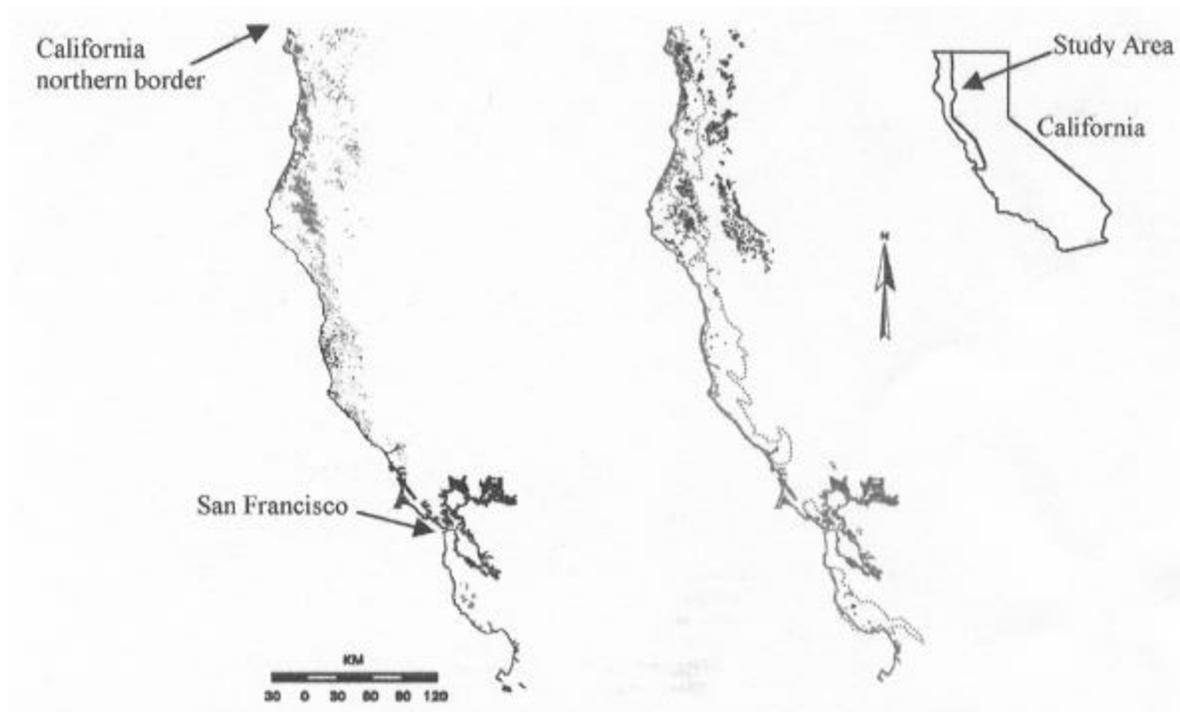


Fig. 2. Location of old-growth forest patches (left map) and survey stations (right map) in the study area in California, USA. The map on the right also shows the fog zone (dotted gray line). Note: The surveyor's definition of old-growth did not always match the definition of old-growth on the GIS map.

Project by Larry Fox, Humboldt State University, California) that we updated with recent aerial photos in the areas with old-growth to keep the minimum mapping unit at 4 ha. On both maps, we delineated old growth forest and other cover types in the study area in ARC/INFO (version 7.1). Old-growth was defined as coniferous forests having dbh ≥ 91 cm and canopy cover $\geq 40\%$. We also mapped topographic and marine features in the GIS (Table 2). Landscape-sized (1600-m radius) circular plots centered on survey stations were overlaid on the GIS maps, and we calculated spatial and other habitat variables within each plot (Table 2). Finally, we used logistic regressions to look for relationships between habitat variables and murrelet occupancy within the plots.

In old-growth forest throughout the study area, 11,392 intensive morning surveys for marbled murrelets (Fig. 2) were conducted according to a standard protocol (Ralph et al. 1994). Because only a small sample of murrelet nests have been located in the study area, we used the bird metric called "occupancy" to identify survey stations where murrelets might be nesting. Occupancy is the classification status of a station or plot as either occupied (proxy for nest sites) or unoccupied based on ground audio-visual surveys. If a bird was seen exhibiting a behavior suggestive of nesting during a 2-hour dawn survey, we classified that station as "occupied". Behaviors suggestive of nesting included observations of the bird flying below the canopy, circling above the canopy, landing or sitting in the canopy, or observations of broken eggshells. If no birds were seen or heard, we classified the station as unoccupied.

After the landscape plots were placed over the point locations of the survey stations, overlapping plots were visually identified and removed to retain independence (removing those that reduced the sample size the least). Number of surveys within each of the remaining plots averaged 39. A landscape plot was classified as occupied if at least one station inside the plot had an "occupied" behavior detected. The plot was classified as unoccupied if all stations within the plot were unoccupied (no birds observed in the entire 804-ha plot). Plots with birds seen or heard, but no occupied behaviors observed, were dropped from the study because their occupancy status was unknown. Thus, our study evaluates inland habitat use in relation to occupancy, not actual nest sites. We would prefer to evaluate actual nest sites as researchers are doing in British Columbia (Centre for Wildlife Ecology, Simon Fraser University); however, such an extensive nest data set based on radiotelemetry is not yet available in our study area.

The variables that we selected as candidates for the logistic regressions at each scale (Table 2) were those we hypothesized to be important based on previous studies (Grenier and Nelson 1995, Hamer 1995, Raphael et al. 1995, Meyer et al. 2002). Variables at the patch scale were measured at or from the center of the plot (topographic, climatic, or distance variables) or averaged over the patch (dbh). We measured landscape variables within the 1.6-km

Table 2. Habitat variables measured in inland circular plots surveyed for marbled murrelets in California, 1990s.^a

<i>Patch Scale</i>	
Elevation (m)	Mean annual precipitation (cm)
Slope (degrees)	Mean maximum summer air temperature (°C)
Distance to roads (m)	Distance to streams (m)
Mean tree dbh in patch (cm) ^b	
<i>Landscape Scale</i>	
Percent landscape in old-growth	Percent landscape in core area (old-growth, landscape) ^c
Mean patch size (ha) (old-growth, landscape)	Density of core areas (no./100 ha) (old-growth, landscape)
Patch density (no./100 ha) (old-growth, landscape)	Mean core area per patch (ha) (old-growth, landscape)
Percent landscape in largest patch (old-growth)	Mean nearest neighbor distance (m) (old-growth)
Density of edges (m/ha) (old-growth)	Mean proximity index (old-growth)
Density of contrast-weighted edges (m/ha) (old growth)	Contagion (%) (landscape)
Presence of unfragmented old-growth in mid-1980s in fog zone	Isolation >5 km
<i>Subregional Scale (distance in km to nearest marine feature indicated)</i>	
Ocean	Major promontory
Major bay	Fine to medium-grained (0.06-12 mm) sandy beach
High summer chlorophyll (mean from 1978-86 >10 mg/m ³)	High spring chlorophyll (mean from 1978-86 >10 mg/m ³)
Nearshore (<30 km) submarine canyons	Spring/summer nearshore cold water areas < 10°C
<i>Regional Scale</i>	
Presence in fog-influenced vegetation zone	Presence in low elevation zone (<1,000 m)

^aSee Meyer et al. (2002) and Meyer (1999) for details on data sources and classifications.

^bDbh was not available in central California, which reduced sample size of patch models by 5.

^cCore area is the interior habitat of a patch that is ≥ 100 m from the edge of the patch.

radius plots using the raster version of FRAGSTATS (McGarigal and Marks 1995, v. 2.0), except the variable “isolation >5 km from other patches containing murrelets”, in which the 5-km threshold was compared to distance from the center of one plot to the center of another. The subregional scale represented an area encompassing marine and terrestrial habitat that might be within a bird's seasonal "home range" (area in which an individual bird occurs throughout the breeding season). Subregional variables were distances measured from the center of the plot to the nearest marine feature of interest. Regional variables were coded as presence in or outside the specified zone (e.g., elevation <1,000 m or fog zone). To evaluate a time lag in response to forest fragmentation, we used a coarse resolution 1985-1986 map of vegetation that covered the entire study area (Redwood Mapping Project, Humboldt State University). We recorded if a relatively unfragmented (>16 ha) old-growth forest patch was present during that period. Patches of old-growth forest highly fragmented before 1985-1986 were too small to identify on such a coarse-resolution map, but forests fragmented after that period still had large patches present on the 1985-1986 map.

Sampling Design and Data Analysis

Our study is a retrospective analysis of available survey data, where the sampling design varied from area to area. Nonetheless, for 75% of the survey stations, researchers randomly or systematically placed stations within potential murrelet nesting habitat (old-growth forest), which reduced surveyor bias in station placement. The rest of the surveys were located near proposed timber sales, which might have caused some unknown bias. Overall, distribution of survey stations was extensive within available old-growth forest throughout the study area (Fig. 2).

In a habitat patch where murrelets are truly present, we assumed 4 surveys provided a 95% chance of detecting the birds based on Miller and Ralph's (1995) analysis. We screened the survey data (obtained from numerous investigators) and only included stations classified as unoccupied if at least 4 surveys had been conducted in the patch where the station was located, if the patch was ≤ 50 ha (often such patches had more than 4 surveys). For patches >50 ha, we divided the patch into 50-ha sections, and ≥ 4 surveys must have been conducted in each section.

The 1994 murrelet survey protocol (Ralph et al. 1994) stated that 4 surveys should be conducted for 2 years in a row to capture the annual variability in use of stations by murrelets. We did not use this 8-survey criteria. Thus, some of our unoccupied stations may have actually been occupied in some years, which could reduce prediction accuracy.

After removing overlapping plots, final sample size was 362 804-ha plots for each scale. The 804-ha plot size (1600-m radius) was selected because it was one of the most predictive sizes for murrelet occupancy in California (Meyer et al. 2002 tested four sizes) and also had a large enough sample size to set aside plots for independent validation of the prediction accuracy. A randomly-selected subset of plots (20%) was set aside as an independent data set that was never used to develop the final logistic regression models. Use of such independent data to validate models and to select the final model helped reduce overfitting (Harrell 2001).

Stepwise logistic regression (backwards and forwards, $P \leq 0.05$) and manual input were used in the initial development of numerous models of alternative combinations of variables (SAS Institute 1990). We eliminated one of a pair of variables (least significant) as candidates if they were highly correlated ($r > 0.8$). We also ensured variance inflation factors of variables were acceptable at values near 1.0 (Menard 1995). To select the best set of variables for each scale, we evaluated the 3 models with the lowest Akaike's Information Criterion (AIC_c , Burnham and Anderson 1998). The one that had a non-significant Hosmer-Lemeshow test statistic ($P > 0.05$) (Hosmer and Lemeshow 1989) and the lowest misclassification of independent plots was our final model. The classification accuracy of each resultant single scale model was compared to the best model that combined scales (which was the multi-scale model, originally developed and reported in Meyer et al. 2002). In the multi-scale model, 3 occupied plots that were outside the fog zone were removed from the analysis because they were statistical outliers. However, these outliers were included in all accuracy assessments of geographic areas that included those plots. Because the model selection procedures often result in inflation of prediction success of the plots (overfitted to the data), we also divided the study area into 3 geographic subsections and tested accuracy within each subsection. The bias due to overfitting is probably not very high if the model performs well in all three subsections (Harrell 2001).

To assess accuracy, plots were classified with the cutoff that produced the least misclassification error (Norusis 1997). We also used Somers' d_{xy} to compare accuracy of models at each scale and geographic subsection, especially when the prevalence (proportion) in occupied plots was different between the compared models. Somers' d is not only insensitive to the prevalence of occupied plots, but has the advantage of not requiring a cutoff (Harrell 2001). This index creates all possible pairs of plots where, in each pair, one plot is occupied and the other is not. The proportion of such pairs in which the occupied plot has a higher predicted probability of occupancy than the unoccupied plot is recorded (concordance) and adjusted so the index ranges from -1 to 1 . Zero is no correlation and 1 or -1 is perfect positive or negative correlation between observed and predicted occupancy. The index is almost identical to the widely used measure of accuracy, area under a "receiver operating characteristic" (ROC) curve, except Somers' d is scaled between -1 and 1 (Harrell 2001).

RESULTS

Many of the variables selected in the best models at each scale were the same as those selected in the multi-scale model (Table 3). The models indicate that, as compared to unoccupied plots, the occupied plots were in the regional fog zone. On a subregional scale, they were close to marine areas of high primary productivity, indicated by high marine chlorophyll concentrations or geographic features that increase productivity such as bays and deepwater submarine canyons. At the landscape scale, occupied plots were in less fragmented old growth (more old-growth core areas) and less isolated from other murrelets (although the landscape matrix around old growth was often fragmented). Birds showed a time lag of at least several years in response to fragmentation, occupying fragmented forests only if the fragmentation was recent (that is, unfragmented forest was present in the previous decade). At the patch scale, murrelets occupied lower elevation sites and the old-growth contained larger trees than unoccupied patches. When variables from all four spatial scales were candidates for one model, the interpretation of the final multi-scale model was almost the same, except the patch variables (elevation, tree dbh) and distance to major bay were not needed, as the other variables were sufficient for accurately predicting murrelet occupancy.

Accuracy in predicting occupancy was high ($\geq 80\%$) for all scales, particularly for the landscape, patch, and multi-scale models ($\geq 93\%$). However, 95% of all occupied plots were in the fog zone (Fig. 2), which suggests the redwood (*Sequoia sempervirens*) zone (= the fog zone in California) mostly delineates the boundary of the species' geographic nesting range in California. The numerous absence records (195 plots) from outside this apparent nesting range may be distorting the model, inflating the accuracy, and thus were excluded. As might be expected, prediction accuracy (using Somers' d) was lower for most of these models when evaluated only within the fog zone with the exception of the multi-scale model, which had the fog zone included as a variable (Fig. 3). Therefore, using only the plots within the fog zone, we developed new regression models. The revised models had variables similar to the original models, indicating the distortion that resulted from including the plots outside of the fog zone was not

Table 3. Logistic regression equations predicting murrelet occupancy (variable differences between the entire study area and fog zone only are bolded). L = logit (p), where p = probability of occupancy. Entire study area: n = 62 for occupied plots and 229 for unoccupied plots. Fog zone: n = 59 for occupied plots and 34 for unoccupied plots.

Scale	Entire study area	Fog zone
Patch	L = 0.113 <i>dbh</i> – 0.0043 <i>elevation</i> – 3.6027	L = 0.0798 <i>dbh</i> – 0.0031 <i>elevation</i> – 2.0854
Landscape	L = 4.1799 <i>old-growth core density</i> – 0.9845 <i>landscape core density</i> – 2.4875 <i>isolation</i> + 1.4099 <i>unfragmented old-growth in mid-1980s</i> + 1.8995	L = 4.366 <i>old-growth core density</i> – 1.1394 <i>landscape core density</i> – 3.3591 <i>isolation</i> + 0.6592 <i>unfragmented</i> <i>old-growth in mid-1980s^a</i> + 3.4342
Subregional	L = –0.2630 <i>bays</i> – 0.0398 <i>canyons</i> – 0.0855 <i>summer chlorophyll</i> + 4.8154	L = –0.2407 <i>bays</i> – 0.1699 <i>canyons</i> – 0.2219 <i>summer chlorophyll</i> + 0.0052 <i>canyons*chlorophyll</i> + 5.6310
Regional	L = 4.7408 <i>fog zone</i> – 4.1896	
Multi-scale	L = 6.9796 <i>old-growth core density</i> + 1.7647 <i>unfragmented old-growth in mid-1980s</i> – 1.2528 <i>landscape core density</i> – 3.8239 <i>isolation</i> – 0.0979 <i>canyons</i> – 0.0906 <i>spring chlorophyll</i> + 13.9246 <i>fog zone</i> – 6.0633.	L = 6.9796 <i>old-growth core density</i> + 1.7647 <i>unfragmented old-growth in mid-</i> <i>1980s</i> – 1.2528 <i>landscape core density</i> – 3.8239 <i>isolation</i> – 0.0979 <i>canyons</i> – 0.0906 <i>spring chlorophyll</i> + 7.8613.

^aAlthough this variable improved the model and its accuracy, its coefficient was not significant ($P = 0.34$).

great (Table 3). The changes improved model accuracy for the independent plots only at the subregional scale (Fig. 3; note that the regional scale was dropped because within the fog zone the regional variables become constant) However, when all plots (training and independent sets) were included, the revised models were more accurate than the unrevised models for the multi-scale (90.2 vs. 83.6%), subregional (85.2 vs. 69.7%), and landscape models (85.2 vs. 84.4%), mostly due to changes in optimal cutoffs. The accuracy at the patch scale remained the same (79.6%).

The individual scale model that produced the best accuracy for just the independent plots in the fog zone (after revision) was the landscape scale (83%), while the other scales had lower accuracy of 72-79% (Fig. 4). Notably, of the single scale models, the subregional scale was useful for predicting where murrelets are not likely to be found (unoccupied plots), whereas the patch scale was best at predicting where the murrelets will be found (occupied plots) (Fig. 4). The multi-scale model performed the best overall (93% accuracy) with 10% higher accuracy than the best individual scale model (Fig. 4). For comparison to other studies, if our study had only a 0.5 prevalence of occupied plots (instead of 0.65) this 10% increase would actually be higher at 15% (using the proportional relationship in Fig. 1).

Because the time lag variable (presence of unfragmented old-growth in mid-1980s) was a landscape variable, we used the landscape model to evaluate the magnitude of the effect of lengthening the temporal scale. When the time lag variable was removed from landscape scale models, accuracy of independent plots decreased from 83% to 79% in the fog zone. This 4% decrease becomes a 6% decrease when adjusted to 0.5 prevalence for occupied plots.

Using the revised fog zone models and their cutoffs, prediction success and Somers'd were high for each area when the fog zone was split into 3 subsections (Table 4). The two methods of measuring accuracy gave fairly similar results, suggesting that the use of prediction success with cutoffs to evaluate the models is acceptable for our study. As was found for the entire fog zone, analysis by geographic subsection in the fog zone showed the multi-scale model produced the best and most consistent results, followed by the landscape scale (Fig. 5).

DISCUSSION

Advantage of Evaluating All Scales

The scale of analysis, spatial and temporal, clearly matters for the marbled murrelet. The multi-scale spatial model improved prediction accuracy by almost one-third of the increase possible beyond random over the best single-scale model, when species prevalence was adjusted to 0.5. Similarly, the model that included past as well as

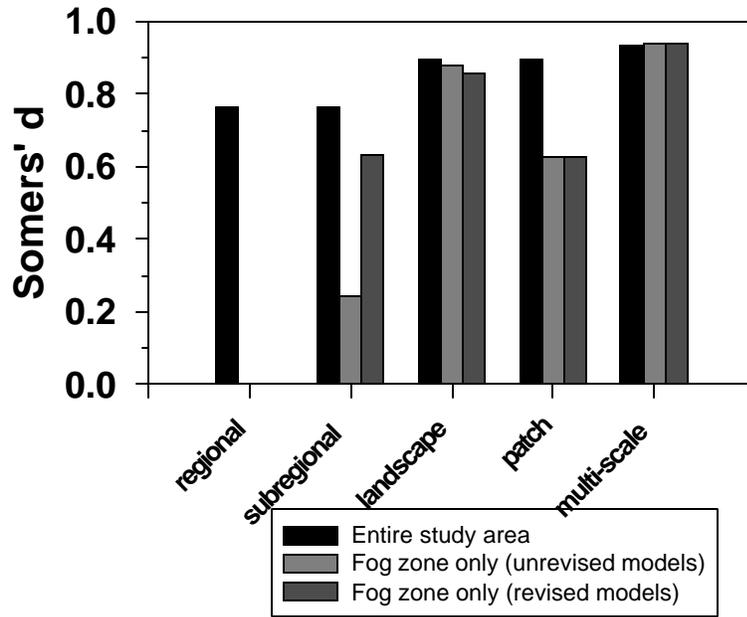


Fig. 3. Relative accuracy of logistic regression models (using Somers' d) in predicting murrelet occupancy of independent plots for each spatial scale compared to the multi-scale model. Results are shown for the entire study area ($n = 73$) and just within the fog zone ($n = 29$), the zone where the majority of murrelets appear to nest in California. The models used for the fog zone were (1) those originally developed for the entire study area (unrevised models) and (2) those developed just for the fog zone (revised models).

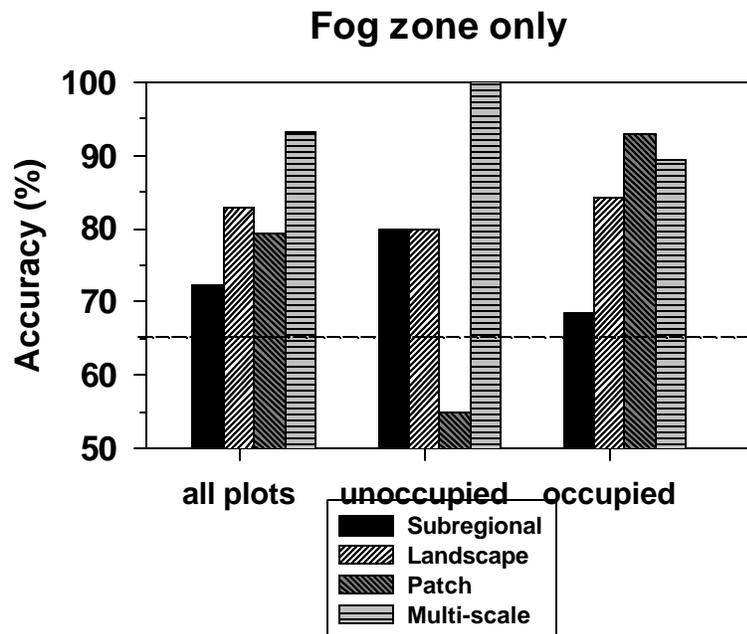


Fig. 4. Accuracy (% predicted correctly) of logistic regression models at different scales in predicting murrelet occupancy of independent plots (revised fog zone models in Fig. 3). The dashed line represents accuracy that would be obtained with no variables in the models, just the constant (correct by chance) to establish a baseline from which accuracy can improve. Classification cutoffs = 65, 60, 50, and 55% for the subregional to multi-scale model, respectively. $n = 19$ for occupied plots and 10 for unoccupied plots.

Table 4. Two measures of accuracy of the multi-scale logistic regression model for geographic subsections of the fog zone in the study area in California. Left of slash is accuracy for the training data set combined with the independent data set; right of slash is for the independent data set only^a. The cutoff for prediction success was 55%.

Measure of Accuracy	Northern third ^b	Middle third	Southern third
Prediction success (%)	89 / 86	92 / 100	89 / 100
Somers' d	0.90 / 0.85	0.91 / 1.00	0.97 / 1.00

^a $n = 55, 49,$ and 18 from north to south for values left of slash. $n = 14, 12$ and 3 for values right of slash.

^bThe location of each third is shown in Fig. 5.

current old-growth conditions increased accuracy by almost one-eighth of the increase possible beyond random over the model without recent historical conditions. Such results demonstrate murrelet use of areas depends on factors measured at multiple scales. If only the patch-level scale is analyzed, the importance of isolation of that patch and forest fragmentation is missed. If only the landscape scale is evaluated, the importance of distance to marine habitat and the fog zone is missed. Nevertheless, analysis at each individual scale provided some new insights. Of the individual spatial scales, the one with the highest accuracy probably contained the factors that most limit the species. For example, landscape scale provided the best single scale model probably because it includes the limiting factors, old-growth forest isolation and fragmentation (Meyer and Miller 2002), in particular, historical fragmentation. Apparently due to site fidelity, the murrelets continue to use a forest patch even after it has been severely fragmented. Such habitat is expected to be poor for the murrelets because they eventually abandon these sites, evidenced by our finding few murrelets occupying forests that were severely fragmented before the mid-1980s (median patch size of unoccupied plots was 4 ha). In support of this finding, marine offshore population sizes of murrelets in the 1990s have also been found to be most limited by nearby old-growth forest fragmentation that occurred prior to the mid-1980s (Miller et al. 2002). In comparison, marine conditions only had a minor effect on the size of those offshore populations. Notably, another study on murrelet inland abundance found patch elevation was more limiting than old-growth fragmentation on the landscape (Meyer et al. 2002), which suggests caution in extrapolating presence/absence results to interpretations about abundance. However, comparison of Meyer et al.'s (2002) methods of audio-visual surveys of murrelet abundance averaged at the landscape scale with work that uses radar to survey the birds (Burger 2001, Cooper et al. 2001) is needed in our study area before one can be confident that elevation is the factor that most limits murrelet abundance in California. Audio-visual detections are not always useful as an index to abundance at local scales (Jodice and Collopy 2000, Rodway and Regehr 2000, Jodice et al. 2001), and more research is needed to evaluate their usefulness when averaged over large spatial scales.

Although marine conditions may not be as limiting, our study shows proximity to productive marine habitat, measured at the subregional scale, is needed to improve the accuracy of predicting inland areas occupied by murrelets. Moreover, in our previous study of inland murrelet abundance (rather than occupancy), inland factors such as elevation and fragmentation most limited relative bird abundance only when measured within local landscapes (≤ 800 ha areas), whereas proximity to marine habitat most limited bird abundance at the broadest landscape scale studied (3200 ha) (Meyer et al. 2002). Our current study of individual scales similarly shows that somewhat large areas (800 ha) far from marine habitat (but within the fog zone) have a low probability of murrelet use, as the subregional scale model was good at predicting many remote unoccupied plots (92% correctly classified when unoccupied plots were ≥ 35 km from productive marine areas, only 40% correct for unoccupied plots < 35 km). Such remote areas may be less desirable because energetic costs can be large when birds are commuting long distances to nest sites (up to 41% of their field metabolic rate in British Columbia, Hull et al. 2001). In contrast, areas closer to marine habitat are probably best predicted using inland characteristics (patch and landscape scales were better at predicting inland plots closer to marine habitat). Notably, patch-level variables were not needed in the multi-scale model, which indicates that the local scale was not needed to improve predictions of murrelet use. Other studies have found slope, dbh, and elevation to be important (Ralph et al. 1995), but perhaps they are not as important to murrelets as variables measured at broader scales. Overall, our study demonstrates that understanding resource selection may require studying habitat requirements at multiple scales, separately and together. Often studies have addressed multiple scales separately (Wiens 1989b, Rahbek and Graves 2001, Chase and Leibold 2002) or together (Carroll et al. 1999, Clark et al. 1999, Miller and Cale 2000), but few have performed both analyses.

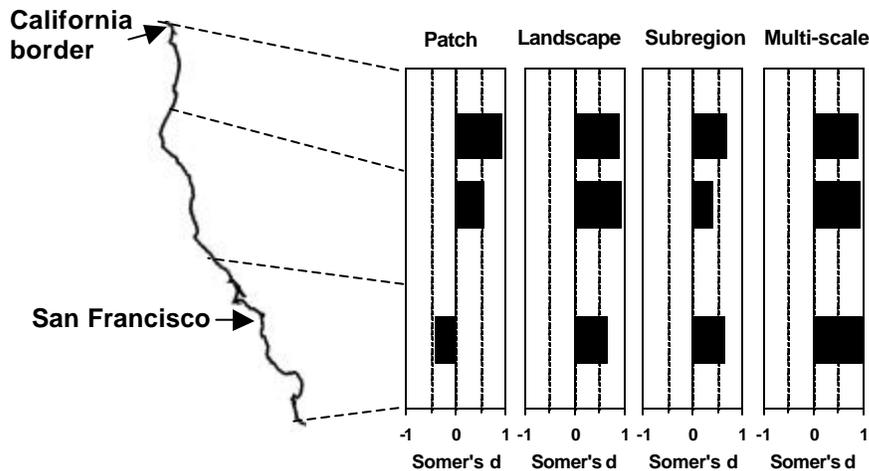


Fig. 5. Accuracy of logistic regressions developed at different spatial scales for predicting murrelet occupancy using all plots (training and independent) in three geographic subsections of the fog zone in the study area (boundaries of subsections shown on coastline map above). The multi-scale model had the highest accuracy most consistently.

We caution that our study provides information on locations where murrelets exhibit behaviors suggestive of nesting, not actual nest sites. Much uncertainty exists as to whether flight below the canopy or circling actually indicates murrelets are nesting in the specific area (Falk Huettmann, personal communication). Furthermore, detection of such "occupied" behaviors is affected by the size of forest canopy openings (Rodway and Regehr 2000), skill of the observer, and the daily variability in number of birds detected in a local area (Jodice and Collopy 2000, Jodice et al. 2001). Fortunately, our approach uses numerous surveys per landscape plot (average of 39), which reduces error associated with classifying an unoccupied plot. If no birds have ever been seen or heard in the plot after many surveys of old-growth forests in the plot, it seems probable that the plot has few or no nesting birds. Our high accuracy for predicting both occupied and unoccupied plots suggests our approach is relatively sound for assessing murrelet occurrence in forest patches, if not actual nest sites. After more nest sites have been identified in California, this study should be repeated using nest sites to test how well our models represent actual nesting areas.

In our modeling approach, we did not include the same variables at every scale as some studies have (Carroll et al. 1999, Rahbek and Graves 2001, Fuhlendorf et al. 2002, Thompson and McGarigal 2002). Thus, we did not assess scaling effects on specific variables. Instead, we used an approach that recognized hierarchically structured variables, where the variables believed to be important to a species shifted with each scale (patch, landscape, subregion, region). Other studies have used a similar approach (Clark et al. 1999, Naugle et al. 1999, Cushman and McGarigal 2002, Fletcher and Koford 2002, Welsh and Lind 2002), although methods of assessing scaling effects other than logistic regression have been used. For example, Cushman and McGarigal (2002) used canonical correspondence analysis in a multi-scale model, which partitioned the variance explained by each scale. Thompson and McGarigal (2002) used repeated measures analysis, where each scale represented a repeated measure. Clearly, there are many ways to assess scaling effects, and this study presents just one approach. Despite the varying methods, most of such studies stress that multi-scale analyses are necessary because any of the individual spatial scales do not give completely accurate results.

Geographic Nesting Range

The regional-scale model was useful in delineating the apparent geographic range of nesting murrelets, as the fog zone (the only variable in the regional model) contained almost all of the occupied plots. Research is needed to determine if the fog zone is an important delimiter of the bird's range in more northern, cooler areas. Murrelets have been observed outside the fog zone along the coast and inland (up to 56 km) in our study area, but most of these murrelets were not exhibiting nesting (occupied) behaviors. Our finding that nesting of this coldwater-adapted seabird is limited to the fog zone did not become obvious until we conducted this study and a study in southern Oregon (Meyer and Miller 2002, Meyer et al. 2002). In southern Oregon, the fog zone that contained murrelets included the western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) zones (Franklin and Dyness 1973). Knowledge of the importance of the fog zone could have saved money spent on an extensive study

conducted outside the zone (Hunter et al. 1998). This discovery stresses the need for studies to be conducted at a broad, regional scale first to identify factors limiting the range of a species.

Absence Data Beyond the Range of a Species

When a regional zone variable, such as the fog zone in our study, is identified that limits the species range, ideally the analysis should be conducted on just plots within the zone (remove 'naughty noughts' as Austin and Meyers (1996) calls them). Otherwise, resource selection functions developed for the entire study area may be distorted or poor at predicting use within the zone where the majority of the individuals of that species occur. Surprisingly, our 5 models that included the 195 unoccupied plots outside the fog zone had variables similar to the models developed for just the fog zone, probably because at least one variable in each full model was partially correlated with the fog zone ($r = 0.6-0.7$ for elevation, isolation, and distance to high marine chlorophyll). However, inclusion of the 'naughty noughts' decreased accuracy because the cutoffs for the entire study area were not optimum for the fog zone (prevalence of occupied plots shifted). Hence, the interpretation, but not accuracy, of a model built on such extraneous absence data might be acceptable when the model includes a variable that delimits the species range (e.g., fog zone). For example, in the multi-scale model, the models with and without the extraneous plots were identical except for the fog zone variable, constant (Table 3), and classification cutoff (55 vs. 22%). The two models' coefficients were identical because the three occupied plots outside the zone were removed as statistical outliers (the 3 possibly were misclassified in the field, see Meyer et al. 2002). The main problem for prediction purposes is finding the correct cutoff for plots in the species range, which is not obtainable using plots outside the range. Therefore, it is still advisable to develop models only within the known geographic range of a species.

Our study demonstrates that logistic regression models can be excellent predictors of habitat use for a wide-ranging species when multiple spatial and temporal scales are addressed. When only one scale is addressed, the accuracy declines, although less so for the scale which contains the most limiting habitat factors. An area of future research is to investigate how scale affects many other wide-ranging species. In particular, a study that compares the accuracy of resource selection functions across many species with different life histories would be a fascinating way to discover if scale matters most for species that have characteristics similar to the murrelet, specifically habitat specialists with large home ranges that show site fidelity or philopatry.

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