# SONG POST AND FORAGING SITE CHARACTERISTICS OF BREEDING VARIED THRUSHES IN NORTHWESTERN CALIFORNIA[1]

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*Abstract.* We used a hierarchical approach to describe habitat characteristics of song posts and foraging sites used by Varied Thrushes (*Ixoreus naevius*) in coastal redwood (*Sequoia sempervirens*) forests of northwestern California. We measured mesohabitat (0.04-ha circular plots) and microhabitat (0.5-m radius) scale attributes centered on occupied and random song posts and foraging locations at four study sites during March–August of 1994 and 1995. Ninety-five percent of song posts were in trees or snags. Male thrushes used song posts with low foliage density near the top of large conifers (microhabitat scale), located on steeper slopes, surrounded by a high density of trees, and centered in drainages closer to water (mesohabitat scale) as compared to random locations. Varied Thrushes foraged predominantly on the ground early in the breeding season, then subsequently included fruit in their diet after the young had fledged. Although many variables were correlated with ground foraging locations, microhabitat foliage density had the greatest explanatory power, indicating thrushes selected foraging locations primarily at the microhabitat scale, and emphasizing the importance of measuring habitat characteristics at the appropriate spatial scale. Abrupt forest edges, such as those produced by clearcuts, may reduce habitat suitability for Varied Thrushes possibly explaining their absence from small forest fragments during the breeding season.

*Key words: foraging locations, hierarchical habitat selection,* Ixoreus naevius, *redwood forests, song posts, Varied Thrush.*

## INTRODUCTION

Within territories, breeding passerines must find suitable sites for foraging, territorial display, and nesting if they are to breed successfully (Hunter 1980). The characteristics of song posts for territorial display and foraging sites are often quite different (Hunter 1980, Collins 1981). Song post location is frequently a function of visibility and conspicuousness (Petit et al. 1988) as well as acoustical transmission (Marten and Marler 1977). In comparison, foraging microsites frequently change as food resources (Hutto 1981, Brush and Stiles 1986) and predation risk vary (Bouskila 1995, Brown and Morgan 1995). Furthermore, the scale at which a site is chosen is not only dependent on the organism itself, but on the type of resource being utilized (Sedgwick and Knopf 1992). Whereas prey items may occur within a very restricted substrate, successful courtship and territorial display by an individual may require a much larger area.

The Varied Thrush (*Ixoreus naevius*) breeds in moist coniferous forests from Alaska south to northern California (Ehrlich et al. 1988, George, in press). Territorial males usually sing high in trees and have a brighter plumage than females. This suggests there might be a visual component in the use of song posts by males. Early in the breeding season Varied Thrushes forage almost exclusively on the ground for invertebrates, which provide the protein needed by the female for egg production and by the nestlings for this period of intense development (Bent 1949, George, in press). Once young fledge, the diet changes to include more fruit, coinciding with the ripening berry crop (Sawyer and Keeler-Wolf 1995).

Habitat loss and fragmentation due to silvicultural practices have occurred over much of the Varied Thrush's range. Because of their narrow habitat requirements during the breeding season, there has been concern regarding possible declines in their distribution and abundance (Hansen et al. 1993). Sharp (1996) detected a decrease in Varied Thrush abundance in national forests of Washington. Hurt (1996) found that

Varied Thrushes are generally absent from small fragments (<16 ha) of mature coastal redwood (*Sequoia sempervirens*) forest in northern California. The reasons for their absence from small forest fragments are unclear, but possible explanations include: differences in microhabitat, food availability, or predation pressure between large and small forest fragments. It is possible that breeding Varied Thrushes require large areas of contiguous forest to meet their foraging requirements or that they are averse to breeding near forest edges.

Whether landscape-level effects influence availability of resources at the microhabitat level is uncertain. Examination of microhabitat use by Varied Thrushes may provide insight into their breeding distribution at a scale more closely associated with ultimate factors affecting fitness. However, the purpose of this study was only to identify, and not correlate, song post and foraging site attributes that might be associated with landscape-level effects, such as area sensitivity and fragmentation.

There were two main objectives of this study. First, we examined song post and foraging habitat requirements of Varied Thrushes in northern California. We hypothesized that Varied Thrushes would use song post or foraging locations that differed in habitat characteristics from those available at random locations. Second, we examined the scale at which Varied Thrushes may be using song post and foraging locations. For this reason we used a hierarchical approach (Hutto 1985, Sedgwick and Knopf 1992), incorporating both mesohabitat and microhabitat variables to characterize song post and foraging locations. We hypothesized that mesohabitat characteristics differ from microhabitat characteristics within song post or foraging locations used by Varied Thrushes or between used and random sites.

## METHODS

### STUDY SITE

We studied Varied Thrushes from March through August of 1994 and 1995 at four locations in Humboldt County, California. Lost Man Creek and Prairie Creek State Park are old-growth coastal redwood forests that are part of Redwood National Park. Grizzly Creek Redwoods State Park is an old-growth redwood forest, but because it is farther from the coast than

the other two sites, it is drier and has a large Douglas-fir (*Pseudotsuga menziesii*) component. The Arcata Community Forest is an 80-year-old, second-growth coastal redwood forest managed for multiple use (Beck 1997).

Redwood forest canopy (>50 percent) dominated the four study sites. The major tree species associates included Douglas-fir, grand fir (*Abies grandis*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), tan oak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), bigleaf maple (*Acer macrophyllum*), and California bay (*Umbellularia californica*) (Sawyer and Keeler-Wolf 1995). Elevation ranged from 10 to 350 m.

### EXPERIMENTAL DESIGN

We used a paired design to compare bird-centered and corresponding random locations to determine whether Varied Thrushes used song posts and foraging locations with attributes that were different from those available at random sites within territories (Larson and Bock 1986, Dunk et al. 1997). To resolve the spatial scale at which birds used foraging and singing locations, we measured habitat in a hierarchical fashion (Petit et al. 1988, Sedgwick and Knopf 1992). At the microhabitat scale, we measured variables within 0.5-m radius plots centered on a location. At the mesohabitat scale, we measured variables within a 0.04-ha circular plot (Noon 1981).

### SELECTING BIRD-CENTERED LOCATIONS

We surveyed for song post and foraging locations during the early morning (05:00–11:00) and late afternoon (15:00–20:00) from 15 May to 1 August 1994 and 25 March to 1 August 1995. Early in the breeding season, we randomly chose a starting location within one of the four study areas. However, soon after surveys began, we were able to recognize individual territories based on locations of singing males, and delineate these on maps of the study areas. Subsequently, we randomly chose territories to begin surveys. We considered song post or foraging observations to be independent if they were >200 m apart (Brown 1985, pers. observ.). Once we observed a singing male and a foraging location for the male, female, and one juvenile during separate surveys within each territory, no further observations were made to insure there

was only one independent observation for each individual. We found song posts by following singing males until the first visual detection. Although such a method may result in a bias towards open perches, we made most initial visual detections when a bird flew, landed, and began singing. We found foraging locations by visually searching for foraging birds and flagging the location where we observed their first foraging maneuver (Bell et al. 1990, Hejl et al. 1990). Because thrushes often were observed foraging on trails, we deliberately searched off trails, throughout the forest, so as not to bias our sample. For both song post and foraging locations, we recorded the date, time, location, and sex (adults only) or age (juvenile vs. adult) of the bird. We measured mesohabitat and microhabitat variables within 2 weeks of observing a bird so that habitat (physical conditions and vegetation phenology) was similar to the time of the observation. Because all plants had leafed out by the time surveys had started, there was little change in vegetation within this period.

## SELECTING RANDOM LOCATIONS

For each bird-centered point, we selected paired random locations within territories by generating a random direction and distance (25–200 m). For song post locations, if the bird-centered point was in a tree, we centered the random location on the tree nearest the random point. If a bird was observed singing on a log or on the ground, then the random point was the center of the random plot. For foraging locations, if the bird-centered point was on the ground, then the random point was the center of the random plot. However, if the bird-centered point was in a shrub or tree, we centered the random location on a shrub or tree nearest to the random point.

## MICROHABITAT VARIABLES

At bird-centered and random song-post locations in trees, we recorded the tree species, estimated tree height, and measured tree diameter at breast height (dbh). For bird-centered song posts, we recorded substrate as tree, snag, log, or ground, and we visually estimated the height of the bird and proportion of foliage density within a 0.5-m radius sphere around the bird (Sakai and Noon 1991).

For bird-centered and random foraging locations, we visually estimated the percent cover of shrub, forb, bare ground, litter, woody debris

(>30 cm and <30 cm diameter), and measured litter depth within a 0.5-m radius circular plot. We measured distance to nearest cover (vegetation or other physical features >15 cm in height) from plot center, estimated proportion of foliage density within a 0.5-m radius hemisphere, and for ground foraging locations, we also measured soil moisture following Hurt (1996). For foraging locations in shrubs or trees, we recorded plant species. We categorized the habitat type in which foraging locations occurred as undisturbed forest or disturbed habitat (trails, roadsides, grassy parks, and yards). For bird-centered points, we recorded substrate as ground, log, shrub, tree, or snag.

## MESOHABITAT VARIABLES

Within 0.04-ha circular plots, we recorded number, dbh, and species of each tree (dbh > 10 cm), number of trees of each species with a dbh < 10 cm and >4 m in height, and number of snags. At the center point of each plot, we measured slope, aspect, and distance to nearest open water. We used the line intercept method (Bonham 1989) to measure shrub and woody debris cover along two perpendicular 22.6-m transects, oriented in a random direction, bisecting the center of each plot. We measured litter depth and visually estimated forb, litter, and bare ground cover inside a 20 × 50 cm Daubenmeir plot frame at 2 m intervals on alternating sides of each transect (Bonham 1989). This yielded 22 estimates of each variable, which we then averaged. We used the point intercept method to measure forest vegetation structure by developing foliage profiles within seven vertical layers (0–1 m, >1–2 m, >2–3 m, >3–5 m, >5–10 m, >10–25 m, and >25 m) at 33 points within each plot (Beck 1997). We used the proportion of points that intercepted vegetation in each layer to calculate total foliage density, foliage height diversity (fhd) (Anderson and Ohmart 1986), and canopy cover.

## STATISTICAL ANALYSIS

We used 1–1 matched-pairs logistic regression (MPLR) (Hosmer and Lemeshow 1989) to compare song posts and foraging locations of Varied Thrushes to paired random locations. We calculated mean differences between paired bird-centered and random locations for each microhabitat and mesohabitat variable. The mean differences were then used in the MPLR analyses.

As part of a model building strategy, we first conducted univariate MPLR on each independent variable to determine which variables might be useful in classifying song post or foraging locations occupied by Varied Thrushes. We included variables that were significant at the 0.25 level in the full model, following the suggestion of Hosmer and Lemeshow (1989). This strategy also served as an efficient means of variable reduction. We controlled for multicollinearity by computing a correlation matrix among the remaining variables. When two or more variables were significantly correlated ($r > 0.60$, $P < 0.001$), we used each correlated variable with all other variables included in the full model in separate multivariate MPLR analyses. We achieved the most parsimonious reduced model by removing variables in a manual, single-step elimination routine and comparing Akaike Information Criteria (AIC) (Akaike 1973) values. We also compared the reduced model to one using a stepwise selection procedure. Finally, we assessed model fit by comparing the estimated coefficients and standard errors for each variable in the reduced model with the estimates of those variables in the full model.

For the song posts analyses, we used 18 microhabitat and mesohabitat variables to differentiate bird-centered and random song posts. Because 57 of 60 song posts were in trees or snags, we used only those observations in MPLR analyses.

Because of the large number of independent variables, we used the basic model building strategy outlined above to conduct separate analyses on microhabitat and mesohabitat variables of foraging locations (James and McCulloch 1990). Ten microhabitat variables were used in the first MPLR and 19 mesohabitat variables were used in the second MPLR. We then combined the variables from the reduced microhabitat and mesohabitat models and entered them into a third MPLR to build the final model. We only used foraging locations on the ground or on logs in the analyses ($n = 43$).

We used standardized differences ($X_i - \bar{X}_i$)/$SD_i$, where $X_i$ is the value for the microplot, $\bar{X}_i$ is the mean value for the mesoplot, and $SD_i$ is the standard deviation for the mesoplot, to evaluate whether song post and foraging microhabitat attributes differed from mesoplot attributes. For most variables, we analyzed the mean standardized differences using a one-sample $t$-test.
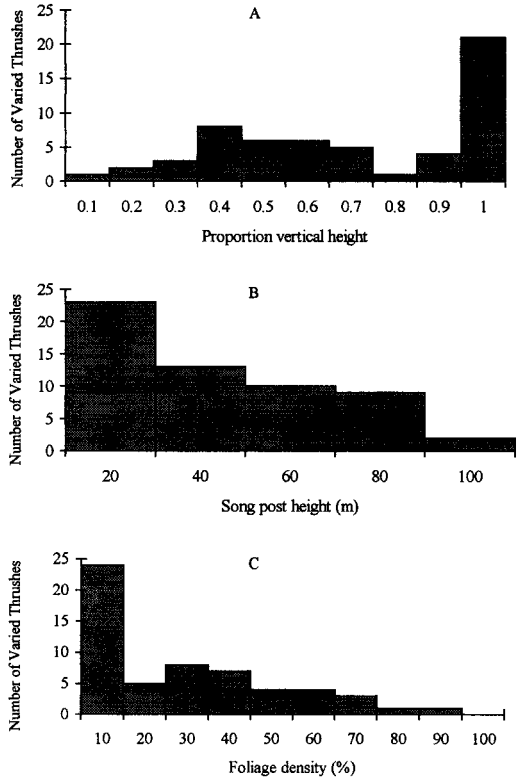


FIGURE 1.   Spatial characteristics of song posts in trees used by Varied Thrushes in Humboldt County, California, 1994–1995. (A) Vertical position of song posts. A proportion of 1 indicates the top 10 percent of trees. (B) Height of song posts. (C) Foliage density within a 0.5-m radius sphere of song posts.

Where standardized difference analysis was not appropriate (e.g., % shrub cover, % cover of woody debris), we used a paired $t$-test to compare microsite cover values with cover values for the plot.

We conducted a contingency table analysis using Cramer's $V$ statistic (Hintze 1996) to determine whether there was an association between the species of tree used by Varied Thrushes as song posts versus randomly chosen trees. We used chi-square goodness-of-fit tests to determine whether vertical position and foliage density of song posts within trees were different than expected. We divided vertical position into five equal proportions of 0–0.2, >0.2–0.4, >0.4–0.6, >0.6–0.8, >0.8–1.0. We divided foliage density into intervals of 0–10 percent, >10–25 percent, >25–50 percent, >50–75 percent, >75–100 percent. A sphere completely

TABLE 1. Summary of mean differences ($\pm$ SE) between paired bird-centered and random sites and results of univariate and multivariate 1-1 matched-pairs logistic regression (MPLR) using habitat variables to explain use of song posts by Varied Thrushes in Humboldt County, California, 1994–1995. $n = 57$ song posts.

| | Univariate 1-1 MPLR | | | Multivariate 1-1 MPLR | | |
| Variable | $\bar{x}$ Difference | Wald $\chi^2_1$ | $P^a$ | Coefficient | Wald $\chi^2_1$ | $P$ |
|---|---|---|---|---|---|---|
| Distance to water (M) | $-29.4 \pm 9.4$ | 7.0 | <0.01 | $-0.02 \pm 0.01$ | 6.5 | 0.01 |
| Slope (°) | $3.3 \pm 1.6$ | 3.8 | 0.05 | $0.06 \pm 0.03$ | 3.5 | 0.06 |
| Song post tree dbh (cm) | $45.1 \pm 16.0$ | 5.6 | <0.02A | $0.01 \pm 0.004$ | 2.6 | 0.11 |
| Song post tree type (conifer/deciduous) | $0.1 \pm 0.1$ | 2.7 | 0.10 | $1.08 \pm 0.68$ | 2.6 | 0.11 |
| Density of trees > 10 cm dbh (ha$^{-1}$) | $53.9 \pm 35.8$ | 2.1 | 0.15 | $0.003 \pm 0.002$ | 2.4 | 0.12 |
| Song post tree height (m) | $9.0 \pm 4.2$ | 4.0 | <0.05A | | | |
| Total foliage density (%) | $2.7 \pm 1.9$ | 1.9 | 0.17 | Model (df = 5)$^b$ | 26.0 | <0.001 |

$^a$ Letters indicate significantly correlated variables ($r \geq 0.60$, $P < 0.001$) included in separate full models for MPLR multivariate analysis.
$^b$ Model AIC (Akaike Information Criteria) = 64.2.
$^c$ $-2$ log likelihood $\chi^2$.

surrounded by foliage would equal 100 percent and would preclude seeing anything inside the sphere.

We used 2-×-2 contingency table analysis to determine whether thrushes used habitat types, categorized as undisturbed forest or disturbed habitat such as trails, roadsides, grass parks, and yards within or adjacent to forests, in different proportions in bird-centered versus random ground-foraging locations. We conducted a contingency table analysis using Cramer's $V$ statistic to determine whether Varied Thrushes used specific shrub species as foraging locations in different proportions than shrub species in the random plots.

We conducted MPLR analyses using SAS (PROC LOGISTIC; SAS Institute 1995). Model selection was based on AIC values and not significance of variable parameters (Lebreton et al. 1992). We performed all other analyses using NCSS 6.0.21 (Hintze 1996). Results reported as $\bar{x} \pm$ SE, are considered significant if $P \leq 0.05$.

RESULTS

SONG POST LOCATIONS

Fifty-seven of 60 (95%) song posts were in trees ($n = 55$, 91.7%) or snags ($n = 2$, 3.3%), two were on logs (3.3%), and one was on the ground (1.7%). All observed singing Varied Thrushes were males.

We found no difference between the proportion of tree species used as song posts and randomly chosen trees (Cramer's $V = 0.44$, $n = 57$). There was no significant difference in the proportion of conifers used as song posts compared to random song posts ($\chi^2_1 = 2.7$, $P = 0.10$).

Based on the results of univariate MPLR, height and dbh of song post tree, distance to water, slope, tree type (conifer vs. deciduous), tree density, and total foliage density met the criteria ($P \leq 0.25$) for inclusion in the full model used in the subsequent multivariate analysis of song post versus random locations (Table 1). However, song post tree height and song post dbh were used in separate multivariate MPLR analysis because both were highly correlated ($r = 0.77$, $P < 0.001$) (Table 1). Song posts tended to be in larger dbh conifers, located on steeper slopes, closer to water, and surrounded by a higher density of trees than random locations in the most parsimonious reduced model (Table 1).

Song post tree dbh (microhabitat variable) was a much better explanatory variable of song post locations compared to random locations than mean tree dbh (mesohabitat variable) (model $\chi^2_1 = 8.0$, $P < 0.005$ and model $\chi^2_1 = 0.4$, $P = 0.52$, respectively). Varied Thrushes used significantly larger dbh trees ($\bar{x} = 126.4 \pm 16.1$ cm) for song posts than mean dbh of all trees ($\bar{x} = 79.8 \pm 8.2$ cm) within each bird-centered mesoplot ($t_{56} = 4.7$, $P < 0.001$).

Song post locations tended to be higher in trees than would be expected by chance ($\chi^2_4 = 25.0$, $P < 0.001$). Twenty-five of 57 (44%) singing Varied Thrushes were positioned in the highest stratum of the trees (Fig. 1A). Twenty-three of 57 (40%) song posts were within 20 m of the ground (Fig. 1B). A greater proportion of Varied Thrushes than expected used song posts with

TABLE 2.   Summary of mean differences (± SE) between paired bird-centered and random sites and results of univariate 1-1 matched-pairs logistic regression (MPLR) using habitat variables included in the full models to explain use of foraging locations by Varied Thrushes in Humboldt County, California, 1994–1995. $n = 43$ foraging locations.

| Variables | x̄ difference | Wald $\chi^2_1$ | $P^a$ |
|---|---|---|---|
| Microhabitat variables | | | |
| Bare ground cover (%) | 23.4 ± 5.9 | 6.8 | 0.009A |
| Litter cover (%) | −24.3 ± 6.1 | 7.5 | 0.006A |
| Litter depth (cm) | −2.7 ± 0.7 | 8.3 | 0.004 |
| Soil moisture (%) | −6.9 ± 2.0 | 7.3 | 0.007 |
| Forb cover (%) | 10.3 ± 8.2 | 1.5 | 0.22 |
| Shrub cover (%) | −75.3 ± 5.5 | 8.7 | 0.003B |
| Wood < 30 cm cover | −6.7 ± 2.1 | 5.4 | 0.02 |
| Foliage density (%) | −59.7 ± 4.8 | 4.4 | <0.04B |
| Distance to cover (m) | 1.3 ± 0.2 | 11.9 | <0.001 |
| Mesohabitat variables | | | |
| Bare ground cover (%) | 14.4 ± 3.8 | 6.7 | <0.01C |
| Litter cover (%) | −15.8 ± 3.8 | 7.3 | <0.007C |
| Litter depth (cm) | −2.1 ± 0.5 | 9.6 | <0.002 |
| Forb cover (%) | 7.3 ± 4.8 | 2.1 | 0.14 |
| Shrub cover (%) | −26.6 ± 3.9 | 13.0 | <0.001 |
| Wood < 30 cm cover | −1.6 ± 0.6 | 5.4 | 0.02 |
| Conifer importance | −0.1 ± 0.1 | 1.9 | 0.17 |
| Canopy cover (%) | −10.5 ± 4.8 | 3.9 | <0.05D |
| Total foliage density | −5.2 ± 1.0 | 4.2 | 0.04D |
| Snag density (ha⁻¹) | −16.9 ± 7.2 | 4.2 | 0.04 |
| Slope (°) | −4.0 ± 1.9 | 3.8 | 0.05 |
| Distance to water (m) | −32.9 ± 9.0 | 7.9 | <0.005 |

$^a$ Letters indicate significantly correlated variables ($r \geq 0.60$, $P < 0.001$) included in separate full models for NPLR multivariate analysis.

low foliage density ($\chi^2_4 = 73.2$, $P < 0.001$). Twenty-four of 57 (42%) song post locations were characterized by <10% foliage density within a 0.5-m radius sphere of the bird (Fig. 1C).

FORAGING LOCATIONS

Thirty-one of 55 (56%) foraging Varied Thrushes were males, 15 (27%) were females, 4 (7%) were juveniles, and 5 (9%) we were unable to identify. We also observed eight juveniles or fledglings being fed by adults on five different occasions. Nineteen of 55 (35%) foraging locations were in undisturbed forest and 36 (65%) were in disturbed habitats, within or adjacent to forests, such as trails ($n = 19$, 35%), roadsides ($n = 12$, 22%), grass park ($n = 3$, 5%), and yards ($n = 2$, 4%). A significantly greater proportion of Varied Thrushes used disturbed habitat types as ground foraging locations compared to random locations ($\chi^2_1 = 53.5$, $P < 0.001$). Forty of 55 (73%) foraging locations were on the ground, 3 (5%) were on logs, 9 (16%) were in berry bushes, 2 (4%) were in trees, and 1 (2%) was in a snag.

Based on univariate MPLR using only microhabitat variables, bird-centered foraging microsites had less litter cover, litter depth, percent soil moisture, shrub cover, wood < 30 cm diameter cover, foliage density, greater distance to nearest cover, and greater bare ground cover and forb cover than random microsites (Table 2).

In the subsequent multivariate MPLR, we controlled for multicollinearity by including shrub cover and foliage density ($r = 0.78$, $P < 0.001$) and litter cover and bareground cover ($r = -0.94$, $P < 0.001$) in separate analyses. The multivariate analysis of microsite variables resulted in two models that were equivalent in their explanatory ability. Ground foraging microsites were surrounded by 60% less foliage density within a 0.5-m radius hemisphere and had 75% less shrub cover and were 1.3 m farther from cover than random microsites (Table 3).

Based on univariate MPLR using only mesohabitat variables, bird-centered plots had less litter cover, litter depth, shrub cover, wood < 30 cm diameter cover, canopy cover, snag density, conifer importance, and total foliage density, and greater bare ground cover and forb cover

TABLE 3. Results of multivariate 1-1 matched-pairs logistic regression (MPLR) using habitat variables to explain use of foraging locations by Varied Thrushes in Humboldt County, California, 1994–1995. Each level of analysis yielded two equivalent models. Model 1 depicts the most parsimonious model for each level, based on the lower AIC (Akaike Information Criteria) value. $n$ = 43 foraging locations.

| Variable | Coefficient ± SE | $\chi^2$ | $P$ | AIC |
|---|---|---|---|---|
| Microhabitat Model I (df = 1) | | 49.1[a] | <0.001 | 12.6 |
| Foliage density (%) | −9.5 ± 4.5 | 4.4[b] | <0.04 | |
| Microhabitat Model II (df = 2) | | 49.8[a] | <0.001 | 14.1 |
| Shrub cover (%) | −9.6 ± 5.1 | 3.4[b] | 0.06 | |
| Distance to nearest cover (m) | −1.2 ± 0.9 | 1.6[b] | 0.20 | |
| Mesohabitat Model I (df = 2) | | 30.7[a] | <0.001 | 33.3 |
| Shrub cover (%) | −5.7 ± 1.9 | 9.2[b] | <0.003 | |
| Litter depth (cm) | −0.2 ± 0.2 | 2.5[b] | 0.12 | |
| Mesohabitat Model II (df = 4) | | 34.0[a] | <0.001 | 34.7 |
| Shrub cover (%) | −5.3 ± 2.2 | 5.6[b] | <0.02 | |
| Litter depth (cm) | −0.3 ± 0.2 | 2.5[b] | 0.11 | |
| Distance to water (m) | −0.02 ± 0.01 | 2.3[b] | 0.13 | |
| Slope (°) | 0.1 ± 0.1 | 1.7[b] | 0.19 | |
| Final Model I (df = 1) | | 49.1[a] | <0.001 | 12.6 |
| Foliage density (%) | −9.5 ± 4.5 | 4.4[b] | <0.04 | |
| Final Model II (df = 3) | | 52.4[a] | <0.001 | 13.8 |
| Microhabitat shrub cover (%) | −14.9 ± 10.2 | 2.1[b] | 0.14 | |
| Distance to nearest cover (m) | −2.2 ± 1.8 | 1.6[b] | 0.20 | |
| Mesohabitat litter depth (cm) | −0.3 ± 0.2 | 1.8[b] | 0.18 | |

[a] −2 log likelihood $\chi^2$.
[b] Wald $\chi^2$.

than random plots (Table 2). Like song post locations, bird-centered foraging locations were closer to water than random locations. However, unlike song post locations, which were on steeper slopes, foraging locations were on more moderate, gradual slopes compared with random locations (Table 2).

In the subsequent multivariate MPLR, we included canopy cover and total foliage density ($r$ = 0.67, $P$ < 0.001) and bare ground cover and litter cover ($r$ = −0.96, $P$ < 0.001) in separate analyses because of significant correlation. Two equivalent models resulted from multivariate analysis of mesoplot variables. In the first model, ground foraging mesoplots had 27% less shrub cover and 2.1 cm less litter depth. The second model included the variables from the first model, and additionally, foraging mesoplots were 32.9 m closer to water and were on slopes that were 4° less than random mesoplots. (Table 3).

After combining the variables from the previous microhabitat and mesohabitat models, the final multivariate MPLR analysis of ground foraging locations yielded two models with equivalent explanatory power. The most parsimonious of the two models was identical to the microhabitat model containing foliage density. The

second model contained mesohabitat litter depth in addition to the variables from the microhabitat model containing shrub cover and distance to nearest cover (Table 3). Thus, it appears that fine scale microhabitat variables have more power in explaining use of foraging locations than larger scale mesohabitat variables.

Although both variables were significant, microhabitat shrub cover was a better explanatory variable of foraging locations compared to random locations than mesohabitat shrub cover (model $\chi^2_1$ = 47.6, $P$ < 0.001 and model $\chi^2_1$ = 28.0, $P$ < 0.001, respectively). Within foraging locations, Varied Thrushes used microsites with significantly less shrub cover than for bird-centered plots (Table 4). This suggests that microsite shrub cover provided a better explanation of foraging locations than shrub cover measured at the mesohabitat plot scale. Foraging microsites also had significantly greater forb cover and less litter depth than what was available within each bird-centered plot (Table 4).

We found a very strong difference between the species of shrubs used by Varied Thrushes as foraging locations compared to random locations (Cramer's $V$ = 1.00, $n$ = 9). All Varied Thrushes foraged in fruiting berry bushes, whereas only two of the shrubs from the random

TABLE 4. Standardized differences in standard deviations (SD ± SE) and mean differences (± SE) in real units between bird-centered foraging location microhabitat (0.5-m circular plots) and mesohabitat (0.04-ha circular plots) attributes used by Varied Thrushes in Humboldt County, California, 1994–1995. $n = 43$ foraging locations.

| Variable | SD | x̄ difference | $t_{42}$ | $P$ |
|---|---|---|---|---|
| Forb cover (%) | 0.3 ± 0.1 | 7.9 ± 3.4 | 2.3 | 0.02[a] |
| Bare ground cover | 0.2 ± 0.1 | 6.4 ± 3.5 | 1.4 | 0.18[a] |
| Litter cover (%) | −0.1 ± 0.1 | −4.0 ± 3.5 | −0.7 | 0.52[a] |
| Litter depth (cm) | −0.3 ± 0.1 | −1.0 ± 0.3 | −2.4 | <0.02[a] |
| Shrub cover (%) | —[b] | −36.4 ± 3.0 | −12.1 | <0.001[c] |
| Wood < 30 cm cover | —[b] | 0.8 ± 0.9 | 0.9 | 0.36[c] |
| Wood > 30 cm cover | —[b] | −3.8 ± 3.5 | 1.1 | 0.28[c] |

[a] One-sample $t$-test of standardized differences.
[b] No standardized differences exist because the line-intercept method does not yield a distribution of values.
[c] Paired $t$-test of mean differences.

locations were berry bushes which contained no berries at that time. Seven of nine birds foraged on red huckleberry (*Vaccinium parvifolium*), one on thimbleberry (*Rubus parviflorus*), and one on salmonberry (*Rubus spectabilis*), whereas at random locations six of nine shrubs were sword fern (*Polystichum munitum*), one was hazelnut (*Corylus cornuta*), one was red elderberry (*Sambucus racemosa*), and one was California huckleberry (*Vaccinium ovatum*). We never observed foraging on berries before 1 June.

## DISCUSSION

### SONG POSTS

In territorial, sexually dimorphic species such as the Varied Thrush, song and plumage advertise a male's fitness, both in terms of interactions with conspecific males, and for courtship and breeding activities with females. Not only are song quality (Morton 1975) and plumage characteristics (Cott 1940) important, but the use of a specific song post location has consequences as well (Hunter 1980). The characteristics of the song post will affect the transmission of both audio and visual information to conspecifics, and to potential predators and interspecific competitors. Marten and Marler (1977) found that acoustic attenuation of all frequencies was most pronounced less than 2 m above the ground in all temperate habitats. However, unlike deciduous forests, coniferous forests showed a small additional reduction in attenuation above 2 m as well, suggesting that Varied Thrushes in this environment may benefit from singing higher in trees. Higher song posts may reduce attenuation in topographically variable landscapes like those found at our study sites, although Marten and

Marler (1977) did not quantify topographical effects. In addition, there may be other reasons for using higher song posts. First there are probably a greater number of song perches available within the canopy of trees, although the well developed, multi-layered subcanopy and understory of redwood forests appears to provide song posts at all heights. Second, visual detection of conspecifics and predators may be enhanced from higher perches. Finally, song posts above the ground are generally more conspicuous, which might prove beneficial in interactions with conspecifics, although the risk from avian predators might increase as well (Endler 1978).

Male Varied Thrushes sang from larger trees than those available both within bird-centered plots and between bird-centered and random locations within territories. Depending on the position of the song post within the tree, large, tall trees may provide more conspicuous song posts than smaller trees, or the use of larger trees may simply reflect the higher probability of landing on a tree with a greater surface area and more perches. The greater tendency to use coniferous trees reflects the larger size of most conifers compared to deciduous trees. Song post trees were surrounded by a higher density of trees compared to random locations. This would account for the greater total foliage density found within bird-centered plots and make song posts less visible, especially over greater distances. Song posts were on steeper slopes than random locations. However, the difference was small (3°), resulting in only a 0.5-m change in song post height for every 10 m change in horizontal distance. Therefore, variability in tree height would appear to overwhelm such a change. Fi-

nally, song posts were closer to water, possibly because territories were centered in drainages.

Many song post characteristics, such as low foliage density perches near the tops of trees, are consistent with the perspective that male Varied Thrushes use conspicuous song posts. Opposing this view, many song posts were in midcanopy trees within 20 m of the ground. More importantly, any advantage conferred by a conspicuous song post would tend to be countered by the low visibility of multilayered, closed-canopy redwood forests. In addition, male Varied Thrushes have a high-contrast, cryptic plumage that would confer low visibility in mature forests (Endler 1993, Gotmark and Hohlfalt 1995). Acoustical characteristics of songs may conceal the location of singing males (Dawson 1923). Therefore, it appears unlikely that Varied Thrushes are using song posts for visual display purposes.

FORAGING HABITAT

The tendency of animals to forage in well-defined microhabitats can be considered a logical extension of patch choice in foraging theory (Hutto 1985, Brown and Morgan 1995). Breeding Varied Thrushes often foraged on the ground for invertebrates (pers. observ.) in disturbed areas, especially along trails, within the forest. Ground foraging locations had less shrub cover, foliage density, woody debris <30 cm diameter cover, litter cover, litter depth, and more bare ground and forb cover at both the mesohabitat and microhabitat scale. However, less foliage density at the microhabitat scale best characterized ground foraging locations (Table 3). This was further supported by microsites having less shrub cover and greater distance to nearest cover, both of which were correlated with foliage density, and is evidence that thrushes used sites with little ground level vegetation present.

Varied Thrushes foraged closer to water, although, unexpectedly, foraging locations had less soil moisture at the microsite level than random locations. The low foliage cover at foraging sites (shrub and litter) can best explain this apparent contradiction. The lack of cover would result in moisture loss from the soil through increased evaporation.

The use of specific foraging locations (patch choice) is strongly affected by diet choice based on the availability of temporally changing food resources and nutritional requirements. Al-though we did not measure food availability and choice, we did observe changes in patch use, similar to those that Hutto (1981) found in western wood warblers. Early in the breeding season, when protein requirements of females and nestlings were presumably high, Varied Thrushes foraged predominantly on the ground for invertebrates (pers. observ.). After the young fledged, thrushes began including fruit in their diet; this was primarily red huckleberries which coincidentally became available in large numbers at that time (1 June). This suggests that Varied Thrushes rapidly changed their foraging behavior as their energetic needs and food availability changed over the season. Thus, in addition to habitat physiognomy, the presence of particular plant species such as fruit bearing shrubs became an important explanatory variable of foraging locations.

SCALE PERSPECTIVES

Our results support the efficacy of using a hierarchical approach, both in terms of measuring habitat characteristics at the appropriate scale of resolution and determining the scale or scales at which animals select habitat for specific activities. Habitat use can be viewed as a hierarchical, scale-dependent process by which an animal chooses locations within a habitat (Hutto 1985). It appears that use of song posts by Varied Thrushes was influenced by both micro and mesohabitat variables because both were included in the final multivariate MPLR model. At the territory-size scale, singing males used song posts on steeper slopes that were closer to water compared to random locations. At the within stand or mesohabitat scale, male Varied Thrushes used sites with higher tree density, whereas at the microhabitat scale, song-post tree size, position within the tree, and foliage density around the perch site were important. The importance of different scales in song perch use is not surprising given the varying scales at which plumage and vocal characteristics may operate in territorial advertisement and predator avoidance.

Foraging site use by Varied Thrushes appears to be influenced primarily by microhabitat attributes. Hilden (1965) and Hutto (1985) suggested that at larger scales, for instance the stand or habitat type, birds were more likely to respond to such proximate environmental cues as vegetation composition and structure in assessing habitat suitability. In contrast, patterns of mi-

crosite use within a habitat may be based on active exploration in response to ultimate factors, such as food or predation risk, or to cues that are closely correlated with ultimate factors. For example, when foraging for red huckleberries, the bright red berries are both a proximate cue that attracts the birds and ultimately are food items for the birds. However, Varied Thrushes may primarily respond to proximate cues such as lack of vegetation cover when choosing ground foraging locations. These proximate cues were probably correlated with two ultimate factors: food availability and risk of predation. Invertebrates may be more available in less vegetated sites because of higher densities, greater visibility, or easier accessibility. Areas with little ground level vegetation would increase the detectability of terrestrial predators and reduce the risk of predation (Bouskila 1995). Once these cues initiated a settling response, thrushes then began actively searching for food items.

Our foraging site analyses emphasize the importance of measuring habitat attributes at the appropriate spatial scale and corroborates earlier studies. Petit et al. (1988) found that mesoplot (0.04-ha circular plot) scale measurements failed to capture fine scale variation in nest site characteristics by Hooded Warblers (*Wilsonia citrina*) (1-m radius plots) and Wood Thrushes (*Hylocichla mustelina*) (5-m radius plots). When we used 0.04-ha circular mesoplots, we sampled not only the actual foraging site, but much of the surrounding forest vegetation, thus incorporating a great deal of heterogeneity into our samples. In contrast, the 0.5-m circular plot used in measuring microhabitat characteristics usually fell within the relatively homogenous habitat of foraging locations and therefore provided a more appropriate scale of resolution.

Our results and those from Hurt (1997) identified various habitat associations at multiple scales that might affect patterns of use of Varied Thrushes in northern California. Both studies also raise the possibility that changes in habitat characteristics at one scale may influence the distribution and abundance of these birds at other scales. For instance, lack of foraging opportunities or appropriate song posts may make small forest fragments less suitable to breeding Varied Thrushes. Chen et al. (1992) found that shrub and sapling cover was higher adjacent to clear cut edges than in the forest interior. Thus small forest fragments may not provide suitable

foraging conditions because of edge-associated effects on the vegetation. In addition, streams may often be absent from small forest fragments, thereby excluding a habitat element that is important both for foraging and song post use. These possible cross-scale interactions deserve further study in Varied Thrushes and other species.

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