BREEDING HABITATS OF THE WOOD THRUSH AND VEERY

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Habitat-related differences in the abundance of bird species are appreciated by every bird-watcher and have received their share of scientific study. In very few cases, however, do we understand why a species occurs in a particular habitat, either in an ultimate (evolutionary) sense or a proximate (behavioral) sense. Before these questions can be adequately approached, a knowledge of the quantitative aspects of species' habitats is necessary. Most information on this subject comes from comparative habitat analyses (e.g., Sturman 1968, Wiens 1969, James 1971, Anderson and Shugart 1974). Vegetation structure has been emphasized heavily in such studies and often has been adequate to measure habitat differences among species. Floristic and physical factors have received less attention although MacArthur (1964) suggested that the latter may be important for at least some species.

This study examines quantitatively the habitats of two woodland thrushes, the Wood Thrush (*Hylocichla mustelina*) and the Veery (*Catharus fuscescens*). My purposes were to determine how and to what extent their habitats differed and to indicate factors which seemed to be favored by each species in its selection of habitats. Some physical and floristic, as well as structural, habitat features were included to examine their effects on the distribution of the two species.

METHODS

I studied thrush territories at two localities in Litchfield Co., western Connecticut. The Pond Mountain area in Kent is a 320-ha deciduous woodland (max. relief = 220 m), with some open fields and thickets. The mature lowland woods are dominated by Sugar Maple (*Acer saccharum*) and White Ash (*Fraxinus americana*), and the uplands by Red and Chestnut Oaks (*Quercus rubra* and *Q. prinus*). The Catlin Wood area in Litchfield is a 20-ha mature lowland forest (max. relief = 10 m) dominated by Eastern Hemlock (*Tsuga canadensis*), White Pine (*Pinus strobus*) and Red Maple (*Acer rubrum*).

Territories of 49 Wood Thrush and 55 Veery pairs at Pond Mountain, and those of 6 Wood Thrush and 6 Veery pairs at Catlin Wood were mapped between 10 May and 15 June 1974. I visited each territory an average of 6 times; each visit averaged about 0.5 h. To map, I plotted positions of males singing and reacting aggressively to recorded songs of their species.

Habitat data were recorded in each territory along 200 m of transect, which was divided according to territory size. In heterogeneous territories the transects were aligned along the most obvious gradient; other-wise, the direction was taken from a table of random numbers. Vegetation cover data were taken at each of 100 points (every 2 m). The kinds and numbers of plants touching a 10 mm diameter peg between 0 and 0.2 m above the ground (C layer) were recorded. Similar data were recorded between 0.2 and 1.0 m (B layer) and between 1.0 and 3.0 m (A layer) using a 25 mm diameter pole. These cover figures are slightly greater than true percent cover because determination of the latter requires dimensionless sampling devices. I noted the type of substrate at the same 100 points. Tree size and distribution were evaluated by point quarter sampling at 25 points (every 8 m). Moisture regimes were recorded according to a scale used by Damman (1964). The scale runs from zero (here converted to -1) for loose sand, rock piles, and gravel, to 8 for permanently inundated soils. It is based on soil features such as texture, state of oxidation, and water table, and is independent of short term weather conditions. For example, sandy loams typically have moisture regimes of 2, whereas anaerobic soils with maximum water level close to the soil surface are classified as 5. I estimated the territory percentage occupied by different successional stages and plant communities. Successional stages were classified as "early": maximum tree height < 14 m; "late": maximum tree height > 14 m, but with many early successional plants remaining (and often a thicker shrub layer); and "mature": tree height ≥ 14 m and with a mature flora. Plant communities are described elsewhere (Bertin 1975, Kershner 1975) according to techniques of the Zurich-Montpelier school (e.g., Shimwell 1971: Ch. 6). Communities were delimited on the basis of floristic similarities and differences which corresponded to differences in soil type, moisture regime, topography, exposure, etc.

Territories of the two thrush species were compared using the Mann-Whitney U-test on parameters taken from the raw data. Structural parameters included percent vegetation cover in A, B, C, and tree layers, tree height and diameter, number of stems ≥ 25 mm dbh per ha, and percentage of territorial area in different successional stages. Physical factors included moisture regime, substrate type, and slope. Floristic parameters included importance values for the 40 commonest tree species and abundance values for the 100 commonest plant species. Each importance value combines density, dominance, and frequency, with 300 as the maximum possible value (for a monotypic stand) (Phillips 1959:44). Plant abundance values refer to total hits on the sampling pole or peg at all 100 sampling points in a territory for the particular plant species. Initially, I compared the amounts of each plant community in territories of the two thrush species, but they did not prove useful in differentiating territories and are not discussed further.

RESULTS

IDENTIFICATION OF IMPORANT HABITAT FEATURES

Territories of both thrush species at Pond Mountain were clustered along streams and
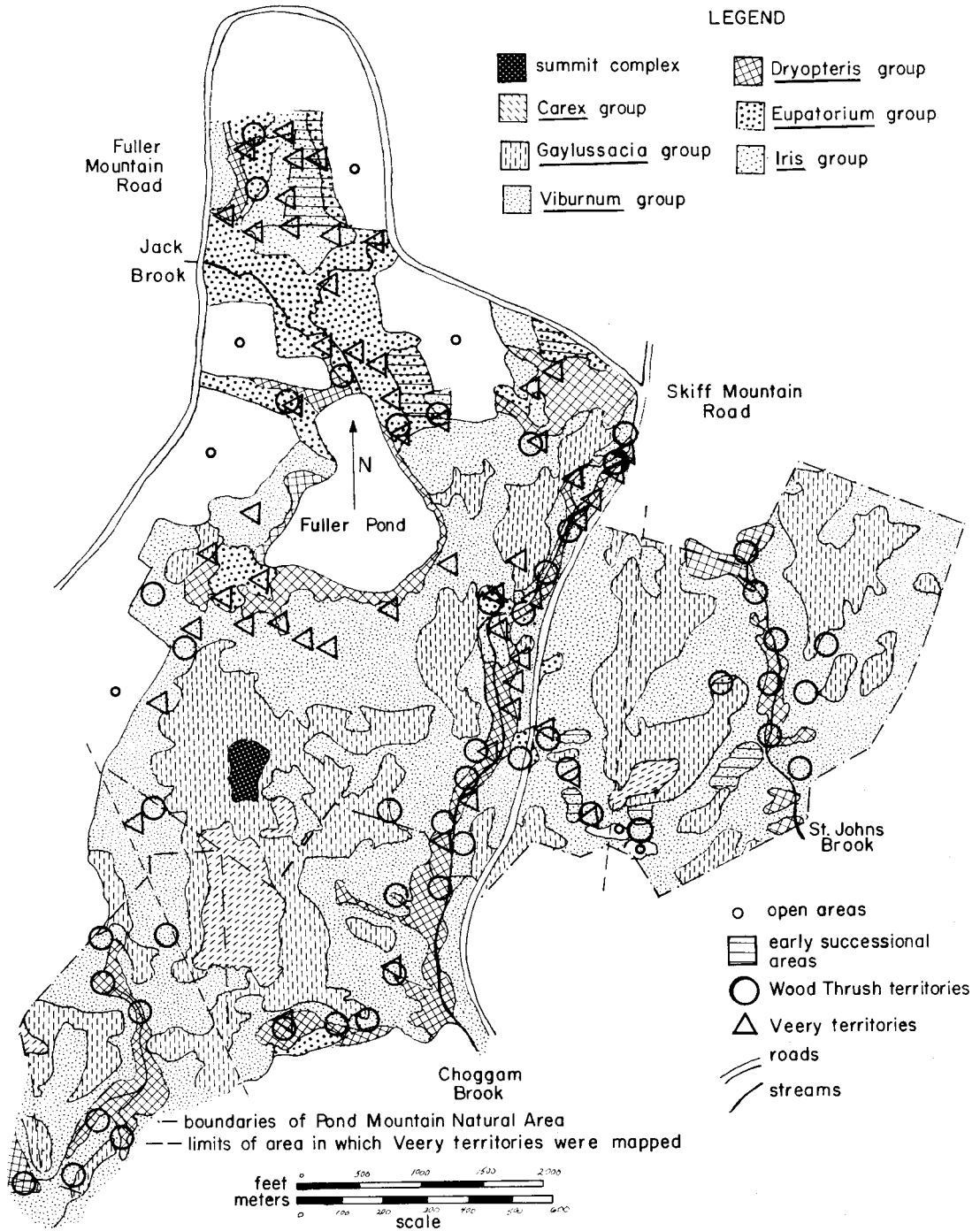
FIGURE 1. Distribution of Wood Thrush and Veery territories at Pond Mountain with respect to plant community groups. Average moisture regimes: summit complex –1.0, *Carex* group 1.0, *Gaylussacia* group 0.5, *Viburnum* group 2.0, *Dryopteris* group 3.5, *Eupatorium* group 4.0, *Iris* group 6.0. Map based on Kershner 1975.

in wetter places (Fig. 1). No similar pattern was observed at Catlin Wood, as this area contained no permanent water courses, and the range in moisture conditions was less than at Pond Mountain. Many environmental factors differed between the wet occupied areas and the drier unoccupied areas. In analyzing them, the availability of each factor in the entire study area had to be considered as this affects the range of habitats occupied. For example, average moisture regimes in most territories of both thrushes was 2 to 3
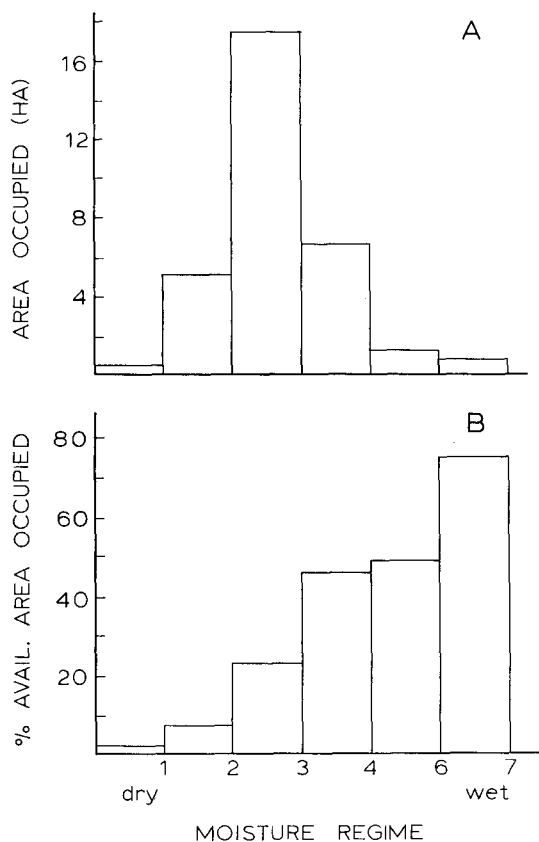
FIGURE 2. (A) Area of mature woodland at Pond Mountain occupied by Wood Thrush territories at different moisture regimes. (B) Percentage of available area at different moisture regimes occupied by Wood Thrush territories in mature woodland at Pond Mountain. No territory included sites with a moisture regime less than 0. Category 5–6 was excluded, as no plant community had this moisture regime.
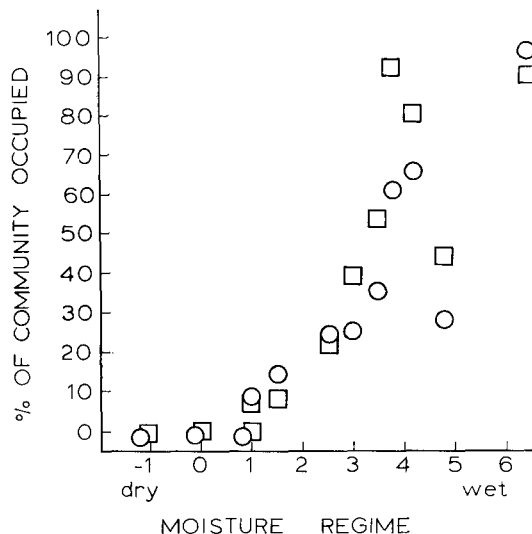

FIGURE 3. Percentage occupancy of plant communities with different moisture regimes in mature woodland at Pond Mountain. Squares denote Wood Thrushes, circles denote Veeries. Correlation of percent occupancy with moisture regime = 0.88 for Wood Thrushes and 0.90 for Veeries, both significant at .05 level.

(Fig. 2A) although regimes between 6 and 7 were preferred (Fig. 2B); this difference reflects the greater amount of available habitat with intermediate moisture regimes.

Habitat availability was taken into account for seven properties of the plant communities. The relative homogeneity of vegetation structure in each mature plant community allowed me to calculate average values of these parameters applicable to each community as a whole. Percentage occupancy of each community was calculated from territory size and composition measurements from this study, and plant community area measurements from Kershner (1975). Average values of the following parameters were calculated for each (mature) plant community: tree, herb (A + B), and shrub (C) layer cover, tree diameter and density, percentage of bare soil exposed, and moisture regime. For each thrush species, percentage of community occupied was re-

lated to these variables in a stepwise multiple regression. This technique is not ideally suited to the present situation because the results can be adversely affected by high correlation of independent variables (e.g., Neter and Wasserman 1974), and, like other statistical techniques, it does not address causation. However, it does indicate which of the independent variables account for the greatest amount of variability in habitat occupancy.

For the Wood Thrush, four variables made significant contributions to the regression: moisture regime ($P < .001$), tree diameter ($P < .01$), herb (A + B) cover ($P < .05$) and shrub (C) cover ($P < .05$). Moisture regime alone accounted for 76.0% of the variability in habitat occupancy. The next highest single variable (percentage of bare soil exposed) accounted for only 37.4% of this variability. The four significant variables together accounted for 98.3% of the variability in the dependent variable. For the Veery, two variables made significant contributions to the regression: moisture regime ($P < .001$) and herb (A + B) cover ($P < .05$). Moisture regime alone accounted for 78.4% of the variability in habitat occupancy, and the next highest single variable (herb cover) accounted for only 38.2% of this variability. These two significant variables together accounted for 86.8% of the variability.

Thus for both thrushes, moisture regime

TABLE 1. Average values of physical and structural parameters showing significant differences between all Wood Thrush and Veery territories.

Parameter	Territory means		
	Wood Thrush	Veery	P[a]
Shrub (A) layer cover (%)	43.9	51.6	0.01
Tree height (m)	16.3	15.0	0.05
Early successional stage (%)[b]	16.2	28.2	0.05
Late successional stage (%)[b]	9.6	17.9	0.01
Moisture regime (average)	2.8	3.4	0.01
Earth exposed (%)[b]	2.4	6.5	0.05

[a] Mann-Whitney U-test.
[b] Percent of territory.

TABLE 2. Significant and near-significant floristic differences between Wood Thrush and Veery territories in mature woodland at Pond Mountain. IV = importance value, PA = plant abundance value.[a]

Plant species	Wood Thrush	Veery	P[b]
Acer pensylvanicum IV	1.2	6.4	< 0.05
A. pensylvanicum PA	2.3	20.8	< 0.01
Betula papyrifera IV	1.6	8.9	< 0.05
Cornus florida PA	7.1	2.7	ns (< 0.07)
Hamamelis virginiana IV	11.7	29.9	< 0.01
H. virginiana PA	13.9	26.5	< 0.05
Maianthemum canadense PA	0.7	3.1	< 0.05
Quercus rubra–velutina PA	2.5	1.7	< 0.05
Uvularia perfoliata PA (B layer)	0.4	0.0	< 0.05
Viburnum acerifolium PA	34.0	15.7	< 0.01

[a] Plant abundances for A, B and C layers combined unless otherwise noted.
[b] Mann-Whitney U-test.

accounted for the most variation in habitat occupancy in mature woodland (Fig. 3) suggesting that it was either the dominant factor in the thrushes' habitat selection or was more highly correlated with this factor(s) than the other dependent variables. The remaining significant (structural) factors probably also played a role in habitat selection or were correlated (to a lesser extent) with factors that do. The factors actually used in habitat selection may not be those included in this analysis.

The importance of proximity to water cannot be evaluated in the above fashion. Water seemed to be important, however, because territories occupied earliest in the season tended to be along small streams, and small springs and seeps sometimes led birds to establish territories in habitats that would otherwise generally be unoccupied. Many Pond Mountain territories of both species were far from water (Fig. 1), however, and Catlin Wood supported large numbers of thrushes in moist areas away from running water. Thus, while running water may be desirable to these birds, it is probably less important than moisture regime or its associated factors.

COMPARISON OF WOOD THRUSH AND VEERY HABITATS

Six structural and physical properties differed significantly between all Wood Thrush and all Veery territories (Table 1). Successional stage seems to be the underlying factor in these differences, with Veeries appearing earlier in succession. (Late successional stage, as defined earlier, is also a sub-mature stage.) On sub-mature sites, trees were shorter and shrub cover greater than in mature woodland. Veery territories were slightly wetter than Wood Thrush territories (more moist), but as the early and late successional sites happened

to be wetter on average than mature woodland (Fig. 1), moisture regime itself was probably not the important factor. The higher percentage of exposed earth may have been in part related to moisture regime and perhaps also to presumed lower litter production on such sites (e.g., Major 1974).

Analysis of importance values from point quarter data showed that plants significantly more common ($P < .05$) in Veery territories were those of early successional and/or wetter areas (Speckled Alder, *Alnus serrulata*; Gray Birch, *Betula populifolia*; Black Cherry, *Prunus serotina*; Apple, *Pyrus malus*; American Elm, *Ulmus americana*; Nannyberry, *Viburnum lentago*). Plants significantly more common in Wood Thrush territories were components of mature forest, often of drier sites (American Chestnut, *Castanea dentata*; Flowering Dogwood, *Cornus florida*; Big-Toothed Aspen, *Populus grandidentata*; Chestnut Oak; Red and Black *Quercus velutina* oaks; Sassafras, *Sassafras albidum*). Floristic data from the transects (plant abundance values) showed similar patterns. Information on site preferences of plants was taken from Kershner (1975). Such preferences may, of course, differ in other geographical areas.

Comparisons including only territories in mature woodland were made to eliminate the effects of successional stage. No structural or physical parameters differed significantly although shrub cover was slightly greater in Veery territories (40.2% vs. 33.0%, $P < .07$).

Several significant floristic differences did exist between territories of the two species (Table 2). Plants of warmer and drier sites,

including Flowering Dogwood, Perfoliate Bellwort (*Uvularia perfoliata*), and the oaks, were more abundant in Wood Thrush territories. Conversely, plants of cooler and moister sites, such as Striped Maple (*Acer pensylvanicum*), White Birch (*Betula papyrifera*) and Canada Mayflower (*Maianthemum canadense*), were more abundant in Veery territories. The plants of the two habitats have similar growth (structural) forms. Canada Mayflower and the bellwort are both small herbs; Flowering Dogwood is a small tree similar in form to Striped Maple, and Witch Hazel (*Hamamelis virginiana*), and White Birch and the oaks are trees of at least moderate size. Instead, it seems that the floristic differences reflect microclimatic differences between territories of the two species.

DISCRIMINANT FUNCTION ANALYSIS

Svardson (1949) and Hilden (1965) suggested that habitat selection involves response to a combination of several environmental stimuli. When the sum of these stimuli exceeds some particular level, the bird settles on the territory. Discriminant function analysis provides a convenient way of combining these factors. The technique involves linear combination of variables into a function that maximizes separation between two or more groups (Rao 1952). With a single discriminant value for each territory, there can be complementary changes in individual terms of the discriminant equation (i.e., $l_i x_i$ of $D = l_1 x_1 + l_2 x_2 + l_3 x_3 + \ldots$) without any change in the discriminant value D. Similarly, an unfavorable state of one habitat variable can be balanced to some extent by an especially favorable state of another (Hilden 1965). The coefficients "l" in the equation are consistent with different weights ascribed to different habitat characteristics.

I used discriminant function analysis to get some idea of habitat overlap and to get an independent indication of the most important properties differentiating territories of the two species. Twelve parameters (the number limited by the statistical technique) were selected from those available in an effort to represent as wide a range of habitat characteristics as possible. These included tree cover, height, density, and average basal area, shrub cover, moisture regime, distance to water, importance value of Gray Birch, and plant abundances (from transect data) of Striped Maple, Flowering Dogwood, Mountain Laurel (*Kalmia latifolia*), and Cinnamon Fern (*Osmunda cinnamomea*). Habitat sep-
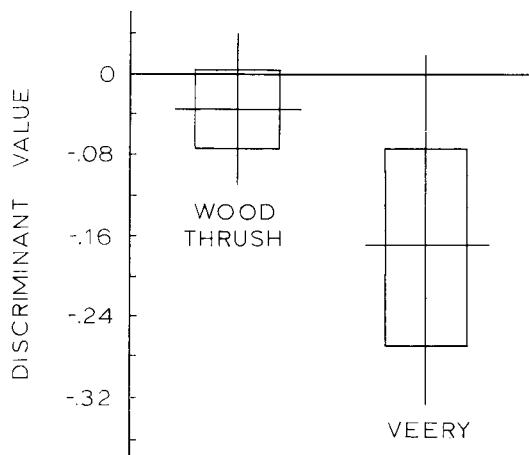

FIGURE 4. Distribution of Wood Thrush and Veery territories in mature woodland at Pond Mountain with respect to a discriminant function. Vertical lines give ranges, horizontal lines give means, and boxes include one standard deviation on each side of means. See text for variables contributing to discriminant function.

aration based on these measurements was significant ($P < .05$) when all territories at Pond Mountain were considered, except those in mature woodland. Based on only those parameters producing strongest separation, the differences were highly significant in both cases ($P < .001$).

In comparisons of all territories, shrub cover was the single most important factor (F value to enter $= 9.48, P < .005$), reflecting the absence of Wood Thrushes from thickets and early successional woodland. The other significant F value in the comparison of all territories (abundance of Flowering Dogwood; $F = 4.40, P < .005$) and the only significant F value in comparison of territories in mature woodland (abundance of Striped Maple; $F = 11.34, P < .005$) were floristic parameters reflecting microclimatic differences between the two species. These results agree well with those of the Mann-Whitney tests (Tables 1, 2).

In mature woodland, Wood Thrushes occupied territories with a much narrower range of discriminant function values than did Veeries (Fig. 4). Ninety percent of the range of Wood Thrush territory values were overlapped by the values of Veery territories, while only 26% of the range of Veery values were overlapped by those of Wood Thrushes. These figures compare favorably with overlap values obtained from territory mapping: 90% of Wood Thrush territories were overlapped to some extent by Veery territories, and 42% of Veery territories were overlapped by Wood

Thrush territories. These figures may indicate that Veeries have broader niches than Wood Thrushes (at least in factors included in the analysis), but they must be interpreted with caution because discriminant overlap values agreed less well with observed overlap when all territories were considered. (Discriminant overlap: 83% for Wood Thrushes, 82% for Veeries; observed territory overlap: 84% for Wood Thrushes, 50% for Veeries.) Furthermore, the discriminant overlaps vary depending on what habitat parameters are included in the analysis. These values are in the same general range as the average Wood Thrush-Veery overlaps (50–60%) obtained by Morse (1971) in Maine using different methods.

DISCUSSION

Wood Thrushes and Veeries are known to favor areas with running water, moist substrate, and high understory cover (e.g., Eaton 1914, Bent 1949, Odum 1950, Beals 1960). My findings suggest that in mature woodland, moisture regime may be more important than understory cover and proximity to running water. It is more highly correlated with features important to thrush habitat selection than these other variables. The frequent presence of high shrub cover in thrush territories may be partly explained by a correlation between this factor and moisture regime. The two showed a weak positive correlation ($r = 0.32$, $0.5 > P > 0.2$).

Wood Thrushes also seem to require one or more trees at least 12 m tall, possibly for song perches. Morse (1971) found Wood Thrushes nesting in stands of young White Pine with a canopy under 9 m; perhaps there were a few neighboring or projecting trees of greater height. My estimate of 12 m is for maximum tree height in the territory rather than average canopy height. Others have noted that Veeries occur on early successional and disturbed sites as well as in mature woods while Wood Thrushes are more restricted to mature woodlands (Pitelka 1941, Dilger 1956, Bond 1957, Beals 1960, Martin 1960, Shugart and James 1973, Magee 1973, 1974).

While the apparent tree height requirement of Wood Thrushes grossly differentiates habitats of the two species, a finer separation occurs in mature woodland. Microclimate seems to be the most important factor, here reflected in abundances of several plant species. These differences are correlated with the geographic distributions of the two thrushes, the Veery being the more northern bird. Veeries are known to inhabit cooler microclimates in southern parts of their range, occurring especially at high elevations, on north-facing slopes, and in wet depressions (Burleigh 1927, DeGarmo 1948, 1951, Adams 1959, Hutton et al. 1968, Alsop 1969, Simmers 1970). My findings suggest that less extreme microclimatic differences may be somehow detected and used in habitat selection in more central parts of the species' range.

Eaton (1914) and Magee (1967) noted unexplained complementary changes through time in numbers of Wood Thrushes and Veeries on particular sites. These changes may be explained if, as suggested here, habitat separation is slight and microclimatic factors are important in this separation. Year-to-year climatic differences during the spring could cause differences in understory microclimate either directly or indirectly through their effects on vegetation development during the spring and subsequent effects of vegetation on microclimate within the forest.

Recent bird habitat studies have largely ignored physical characteristics (e.g., James 1971, Anderson and Shugart 1974). My study shows that factors such as moisture regime or postulated microclimatic variables may be more highly correlated than vegetational structure with abundances of certain bird species. Even where bird abundance correlates with vegetation structure, physical factors can underlie such relationships and should not be neglected. (The reverse, of course, also applies.) I suspect that species most sensitive to physical variables such as substrate type and moisture regime would be those nesting and/or feeding on the ground. Plant abundances may prove to be convenient indicators of physical factors such as moisture regime and microclimate because they are sensitive to subtle changes in such properties, reflect them over periods of time, and are often easier to measure than the physical variables themselves.

In this study I considered only a few physical variables, owing to time and equipment limitations. Others that are probably important include light intensity, temperature, humidity and wind velocity.

PROXIMATE AND ULTIMATE FACTORS IN HABITAT SELECTION

My approach did not permit identification of proximate factors involved in habitat selection although it suggests avenues for more detailed and experimental investigation.

The absence of Wood Thrushes from early successional habitats may result either from preference or competitive interactions. Com-

petition with Veeries for these habitats seems unlikely because Wood Thrushes do not occupy such habitats outside the Veeries' range (pers. observ.). Diffuse competition with species better adapted to such habitats is possible but I did not evaluate it.

The requirement of minimum tree height may be related to singing as has been suggested for the Tree Pipit (*Anthus trivialis*; Lack 1933, 1937, Lack and Venables 1939) and several other species. Tree height is an obvious feature that may actually be a proximate cue in habitat selection. Wood Thrushes sing their prolonged evening serenades from the tops of tall trees while Veeries sing mostly between heights of 2 and 8 m, even in mature woods (Eaton 1914, Forbush 1929, this study). It seems unlikely that the ultimate (in an evolutionary sense) advantage of tall trees (i.e., greater than about 12 m) is related to singing, however. Presumably if female Wood Thrushes are attracted to males with tall trees in their territories, it is because their fitness is thereby enhanced.

The reasons for greater fitness in such habitats are unclear. Wood Thrush nests are regularly placed below 12 m (22 of 24 observed nests were below 6 m), making the extra tree height unimportant for elevating the nest. Wood Thrushes rarely, if ever, forage in the canopy (Dilger 1956, pers. observ.), so the extra height is not directly used for that. If taller trees produce more leaf litter and a greater litter fauna, taller woods may be advantageous to Wood Thrushes because they frequently forage by bill-sweeping in leaf litter (Clark 1971, pers. observ.). Veeries, by contrast, forage more by sight (pers. observ.), and their feeding may not be affected by litter depth. Predation may vary with habitat, as Gorman (1974) found for Common Eiders (*Somateria mollissima*), although why Veeries should not be similarly affected is unclear.

In mature woodland several proximate factors may be used in discerning appropriate habitats. If, as I suggest, the observed floristic differences reflect microclimatic differences, the thrushes may perceive these directly. Factors such as relative humidity and temperature near the ground may be detectable by birds, as has been suggested by Moreau (1934) for some African species, although the sensitivity of birds to such factors is apparently unknown. Calder (1973) suggested that some hummingbirds select nest sites on the basis of microclimatic indicators although it is unclear what these are. The thrushes may discriminate features of vegetation (e.g., leaf shape). Klopfer (1963, 1965) has shown that Chipping Sparrows (*Spizella passerina*) discriminate pine and oak foliage, and that exposure to foliage at an early age affects subsequent habitat preferences. The vegetation differences I found involve plant species whose foliage is more similar than pine and oak (all were broad-leaved species) and which were usually not dominant components of the local vegetation, making this hypothesis less likely. The possibility remains that some unmeasured factor, such as light intensity, is used as a proximate cue.

The ultimate causes of this habitat difference are probably related to physiological differences between the species, reflected in their different latitudinal distributions (Holmes and Sawyer 1975). These differences presumably allow Veeries to maintain an energy balance more easily in cooler microclimates in the southern parts of their range, while the reverse is true for Wood Thrushes in the northern parts of their range.

Studies such as this one, which relate habitat characteristics to species abundance, do not explain why birds occupy particular habitats although they are a necessary first step. They point to factors which appear regularly in bird territories and which may be correlated with proximate factors in habitat selection. Proximate factors may perhaps best be identified by experimentally holding confounding factors constant. To unravel the ultimate factors will require knowledge of the proximate factors, fuller understanding of the species' life history, and probably a healthy amount of evolutionary inference.

SUMMARY

Habitat characteristics of 55 Wood Thrush and 61 Veery territories in western Connecticut were examined quantitatively to determine preferred habitat features and interspecific habitat differences.

Both species tended to select sites with the wettest ground. Proximity to water and density of understory cover may have been important to a lesser degree. Wood Thrushes required trees greater than about 12 m in height, perhaps for use as song perches. The major habitat difference was the absence of Wood Thrushes from thickets and early successional woods, which contained Veeries. In mature woodland, Veeries occupied sites which, on average, had cooler microclimates, as reflected in abundances of certain plant species. Possible proximate and ultimate

factors involved in habitat selection are discussed.

The results suggest that for some bird species, physical factors may be important habitat characteristics and should not be neglected in habitat analyses. Plant abundances may in some instances serve as useful indicators of physical habitat characteristics.

ACKNOWLEDGMENTS

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