The measurements provided here are of use to workers attempting to identify species and sex of problematic museum specimens for these two sandpipers. This species-separating information must be applied with caution, since the possibility of confusion with other sandpiper species, especially Palearctic ones, exists. For North America, though, only the skull of *C. minutilla* is likely to be similar in size to *C. pusilla,* and this species has a distinctive bill shape (Prater et al., Guide to the Identification and Ageing of Holarctic Waders, Maud and Irvine, Tring, Herts., England, 1977).

Macrohabitat use, microhabitat use, and foraging behavior of the Hermit Thrush and Veery in a northern Wisconsin forest.—*Catharus* is one of several genera of North American passerines (e.g., *Dendroica, Empidonax, Parus, Toxostoma, Vireo*) that has received particular attention from ecologists (Grinnell, Auk 34:427–433, 1917; MacArthur, Ecology 39: 599–619, 1958; Lack, Am. Nat. 103:43–49, 1969; Beaver and Baldwin, Condor 77:1–13, 1975; James, Wilson Bull. 88:62–75, 1976). These researchers addressed the question of how series of congenerics differ ecologically to promote sympatric coexistence. Dilger (Auk 73:313–353, 1956a; Wilson Bull. 68:170–199, 1956b; Syst. Zool. 5:174–182, 1956c) arranged the four *Catharus* thrushes and the related *Hylocichla mustelina* along a synthetic gradient based on morphology, behavior, macrohabitat use, and geographical and elevational distributions. Of these factors, subsequent studies of interspecific interactions focused on macrohabitat use (Morse, Wilson Bull. 83:57–65, 1971; 84:206–208, 1972; Sealy, Condor 76:350–351, 1974; Bertin, Condor 79:303–311, 1977; Noon, Ecol. Monogr. 51:105–124, 1981). Relatively little information exists on the behavioral mechanisms behind the observed patterns.

To examine the relationship of *Catharus* thrushes to their habitat, I chose two sympatric species occupying adjacent, intermediate positions on Dilger's morphological-ecological gradient, the Hermit Thrush (*C. guttatus*) and the Veery (*C. fuscescens*). Data were collected for interspecific comparisons of habitat relationships at three levels of detail: (1) the structure of the two species' habitats (macrohabitat use); (2) species' use patterns for vegetation types and height strata within these habitats (microhabitat use); and (3) movement rates and lengths and prey capture methods (foraging behavior).

Based on the observations of earlier workers (Bent, U.S. Natl. Mus. Bull. 196, 1949; Dilger, 1956b, c; Morse 1971; Eckhardt, Ecol. Monogr. 49:129–149, 1979; Noon 1981), I made the following predictions. (1) Hermit Thrushes would occupy available sites dominated by coniferous vegetation, while Veeries would occupy sites dominated by deciduous vegetation. (2) Hermit Thrushes would be active primarily on the ground, whereas Veeries would

TABLE 1

TREE SPECIES AND SHRUB GENERA IN HERMIT THRUSH AND VEERY TERRITORIES

Vegetation category[a]	Species or genera[b]
Hardwoods	*Betula papyrifera*
	Acer saccharum
	Quercus borealis
	Acer rubrum
	Prunus spp.
Aspens	*Populus tremuloides*
	Populus grandidentata
Conifers	*Pinus resinosa*
	Picea mariana
	Pinus strobus
	Abies balsamea
	Picea glauca
	Tsuga canadensis
Shrubs	*Corylus*
	Alnus
	Viburnum
	Cornus
	Rubus
	Vaccinium
	Lonicera
	Amelanchier
	Campostoma
	Salix
	Myrica

[a] Categories based on growth form and foliage structure.
[b] Taxa are ranked in order of decreasing abundance within each category.

engage in more arboreal activities. Within the trees, Veeries would concentrate their activities in deciduous species and Hermit Thrushes would selectively use conifers. (3) Hermit Thrushes would rely more frequently on the active search patterns associated with ground foraging, whereas Veeries would employ more arboreal and aerial prey captures and sit-and-wait foraging tactics.

Study area and methods. — The study area was centered at the University of Wisconsin Trout Lake Station and the adjacent Mann Creek Wildlife Area, Vilas Co., Wisconsin (46°01′N, 89°40′W). The region is primarily forested with a mixture of conifers, aspens, and northern hardwoods (Table 1). Both thrushes were common and their territories frequently adjoined or overlapped.

I recorded vegetational data for three representative territories of each species. A territory was defined as an area regularly occupied by a singing male thrush. For each territory, these data consisted of the following measures: (1) tree identity and size (Tables 1, 2), (2) overstory structure (Table 2), and (3) understory composition and structure (Tables 1, 2).

For habitat analysis I classified woody species in four vegetation types based on overall

TABLE 2
VEGETATION STRUCTURE OF HERMIT THRUSH AND VEERY TERRITORIES[a]

| | Percent occurrence of tree types and size classes | | | | | |
| | Tree types[b] | | | Tree size classes[b] | | |
	% hardwoods	% aspens	% conifers	% saplings (BA < 100 cm^2)	% intermediate (100 cm^2 ≤ BA < 300 cm^2)	% mature (BA ≥ 300 cm^2)
Hermit Thrush (N = 134)	24%	57%	19%	69%	12%	19%
Veery (N = 126)	21%	59%	20%	56%	17%	27%

| | Structure of canopy and understory | | | | | | |
| | Canopy structure[c] | | | | Understory structure[d] | | |
	Foliage 3 m–9 m only	Foliage >9 m only	Foliage 3 m–9 m and >9 m	No foliage	Low herb growth (<0.25 m)	Tall herb growth (0.25–1.0 m)	Low woody growth (<1.5 m)	Tall woody growth (1.5–3.0 m)
Hermit Thrush	15%	25%	42%	18%	19%	19%	34%	28%
Veery	12%	20%	51%	17%	15%	18%	37%	30%

[a] Based on three territories for each species.
[b] Based on stem counts of trees >1 m in height in six randomly located 0.01-ha circular quadrats (two per territory).
[c] Canopy structure is presented as the percentage of 60 randomly located vertical sightings (20 per territory) which intersected vegetation at 3 m–9 m, >9 m, both heights, or neither.
[d] Understory structure is presented as the percentage of 600, 1-m transect segments (200 per territory, collected along two 100-m transects) which contained vegetation in four growth categories.

growth form and foliage structure (Table 1): (1) shrubs, (2) hardwoods, (3) aspens, and (4) conifers. I also delineated five height strata: 0 m, 0–3 m, 3–6 m, 6–9 m, and >9 m—hereafter referred to as ground, 3 m, 6 m, 9 m, and >9 m.

I collected behavioral data on eight pairs of Hermit Thrushes and seven pairs of Veeries between 1 June and 15 August 1976. I observed these territorial birds on a regular basis and followed them for several hours during each observation period. Data from all sequences and individuals were eventually pooled, since a qualitative inspection of the results revealed no appreciable intergroup variability. Observation time totalled 430 min for the Hermit Thrush and 432 min for the Veery.

Behavioral data consisted of chronological records written in a notebook and timed with a stopwatch calibrated in 0.01-min intervals. Individual birds were visually located and chronicled until I lost sight of them. Typically, continuous timings lasted only a few min ($\bar{x}$ = 1.8 min, SD = ±2.9, N = 449). For each movement, the following information was recorded: (1) starting perch location, including ground, tree or shrub species, size category for trees, and height; (2) movement length and type: nonfeeding which included simple travel, aggressive interactions, nest visits, etc.; or feeding which included attempted or realized prey captures; and (3) subsequent perch location (same data as starting location). I visually estimated heights and distances.

In analyzing microhabitat use, I included both feeding and nonfeeding activities. An animal's ability to move through an environment, defend a portion of it, or care for its young can be as important in determining the suitability of a particular habitat as the animal's success at procuring food (Pleszczynska, Science 201:935–937, 1978; Gatz, Tulane Studies Zool. Bot. 21:91–124, 1979; Moermond, Behaviour 70:147–167, 1979).

When a bird did attempt to capture prey, I recorded feeding method, location, and
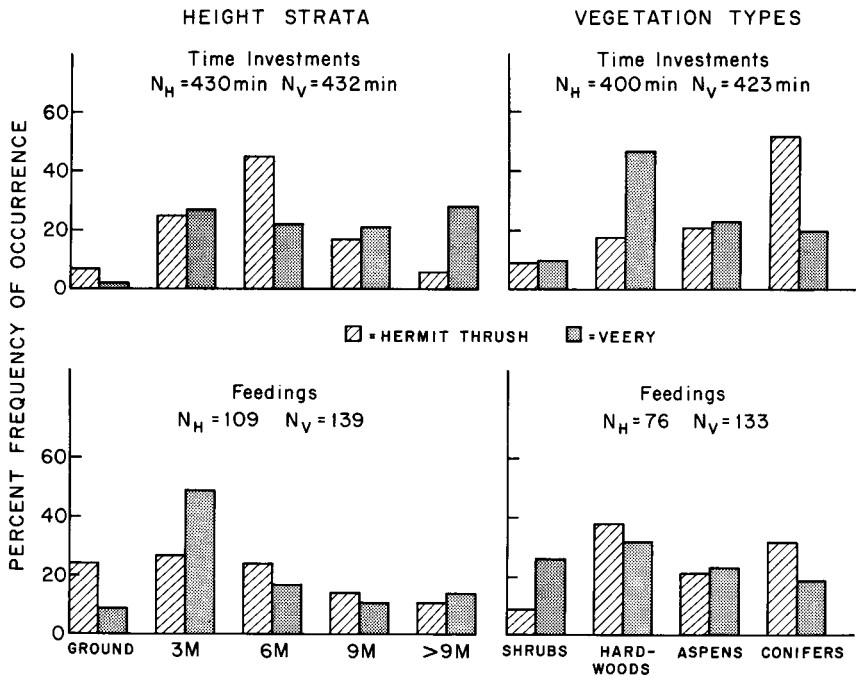
FIG. 1. The distribution of time investments and feedings among five height strata and four vegetation types for the Hermit Thrush and Veery.

outcome. I recognized the following prey capture methods in the vegetation: (1) glean—the bird hopped toward and then picked prey from foliage or woody stem while perched; (2) hover—the bird flew toward and captured prey located on foliage or woody stem; (3) hawk—the bird captured prey in mid-air; and (4) trunk-pounce—the bird flew toward prey located on a vertical surface, usually a tree trunk. The bird contacted the surface with its feet; clinging for a few seconds, it picked off the prey then resumed flight. The first three methods generally follow the terminology used by Robinson and Holmes (Ecology 63:1918–1931, 1982). The fourth method, trunk-pounce, is a distinct behavior frequently used by thrushes, including the American Robin (*Turdus migratorius*).

I also recorded the thrushes' foraging methods and feeding frequencies on the forest floor. Terrestrial travel involved short hops and runs. Prey captures consisted of ground gleans and probes (Holmes et al., Ecology 60:512–520, 1979).

Besides prey capture methods, I used movement rates and the distance of feeding moves, compared across arbitrarily determined length categories, to characterize the thrushes' foraging behavior. I used the distribution of intermove time intervals, based on 0.10-min categories, to compare the two species movement rates in the vegetation. Similarly, I recognized four categories in analyzing length distributions for the two species' feeding moves: 0–3 m, 3–6 m, 6–9 m, and >9 m.

Chi-square tests were used to analyze vegetational and behavioral data (Siegel, Nonparametric Statistics for the Behavioral Sciences, McGraw-Hill, New York, New York, 1956).

Macrohabitat use and structure.—The two thrushes occurred in stands of second-growth

TABLE 3
SUMMARY OF HERMIT THRUSH AND VEERY FORAGING BEHAVIOR IN VEGETATION

		Movement patterns		
Species	N	Median rates of movement (moves/min) (upper boundary of 1st, 3rd quartiles)	N	Median feeding move lengths (m) (upper boundary of 1st, 3rd quartiles)
Hermit Thrush	334	3.8 (1.3, 11.1)	73	3.0 (0.6, 4.6)
Veery	550	3.6 (1.7, 10.0)	109	4.6 (1.0, 7.6)

		Frequency distribution of prey capture methods			
Species	N	% Glean	% Hover	% Hawk	% Trunk-pounce
Hermit Thrush	81	19	54	17	10
Veery	137	22	49	16	13

forest containing both deciduous and coniferous trees (Table 1), with sapling aspens being most abundant. Over half of both species' territories were covered by an overstory with a maximum height of about 20 m. A well-developed understory of bracken ferns (*Pteridium aquinlinum*), shrubs, and tree seedlings extended from the ground to 3 m on over 80% of the area contained in thrush territories.

Vegetation sampling (Table 2) revealed no significant differences ($P > 0.05$) between the two species territories in the distribution of tree types ($\chi^2 = 0.22$, df = 2, NS), tree sizes ($\chi^2 = 4.76$, df = 2, NS), overstory structure ($\chi^2 = 1.27$, df = 3, NS), or understory structure ($\chi^2 = 4.16$, df = 3, NS).

A simple macrohabitat difference between coniferous and deciduous vegetation did not separate the Hermit Thrush and Veery on my study sites. Both species occupied what Dilger (1956b) termed "disturbed coniferous forest." Co-occurrence of the Hermit Thrush and Veery in the same macrohabitat is not unusual (Dilger 1956b, Morse 1971, Holmes et al. 1979). In Maine, the two species chiefly occupy opposite ends of the forest moisture gradient, with Hermit Thrushes nesting in dry pine-oak stands and Veeries nesting in damp deciduous woodlands (Morse 1971). However, both species occur in some mesic, mixed conifer-hardwood stands that, based on Morse's description, appear to be similar to my sites.

Microhabitat use patterns.—The Hermit Thrush and Veery differed significantly in their distribution of time spent among the five height strata ($\chi^2 = 110.10$, df = 4, $P < 0.001$; Fig. 1). Total time spent on the ground by Hermit Thrushes was over three times greater than that spent by Veeries. Hermit Thrushes concentrated their activities in the two lower strata of vegetation, while Veeries spent time evenly among the height categories.

The species' feeding patterns also differed significantly with respect to height ($\chi^2 = 19.61$, df = 4, $P < 0.001$; Fig. 1). Hermit Thrushes did about one-quarter of their feeding on the forest floor, whereas ground feedings accounted for less than one-tenth of the prey captures observed for Veeries. Within the vegetation, both species fed chiefly below 6 m, but it was the Veery that concentrated on the lowest stratum.

The thrushes' time investment patterns support my predictions. The Hermit Thrush appeared more terrestrial and was active most commonly in the lowest forest growth. In

contrast, the Veery appeared to be more arboreal, ranging throughout the canopy, and thus potentially encountering a different set of prey and avian competitors (Dilger 1956b). However, territorial defense may have influenced vertical patterns in the vegetation more strongly than food resources (Morse, Ecology 49:779–784, 1968; Williamson, Ecol. Monogr. 41:129–152, 1971). The divergent time investments reflect differences in song sites. Hermit Thrushes concentrated their singing in the 6 m stratum (57% of observations), while Veeries sang most frequently at >9 m (46%).

Actual feeding patterns suggest a less distinct vertical separation between the species. Despite the fact that Hermit Thrushes foraged on the ground more than Veeries, terrestrial feeding was relatively uncommon in both species. Holmes et al. (1979) observed that both Hermit Thrushes and Veeries did over 40% of their foraging on the forest floor of the old-growth hardwood stands at Hubbard Brook, New Hampshire. Based on my continued observations, I think that ground foraging is infrequent at my study sites, perhaps because the dense ground cover of the second-growth forest presents conditions less amenable to this activity (Smith, Behaviour 48:276–302, 1974). However, when ground foraging does occur, movement and feeding rates are high. While Hermit Thrushes spent only 8% of their time on the forest floor, ground foraging produced 24% of all prey captures.

Within the vegetation the Veery, as well as the Hermit Thrush, fed principally in the forest understory and midstory (Fig. 1). However, shrubs served as the most important foraging site for Veeries in the understory (52% of feedings in 3 m stratum), whereas saplings and low tree growth were more important for Hermit Thrushes (79% of feedings). This relationship illustrates the role of both vegetation type and height in the partitioning patterns exhibited by the two thrushes within their common macrohabitat.

The two species differed significantly in their distribution of time investments among the four vegetation types ($\chi^2 = 10.77$, df = 3, $P < 0.02$). Hermit Thrushes spent more time in conifers while Veeries concentrated their activities in hardwoods (Fig. 1). Significant differences also existed between the thrushes' distributions of feedings among the vegetation types ($\chi^2 = 110.88$, df = 3, $P < 0.001$). Hermit Thrushes fed more in conifers; Veerys fed more in shrubs (Fig. 1). Both species made little use of aspens, relative to these trees' abundance in the environment.

Habitat partitioning based on differential use of broadleaf and coniferous trees is a common pattern among insectivorous birds (Klopfer, Behavioral Aspects of Ecology, Prentice-Hall, Engelwood Cliffs, New Jersey, 1962; Morse, Ecology 54:346–355, 1973; Partridge, Anim. Behav. 24:534–544, 1976). This pattern has been related to interspecific morphological differences, particularly differences in leg and bill structure, similar to those existing between the Hermit Thrush and Veery (Dilger 1956b, c). At my study site this partitioning mechanism operated within rather than between macrohabitats.

The Veery's frequent use of shrubs provides another source of segregation. Other studies (Dilger 1956b, Noon 1981) have reported that a well-developed shrub layer, such as commonly associated with disturbed woodland habitats, characterizes Veery territories.

Foraging behavior. —I expected the two thrushes to differ in their foraging behavior, based on differences in their morphology (Dilger 1956b, c) and their environment (Holmes and Robinson, Oecolgia 48:31–35, 1981). This was not the case. Hermit Thrushes did more ground foraging than Veeries, but as previously discussed, this behavior was used infrequently by both thrushes. The species did not differ significantly ($P > 0.05$) in their movement rates ($\chi^2 = 12.57$, df = 10, NS), feeding move lengths ($\chi^2 = 2.55$, df = 3, NS), or prey capture methods ($\chi^2 = 4.42$, df = 3, NS) in the vegetation (Table 3).

The behavior of both thrushes in the vegetation (Table 3) was intermediate between that of sit-and-wait species (e.g., the Olive-sided Flycatcher [*Nuttallornis borealis*] and Cassin's Kingbird [*Tyrannus vociferans*] [Eckhardt 1979; Landres and MacMahon, Auk 97: 351–365, 1980]) and widely foraging species (e.g., the Yellowthroat [*Geothlypis trichas*] and

Blackpoll Warbler [*Dendroica striata*] [Eckhardt 1979; Sabo, Ecol. Monogr. 50:241–259, 1980]). Noon (1981) suggested that the Veery was less well-adapted for and less dependent on true aerial prey captures, when compared to the most arboreal *Catharus*, Swainson's Thrush (*C. ustulatus*), because of the higher vegetation densities typical of Veery habitats. Veery and Hermit Thrush foraging was dominated by foliage-directed prey captures requiring flight and resembled the foraging strategy employed by other midstory species, such as tanagers (*Piranga* spp.) and small tyrant flycatchers (*Empidonax* spp.), which Robinson and Holmes (1982) termed "open-perch searching" (Williamson 1971, Eckhardt 1979, Holmes et al. 1979).

Frakes and Johnson (Condor 84:286–291, 1982) reported a parallel case of convergence in foraging behavior for two *Empidonax* flycatchers. These species typically occupied separate macrohabitats and displayed distinct foraging patterns, but where they co-occurred in intermediate environments, their foraging proved very similar. Habitat structure apparently plays a role in determining foraging strategy independent of interspecific interactions (Maurer and Whitmore, Wilson Bull. 93:478–490, 1981; Seidel and Whitmore, Wilson Bull. 94:289–296, 1982).

Conclusions.—The Hermit Thrush and Veery at Trout Lake were similar both at the level of macrohabitat structure and the level of foraging behavior. The clearest evidence for resource partitioning occurred at the level of microhabitat use, with the thrushes differing significantly in their overall activity and feeding patterns among height strata and vegetation types within their shared macrohabitat.

My observations support the general premise that large scale separations among similar species along particular resource axes, e.g., prey type or habitat type, should have their evolutionary origins in smaller scale differences among co-occurring local populations (Wiens and Rotenberry, Ecol. Monogr. 50:287–308, 1980).

Interspecific song learning in a wild Chestnut-sided Warbler.—Vocal learning involving imitation is the prevalent mode of song development in songbirds. The evidence for vocal learning both from experimental studies and from local song variants shared among neighbors (dialects) indicates that songbirds generally learn from their own species, and that a genetically determined signal recognition center ("auditory template") constrains song learning within the species (Marler, *in* Function and Evolution in Behaviour, Baerends, Beer, and Manning, eds., Clarendon Press, Oxford, 1975; Payne, Auk 97:118–134, 1980; Marler and Sherman, J. Neuroscience 3:517–531, 1983). However, an increasing number of field and experimental studies have shown instances where birds learn the song of other species (Baptista, Z. Tierpsychol. 30:266–270, 1972; Wilson Bull. 93:265–267, 1981; Baptista and Morton, Auk 98:383–385, 1981; Eberhardt and Baptista, Bird-Banding 48:193–205, 1977; Kroodsma et al., Wilson Bull. 95:138–140, 1983). Evidence of vocal learning in the Parulinae (wood warblers) comes from one experimental Chestnut-sided Warbler (*Dendroica pensyl-*