

SPATIAL PATTERNS, FORAGING TACTICS, AND DIETS OF GROUND-FORAGING BIRDS IN A NORTHERN HARDWOODS FOREST

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ABSTRACT.—Seven species of ground-foraging birds bred syntopically in a northern hardwoods forest in New Hampshire. Spatial overlap was extensive, although some species were patchily distributed, apparently in response to local variations in habitat characteristics. Three groups of species were distinguished on the basis of their food-searching/foraging tactics: (1) those that hopped or walked slowly on the ground while searching and gleaning prey from the surface of the litter and nearby foliage (Ovenbird, *Seiurus aurocapillus*; Dark-eyed Junco, *Junco hyemalis*), (2) those that pried into substrates and searched methodically for hidden or buried prey (Wood Thrush, *Hylocichla mustelina*; Winter Wren, *Troglodytes troglodytes*), and (3) those that searched near and far substrates (up to 3 m) both on the ground and in the sapling, subcanopy, and, occasionally, canopy layers (Veery, *Catharus fuscescens*; Hermit Thrush, *C. guttatus*; Swainson's Thrush, *C. ustulatus*). Species within each of these three searching modes differed in macrohabitat occupied, microhabitat used, in relative use of prey-attacking methods, and/or in diet. Each species appears to use a unique combination of habitat characteristics (e.g., vegetation density on vertical and horizontal axes, food resources). Thus, bird foraging tactics and morphology combined with habitat structure constrain which species will be present in a given location and hence influence bird community patterns. Received 15 Sept. 1987, accepted 25 Feb. 1988.

Ecological relations of ground-foraging birds have been examined by Dilger (1956a, b), Morse (1971, 1972), Bertin (1977), Noon (1981), James et al. (1984), and others. Most of these studies have emphasized the importance of spatial segregation among guild members (James et al. 1984), morphological adaptations (Dilger 1956b), or the possibility that interspecific territoriality may play a key role in determining habitat use (Morse 1971, Noon 1981). Such analyses have largely been conducted at what Paszkowski (1984) called the "macrohabitat" level. Few attempts have been made, however, to understand the ways in which these species actually utilize their habitats, especially in terms of how and where syntopic species obtain food and what types of food are taken. An exception is the study by Paszkowski (1984) which showed that two thrush species in Wisconsin were generally similar in their macrohabitat use but differed in how they searched for food among height strata and vegetation types.

In this paper, we examine the spatial overlap, foraging behavior, and diets of seven species of ground-foraging birds that co-occur in a northern

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hardwoods forest in New Hampshire. These include four turdine thrushes (Wood Thrush, *Hylocichla mustelina*; Swainson's Thrush, *Catharus ustulatus*; Hermit Thrush, *C. guttatus*; Veery, *C. fuscescens*); a wren (Winter Wren, *Troglodytes troglodytes*), a paruline warbler (Ovenbird, *Seiurus aurocapillus*), and a fringillid (Dark-eyed Junco, *Junco hyemalis*). All seven forage for insects and other invertebrates mostly in forest litter and lower shrub levels. In multivariate analyses, these species cluster together into a ground-foraging guild based on foraging maneuver and substrate use (Holmes et al. 1979). In this paper, we address the degree to which these species actually co-occur within the study area, how they search for and capture prey, what food items are actually taken, and discuss what factors determine the ecological relations among these species in this forest.

STUDY AREA AND METHODS

This study was conducted between 1974 and 1978 on the 10-ha study plot in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, USA, described by Holmes and Sturges (1975) and Holmes et al. (1986). The study plot was located in unfragmented, second growth northern hardwoods dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). The forest floor was covered with a thick layer of dead leaves and other forest litter. The shrub layer (0.2–2 m) consisted of the seedlings and small saplings of beech and sugar maple, hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), mountain maple (*A. spicatum*), one common fern (*Dryopteris spinulosa*), and a variety of low-growing forbs. The sapling layer (2–8 m) contained the saplings of the dominant trees and some striped and mountain maple. The subcanopy (8–14 m) was relatively open compared to the denser overlying canopy (> 14 m). Further descriptions of the forest are given by Siccama et al. (1970), Bormann and Likens (1979), and Holmes et al. (1986).

The vegetation of the study area appeared fairly homogeneous, although local variations occurred. The density of vegetation in the shrub and herbaceous layers varied with the topography and was influenced by the occurrence, frequency, and age of gaps created by fallen trees. Understory vegetation was particularly dense in the gaps and along a stream that crossed the plot near the north end. The southern half of the study plot was better drained, drier, and had a less dense shrub layer and a more open forest floor.

Birds were censused and their distributions mapped on the 10-ha plot between late May–early July in each year, 1974–1978. Censuses involved modified spot-mapping, systematic mist-netting, and observations of color-marked birds (Holmes and Sturges 1975, Holmes et al. 1986). The locations of all observed individuals, including chases, fights, and counter-singing events, and of nests when found, were plotted on a gridded map of the study area and activity (=“territorial”) boundaries drawn. The distribution of each species on the study plot was then summarized by superimposing its territory maps for all five years and scoring the number of years that territories of that species covered at least 50% of each of the 40, 0.25-ha (50 × 50 m) quadrats which comprised the study plot (see Fig. 1).

Bird foraging behavior was quantified during June and early July, 1974–1978, using the protocol and techniques described by Holmes et al. (1979) and Robinson and Holmes (1982, 1984). Each time a bird was observed to attack a prey item, we recorded the substrate to which the maneuver was directed (litter, foliage of herbs, ferns, and trees, including seedlings

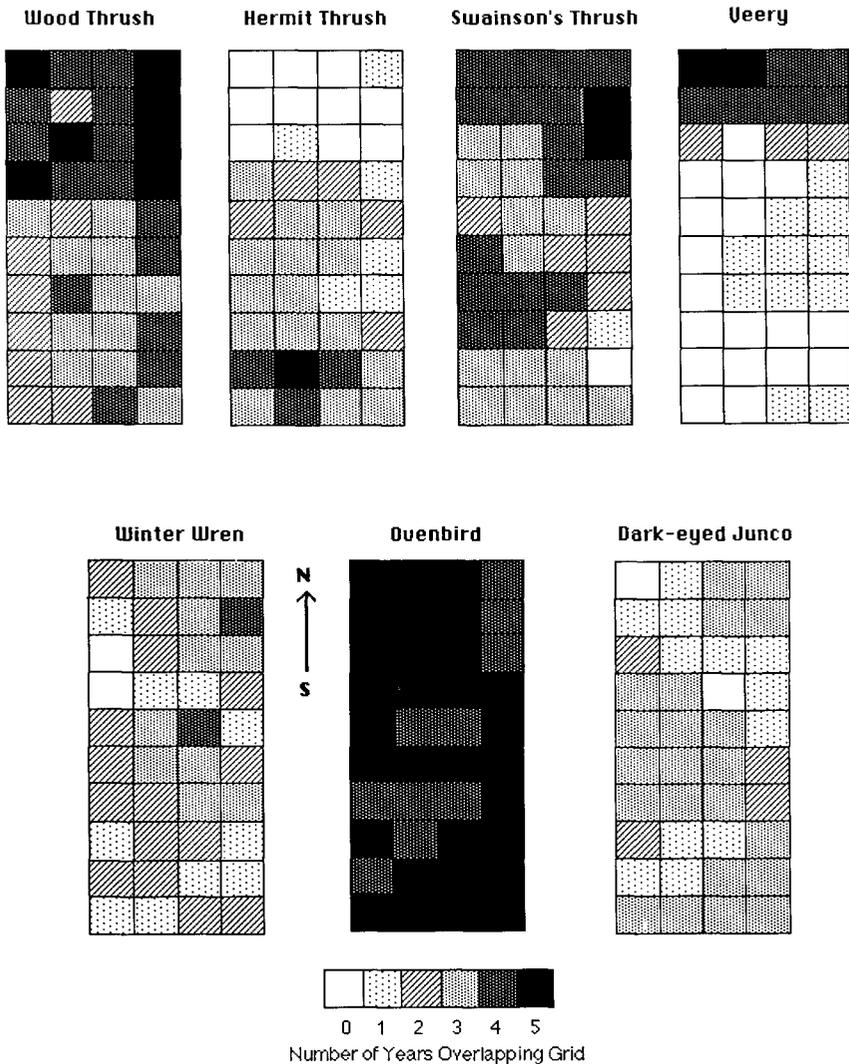


FIG. 1. Spacing patterns of the seven bird species in the ground-foraging guild on the 10-ha study plot at Hubbard Brook, 1974–1978. Patterning (see key) in each of 40, 50 × 50 m, quadrants represents the number of years (0–5) that 50% or more of territories of each species overlapped that square (see text).

and saplings, bark, air), the type of attack methods used, and the height above ground. Prey-attacking maneuvers used by foraging birds were categorized as follows: glean, in which a walking or perched bird picked prey from the surface of a plant or the ground; probe, in which a bird's beak moved, disturbed, or entered the substrate (e.g., leaf litter, loose bark)

to obtain prey; hover, in which a flying bird snatched or grabbed prey from the surface of a substrate, sometimes after a slight pause or hover; jump-hover, in which a bird jumped from the ground and plucked prey, usually from the undersurface of a leaf; dive-glean, in which a bird perched above the ground on a low branch, log or rock, flew downwards, usually landing, and then grabbed (=gleaned) prey from the surface of the litter (equivalent to the ground-pounce of Holmes and Recher 1986), and hawk, in which a flying bird chased and captured air-borne insects.

Once a bird was observed foraging, we followed it for as long as possible. This was desirable for two reasons. First, ground-foraging birds were very difficult to observe in the dense shrub layer of this forest, so that once a foraging bird was located, it was opportune to observe it for as long as possible. Second, we felt long sequences might reveal more about the foraging behavior of these species than the initial observation which would likely involve a more conspicuous act and lead to biases in the results. In the analyses, we provide data in two ways: (1) those based on the first maneuvers of each sequence, and (2) those from the cumulative number of foraging maneuvers from all sequences. All statistical comparisons (χ^2 tests on frequency data), however, are based on the data from first observations only, following the rationale of Morrison (1984). Four to 18 individuals of each species were observed each season, the number varying with the species' abundance on the study area (see Holmes et al. 1986); no individual bird was observed more than once per day, and usually less than once per week. For all species, our data include observations from the entire breeding season over three years, which should reduce any effect of short-term fluctuations in resource availability on our sample.

We also gathered information on the patterns of hopping and flying employed by each species in their search for food. These were often difficult observations to obtain because of the dense shrub layer in the study area and the shyness of these ground-foraging species. Thus, most of such observations are qualitative. However, for the three *Catharus* thrushes, we were able to quantify, with reasonably large sample sizes, the frequencies at which they hopped and flew between perches while foraging and the distances flown between perches. By combining all of the sequences for each species, we calculated their overall hop and flight rates, following the procedures of Moermond (1979), Eckhardt (1979), and Robinson and Holmes (1984). For these species, we also estimated the distances and angles flown on flights terminating in hovering prey-catching maneuvers, as an index to the radius over which they searched for and captured prey (Robinson and Holmes 1982).

To determine diets, we caught birds in mist nets in areas with comparable vegetation structure 1–2 km away from the main study plot, and gave them an emetic, potassium antimony tartrate (1% solution, given 0.1 cm³ per 10 g body weight) following the techniques of Prys-Jones et al. (1974). Details of the method and our procedures in this operation are described in Robinson and Holmes (1982) as are several caveats concerning interpretations of such data.

RESULTS

Densities and dispersion patterns.—Ovenbirds, Wood Thrushes, and Swainson Thrushes, the most common ground-foraging species at Hubbard Brook (Holmes et al. 1986), were relatively evenly dispersed over the entire 10-ha study area, although the latter two species showed some concentration towards the north (Fig. 1). In contrast, Veeries were localized each year in the northern end of the plot (Fig. 1), primarily along the stream, while Hermit Thrushes occupied the southern half away from

the stream where understory vegetation was less dense. Winter Wrens and Dark-eyed Juncos were patchily distributed, with two or three regions of the plot being used more frequently than the intervening areas (see Fig. 1).

Males of all species sang frequently and actively chased intruders in their defense of territory. All such interactions observed were with conspecifics; no interspecific aggression was recorded in any year of the study for any species. Despite the strong intraspecific responses, however, the thrushes, especially the Wood Thrush, often trespassed on neighboring conspecific territories. For example, on several occasions, individually color-marked male Wood Thrushes were observed and caught in nets in mid-breeding season up to 300 m from their home area and nesting site, across one to several conspecific territories. Some of these individuals were probably returning from long territorial conflicts which took them far from their own territories; in other cases, the birds appeared to be feeding and gave no vocalizations. From these few observations, it seems that activity ranges of these thrushes may overlap intraspecifically, and territories may not be very exclusive. Each thrush pair, however, did concentrate its activity within a core area in which the nest was located, and these activity centers were clearly evident from our composite field maps. In contrast to the thrushes, individual Ovenbirds, Dark-eyed Juncos, and Winter Wrens were consistently present in the same areas through each season and were frequently seen or caught near the sites where they were originally netted or observed.

Use of vertical strata for foraging.—Although all seven species have been classified as “ground”-foragers (Holmes et al. 1979), not all foraged extensively on the ground (Table 1). There were statistically significant differences between the frequency distributions of foraging heights for each species when first and all observations were compared ($P < 0.001$ for each intraspecific comparison, Table 1). Since foraging heights in a sequence are clearly correlated (Morrison 1984), we use only the data from the first observations for our interpretations below.

Based on these first observations, all pairwise comparisons of foraging heights among the seven species were significantly different ($P < 0.001$, except for the Wood Thrush and Ovenbird comparison where $P < 0.05$). The forest floor was used most frequently for foraging by all species except the Winter Wren, which foraged more in the shrub layer (Table 1). Wood Thrushes, Veeries, Ovenbirds, and juncos directed $\geq 65\%$ of their foraging attacks toward prey in the ground layer, while Hermit Thrushes, Swainson's Thrushes, and Winter Wrens foraged on the ground $< 50\%$ of the time (Table 1). The shrub layer was the second most used stratum for all species but the Winter Wren, for which it was the most frequently used

TABLE 1
VERTICAL DISTRIBUTION OF FORAGING BY BIRDS IN THE GROUND-FORAGING GUILD AT HUBBARD BROOK, BASED ON THE FIRST (1ST) AND ALL
(ALL) PREY ATTACKS IN OBSERVED SEQUENCES

Species	N	Percent of prey attacks in each stratum									
		Ground (0-0.2 m)		Shrub (0.3-2 m)		Sapling (2.1-8 m)		Subcanopy (8.1-14 m)		Canopy (>14 m)	
		1st (all)	1st (all)	1st (all)	1st (all)	1st (all)	1st (all)	1st (all)	1st (all)	1st (all)	1st (all)
Winter Wren	52 (407)	37.7 (33.4)	54.7 (57.1)	7.6 (9.5)	—	—	—	—	—	—	—
Wood Thrush	54 (204)	87.0 (92.2)	11.1 (6.8)	1.9 (1.0)	—	—	—	—	—	—	—
Hermit Thrush	41 (197)	46.4 (55.9)	26.8 (22.8)	17.1 (9.6)	7.3 (11.2)	—	—	—	—	—	—
Swainson's Thrush	123 (394)	46.3 (58.8)	20.3 (21.8)	13.0 (8.2)	10.6 (5.6)	—	—	—	—	—	—
Veery	27 (127)	70.4 (74.0)	22.2 (24.4)	3.7 (0.8)	3.7 (0.8)	—	—	—	—	—	—
Ovenbird	78 (482)	82.7 (88.4)	12.0 (10.0)	4.0 (1.4)	1.3 (0.2)	—	—	—	—	—	—
Dark-eyed Junco	102 (591)	64.7 (63.8)	19.6 (20.4)	11.8 (12.5)	3.9 (3.1)	—	—	—	—	—	—

stratum. Juncos and Swainson's and Hermit thrushes foraged for prey in the sapling layer (2.1–8 m) more often than did the other species. Hermit and Swainson's thrushes foraged higher than the other species in this group, especially the latter for which 10% of its prey attacks were in the forest canopy (Table 1).

Use of substrates for foraging.—All seven species took prey primarily from forest litter, foliage, and bark (Table 2). They differed significantly from each other, however, in their use of foraging substrates ($P < 0.01$ for each pairwise comparison among the seven species). The frequency distributions of substrate use differed significantly when first observations and all observations were compared ($P < 0.001$ for comparisons within each species). These differences were due mostly to more foliage- and less litter-use in the first-observation data than in the cumulative observations (Table 2). Since the act of attacking a prey on foliage, which usually involves flight, is probably more conspicuous, it would seem more likely to catch the observer's eye, and hence bias the results. For the same reason, the extent of ground, air and herb-fern foraging was underestimated by use of first observations only. Because of these findings, we base the following descriptions of substrate use on the cumulative data from all sequences.

All species, except the junco and wren, direct >50% of their foraging attacks toward prey on or in the forest litter (Table 2). The apparent discrepancy between the data for the ground layer in Table 1 and the ground-litter substrates in Table 2 reflects the fact that some foraging in the ground layer was on herbs, ferns, and low seedling foliage. The Wood Thrush foraged most often in the forest litter and Winter Wren the least often. Veery, Swainson's Thrush, and Hermit Thrush attacked prey frequently on tree foliage and to a lesser extent on tree bark (Table 2). Swainson's and Hermit thrushes, Winter Wrens, and juncos attacked flying prey at low but measurable frequencies (Table 2). For the Winter Wren, 50.1% of all maneuvers were directed towards prey on bark (Table 2); of these, 50% were directed toward the bark on tree trunks and exposed roots, mostly near the bases of trees, 41% toward fallen dead wood, usually logs and branches lying on the ground, and the remaining 9% toward prey on the bark of twigs or branches near the ground.

Prey-attacking behavior.—The most frequently used prey-attacking maneuvers were probes, gleans, and hovers (Table 3). Based on first maneuvers only, the species differed significantly in their use of prey-attack maneuvers ($P < 0.001$ for all pairwise comparisons, except for Ovenbird and Winter Wren which differed at $P < .05$). The frequencies of foraging maneuver use also differed significantly between the first observation data and those from all observations within each species ($P < 0.001$ for each

TABLE 2
FORAGING SUBSTRATE USE BY BIRDS IN THE GROUND-FORAGING GUILD AT HUBBARD BROOK, BASED ON THE FIRST (1ST) AND ALL (ALL) PREY
ATTACKS IN OBSERVED SEQUENCES

Species	N		Percent of prey attacks on each substrate				
	1st (all)	1st (all)	Ground/litter	Herb/fern	Foliage	Bark	Air
			1st (all)	1st (all)	1st (all)	1st (all)	1st (all)
Winter Wren	55 (391)	14.5 (18.2)	9.1 (6.4)	25.4 (21.2)	49.2 (50.1) ^a	1.8 (4.1)	
Wood Thrush	53 (203)	64.1 (85.6)	0.0 (2.0)	22.6 (8.9)	11.4 (2.5)	1.9 (1.0)	
Hermit Thrush	40 (202)	30.0 (50.6)	2.5 (7.4)	27.5 (26.7)	27.5 (7.4)	12.5 (7.9)	
Swainson's Thrush	112 (370)	41.1 (51.9)	0.8 (2.1)	37.5 (33.2)	17.0 (8.7)	3.6 (4.1)	
Veery	25 (123)	36.0 (56.0)	4.0 (3.3)	44.0 (35.8)	16.0 (4.1)	0.0 (0.8)	
Ovenbird	74 (464)	52.1 (65.6)	0.0 (0.0)	42.3 (29.4)	4.2 (3.3)	1.4 (1.7)	
Dark-eyed Junco	96 (557)	39.6 (37.4)	14.6 (18.7)	37.5 (34.6)	7.3 (4.6)	1.0 (4.7)	

^a See text for further breakdown.

TABLE 3
 PREY-ATTACKING MANEUVERS OF BIRDS IN THE GROUND-FORAGING GUILD AT HUBBARD BROOK, BASED ON THE FIRST (1ST) AND ALL (ALL)
 MANEUVERS IN OBSERVED SEQUENCES

Species	Percent of prey attacks by maneuver type													
	N		Probe		Glean		Jump/hover		Hover		Dive/glean		Hawk	
	1st (all)		1st (all)		1st (all)		1st (all)		1st (all)		1st (all)		1st (all)	
Winter Wren	52 (397)		28.9 (24.9)		50.0 (61.3)		3.8 (2.5)		15.4 (6.8)		—		1.9 (4.5)	
Wood Thrush	51 (193)		56.8 (72.5)		21.6 (18.5)		—		19.6 (7.5)		—		2.0 (1.5)	
Hermit Thrush	42 (232)		11.9 (20.3)		40.5 (43.9)		0.0 (0.4)		31.0 (23.7)		0.0 (5.7)		16.6 (6.0)	
Swainson's Thrush	117 (377)		14.5 (14.5)		29.1 (25.1)		0.0 (0.5)		47.9 (37.9)		5.1 (17.5)		3.4 (4.5)	
Veery	25 (136)		8.0 (7.4)		52.0 (40.6)		0.0 (0.7)		40.0 (33.3)		0.0 (15.1)		0.0 (2.9)	
Ovenbird	74 (456)		16.9 (16.4)		60.6 (62.3)		1.4 (9.1)		19.7 (10.8)		—		1.4 (1.4)	
Dark-eyed Junco	99 (566)		7.1 (6.9)		59.6 (62.7)		12.1 (20.5)		19.2 (5.7)		—		2.0 (4.2)	

intraspecific comparison). This was most likely related to the conspicuousness of the behaviors, since the maneuver which is accompanied by the most movement (hover) was recorded more frequently in the first observation data set for all species, while there was no consistent pattern for glean and probes (Table 3). Hermit Thrushes were often first seen while hawking insects (Table 3). And, finally, the rarer prey-attacking maneuvers, such as jump-hover and dive-glean, were recorded more frequently in the full sequence data (Table 3). These findings indicate that data from the longer sequences provide more information concerning the range of foraging maneuvers used by these often secretive species. As a consequence, we base the following analysis of prey-attack behavior on the cumulative data.

Of these seven species at Hubbard Brook, the Wood Thrush was the only species to use the probing maneuver more than 50% of the time. It probed mostly among dead leaves on the ground surface, but occasionally dug deeper into the leaf litter; it also gleaned prey from the ground surface. Both the Ovenbird and Dark-eyed Junco frequently gleaned prey or, especially in the case of juncos jumped to pluck prey from the undersurfaces of leaves they could not reach from the ground. Winter Wrens were primarily gleaners on all substrates, but also extensively probed bark on fallen dead wood and less commonly in the litter (see Table 2). They also hopped into knotholes and the cracks between exposed roots of upturned trees when searching for food.

The *Catharus* thrushes used more aerially-active foraging maneuvers, e.g., hovers, dive-gleans, and even hawking actions, and rarely probed, relative to other species (Table 3). Swainson's Thrushes were often seen to perch on low twigs and branches and to search the litter below it, while Veeries sometimes perched on rocks or logs, especially near streams, and searched the banks and foliage on either side. When prey were spotted from these sites, both Swainson's Thrushes and Veeries would dive to the ground and snatch the prey (i.e., dive-glean, Table 3). Lengths of hover flights averaged 1.1 ± 0.7 SD m (N = 58) for the Swainson's Thrush and 0.8 ± 0.7 SD m (N = 13) for the Veery, which suggest (cf. Robinson and Holmes 1982) that they both visually searched substrates up to a meter away.

Search rates and locomotor patterns while foraging.—From qualitative observations, Ovenbirds, Dark-eyed Juncos, and Wood Thrushes, once in a foraging area, searched for prey primarily by hopping or walking along the ground; they rarely flew between perches used for searching. Ovenbirds walked more or less continuously, pausing only to glean prey, often with quick pecking motions, from the surface of the litter. Dark-eyed Juncos behaved similarly, except that they hopped rather than walked

and seemed more deliberate in their gleaning actions. Winter Wrens methodically searched low substrates by hopping slowly, apparently examining crevices and other places for hidden prey. Wood Thrushes typically hopped several times in succession, then paused to visually search nearby substrates or to dig in the litter. In this respect, they foraged much like *Turdus* thrushes (Smith 1974, Paszkowski 1982).

The *Catharus* thrushes, particularly Swainson's and Veery, differed from other species in their search behavior by flying more often. While searching for food, they typically flew from one perch to another, hopped several times along a branch or occasionally on the ground, and then flew on to another branch to continue searching. Foraging Swainson's Thrushes changed perches, on average, by flying 6.1 times/min and hopping 5.0 times/min ($N = 898$ sec), while Veeries flew 5.8 times/min and hopped 6.5 times/min, ($N = 240$ sec). Thus, these two species flew and hopped about equally and had similar searching patterns. In contrast, Hermit Thrushes hopped more than they flew (2.6 flights/min, 17.6 hops/min, $N = 235$ sec). The distances moved in flights between perches while searching for food were similar for Swainson's Thrushes and Veeries, averaging 1.7 ± 1.2 m ($N = 60$) and 1.6 ± 0.9 m ($N = 20$) respectively (Hermit Thrushes not included due to small sample size).

Diets.—Diet samples were collected from mid-June to mid-July, and contained only animal, mainly insect, remains (Table 4). Coleoptera, most of which were adults, were the most frequently found item in all samples, probably because their body parts, especially elytra, persisted longer in the stomachs than those of other types of prey (Robinson and Holmes 1982). Also, the same major Coleoptera families were represented in samples from most bird species: Carabidae, Cantharidae, Scarabeidae, Curculionidae, Cerambycidae, and Elateridae (Table 4), all of which occur on the forest floor and on vegetation. Hymenoptera were represented primarily by ants and wasps (families Ichneumonidae and Braconidae). Lepidoptera were mostly larvae in the families Geometridae and Noctuidae (Table 4) which dominate the leaf-dwelling caterpillar fauna at Hubbard Brook (Holmes and Schultz 1988). Most Diptera in the samples were adult crane flies (family Tipulidae).

Diets of the five species, for which we had a reasonably large number of emetic samples, differed significantly at the ordinal level ($P < 0.001$ for all pairwise comparisons except the Veery and Ovenbird for which $P < 0.05$; analyses were not performed at family level due to small sample sizes in some categories). Comparisons among species indicate that Hermit Thrushes took relatively more Coleoptera, while Swainson's Thrushes had the highest proportion of Hymenoptera, mostly ants (Table 4). Hermit Thrushes and Ovenbirds took relatively large numbers of Lepidoptera

TABLE 4
DIETS OF BIRDS IN THE GROUND-FORAGING GUILD AT HUBBARD BROOK, 1974-1976,
BASED ON EMETIC SAMPLES. VALUES REPRESENT PERCENT OF EACH TAXON IN THE SAMPLE
OF IDENTIFIABLE PREY ITEMS

Taxa	N (n) ^a =	Wood Thrush 329 (60)	Hermit Thrush 82 (18)	Swainson's Thrush 186 (34)	Veery 101 (18)	Ovenbird 119 (30)
Lepidoptera		11.9	19.5	9.7	12.9	19.3
Larvae ^b		11.6	19.5	9.1	12.9	19.3
Adults		0.3	—	0.6	—	—
Hemiptera		2.4	1.2	0.5	4.0	3.4
Hymenoptera		17.3	12.2	32.8	12.9	15.1
Formicidae		14.0	9.8	27.4	8.9	8.4
Other ^c		3.3	2.4	5.4	4.0	6.7
Coleoptera		38.0	64.7	44.7	41.5	36.1
Larvae		4.6	12.2	4.3	—	4.2
Adults		33.4	52.5	40.4	41.5	31.9
Carabidae		7.0	13.5	5.4	3.0	2.5
Cantharide		1.8	7.3	2.7	14.8	3.4
Staphylinidae		0.9	—	—	1.0	—
Scarabeidae		1.5	2.4	2.2	6.9	4.2
Curculionidae		4.0	7.3	2.7	1.0	5.0
Cerambycidae		0.9	2.4	2.7	2.0	0.8
Elateridae		5.2	8.5	17.7	9.8	5.9
Other		12.1	11.1	7.0	3.0	10.1
Diptera		18.5	2.4	9.1	18.8	20.2
Larvae		2.7	—	—	5.9	—
Adults		15.8	2.4	9.1	12.9	20.2
Tipulidae		4.0	2.4	4.8	9.9	5.0
Other		11.8	—	4.3	3.0	15.2
Arachnida		1.8	—	1.6	5.0	4.2
Mollusca		4.9	—	0.5	4.0	1.7
Other		5.2 ^d	—	1.1	0.9	—

^a N = Number of identifiable prey items, n = number of birds from which emetic samples were obtained.

^b Identifiable Lepidoptera larvae were mostly in the families Geometridae and Noctuidae.

^c Adult flying Hymenoptera, including Ichneumonidae and Braconidae.

^d Included several Diptopoda (millipedes) and Chilopoda (centipedes).

larvae, while Wood Thrushes, Veeries, and Ovenbirds fed more often on Diptera, especially tipulid adults (Table 4). Ovenbirds and Veeries both fed relatively often on Hemiptera, mostly leafhoppers, and spiders, while Veeries and Wood Thrushes took small snails (Table 4). Wood Thrushes also took measurable numbers of millipedes and centipedes which occur in the forest litter where this species concentrates its feeding. Also, one Wood Thrush sample had vertebrae of *Plethodon cinereus*, a common salamander that lives in the litter at Hubbard Brook.

DISCUSSION

Ecological relations among ground-foraging birds.—Even though all seven species in the ground foraging guild occurred syntopically on the 10-ha plot, some differences occurred in distribution and local habitat use, especially by the junco, wren, Hermit Thrush, and Veery. Although not quantified, the areas occupied most frequently by juncos had a more open understory with relatively dense herbs and ferns compared to the less occupied parts of the plot. Such areas occurred where the canopy was complete and had not been disturbed recently by tree falls. The wrens were often in or near the canopy gaps where understory vegetation was thickest and where upturned root systems provided suitable nesting sites. They have thus been responding, at least in part, to areas of local disturbance. Veeries and Hermit Thrushes concentrated their activities at opposite ends of the study area, the former near the north end where the shrub layer was relatively dense along the stream, the latter in better drained areas with more open understory. We have no evidence that their separation was due to interspecific competition (cf. Morse 1971, Noon 1981), and it may simply reflect differences between the species in habitat preferences (James et al. 1984). Veeries have been reported to occur in more mesic and thickly vegetated habitats (Morse 1971, Bertin 1977), such as those at the north end of our study area. Hermit Thrushes are usually considered a bird of forest interiors (Dilger 1956b).

Besides subtle differences in habitat selection, the species in the ground-foraging guild at Hubbard Brook also differed from each other in microhabitat use and/or in foraging behavior, which may be the basis for the significant differences in diet. Three major ways in which these species searched for prey (searching modes, *sensu* Robinson and Holmes 1982) can be distinguished, and within each of these, further differences occurred in foraging tactics, microhabitats searched for prey, and/or in body size.

(1) Near-surface searchers. Two species, Ovenbird and Dark-eyed Junco, searched for and gleaned prey from nearby substrates while walking or hopping more or less continuously along the ground. In this respect, their foraging patterns are analogous to those of the *Dendroica* warblers which use this same approach among tree foliage (Robinson and Holmes 1982). The junco searched more foliage and foraged more often in the vegetation strata above the litter than did the Ovenbird, which probably results in their capturing a greater number of caterpillars. Juncos also employed the jump-hover maneuver more frequently than did the Ovenbird, which was used to pick prey from foliage surfaces overhead. The slow, smooth walking gait of the Ovenbird and its rapid striking gleans resulted in the capture of adult Diptera and other active prey (Table 4) which may often be able to escape being caught when approached by birds

using other foraging methods. The longer and more pointed beak of the Ovenbird may increase its success in catching highly mobile prey. Thus, Ovenbirds and juncos, both of which use the ground and low shrub layer extensively, have unique searching and prey-capturing styles.

(2) Manipulative searchers. Another distinctive foraging pattern was exhibited by Wood Thrushes and Winter Wrens. Both species actively manipulated their foraging substrate to find hidden or buried prey. The larger Wood Thrush concentrated its foraging activities in the loose leaf litter, where it moved relatively slowly, probed and turned over litter, and took beetles, ants, adult tipulids, snails, millipedes, centipedes, and even small vertebrates. The Winter Wren also manipulated substrates to obtain prey, but did this by searching methodically among the fallen dead wood, root masses of upturned trees, and dense foliage near the ground, where it probed into crevices and under loose bark or gleaned prey from surfaces where they were hiding. In other sections of the forest, we have witnessed Winter Wrens probing clusters of dead leaves suspended in the shrub layer vegetation (S. K. Robinson, pers. observ.). In this behavior, the wren is similar to the Black-capped Chickadee (*Parus atricapillus*) which often concentrates its foraging on specific substrates (e.g., dead leaves) where it searches for hidden prey (Robinson and Holmes 1982). Although we do not have quantitative data on foods taken by Winter Wrens, we have observed them take spiders, harvestmen (Phalangida), and other invertebrates located on bark near the ground, suggesting that this searching of special substrates and foraging method lead to the detection and capture of prey different from those obtained by Wood Thrushes and other members of the foraging guild. The wren, being a much smaller species, probably takes smaller sized prey than the larger Wood Thrush.

(3) Variable-distance searchers. The three *Catharus* thrushes searched substrates both near and far from a particular perch and often took flight to catch more distantly sighted prey. In this respect, their searching behavior is similar to that of the canopy-foraging vireos and Rose-breasted Grosbeak (*Pheucticus ludovicianus*) (Robinson and Holmes 1982). Each thrush species, however, seemed to have a particular way of foraging that differed from the others. Veeries foraged more on the ground than its congeners and took a larger proportion of Diptera, especially adult tipulids which are often on the litter surface. Hermit and Swainson's thrushes foraged from the ground layer to the canopy, but Swainson's Thrushes were more arboreal, foraging more often among the canopy foliage. This is consistent with the morphology of these two species in that the Swainson's Thrush has a shorter tarsometatarsus which is related to a more arboreal existence (Dilger 1956b). At Hubbard Brook, Hermit Thrushes gleaned prey from nearby substrates, while Swainson's Thrushes did more

hovering and used the dive/glean maneuver more frequently. Finally, Hermit Thrushes took a larger proportion of beetles, particularly cantharids, while Swainson's Thrushes fed more heavily on elaterid beetles and especially on ants (see Table 4), indicating that their different searching and foraging patterns led to differences in foods taken.

Guild and community structure. — The seven species of ground-foraging birds thus differ in one or more aspects of their use of space (horizontal or vertical), foraging behavior, and diet. The question that then arises is what determines the particular number and combination of ground-foraging species existing in this, or any, particular forest habitat? Why are there seven species in this forest at Hubbard Brook, and especially, why are there four species of thrushes, when this is an unusually high number (Noon 1981) to be found together?

The most parsimonious answer to these questions lies in the structure and resources of the Hubbard Brook forest during the period of study. Each species with its characteristic morphology and behavior may respond to specific features of the habitat, which in turn lead to their occurrence in a particular site. The study area at Hubbard Brook in the mid-1970s when this research was conducted was a second-growth forest, approximately 65 years post-logging. The forest contained a dense but somewhat patchy shrub layer, and thus represented a particular stage in mid- to late-forest succession following disturbance (Aber 1979). Forest stands with these particular plant species, vegetation characteristics, and the associated invertebrates may provide a particular set of microhabitats, food resources, or some combination thereof that allows each of the seven species to settle, feed, and reproduce successfully. At Hubbard Brook, as we have demonstrated, ground-foraging birds can make a living by searching for prey in the litter, on the surface of the litter, on herbaceous and low sapling foliage, and, for those with the morphological and behavioral capabilities of perching and moving through the trees, on the foliage of shrubs and saplings. In a forest with either a more open or a more closed understory, there would be different constraints or opportunities for species occupying this layer. In this context, it may be significant that the composition and abundances of species in the ground-foraging guild at Hubbard Brook has changed considerably since 1978 when this study was completed (Holmes et al. 1986). By the mid-1980s, the shrub and sapling layers had become denser, and all thrush species had declined in abundance, particularly the Wood Thrush which requires more open litter for foraging. These changes suggest the need for comparative studies of ground-foraging birds in sites differing in specific ways and or in habitats that have been experimentally manipulated. These would help to identify more clearly the proximal factors that are important in habitat selection and

in determining the requirements for each species. As far as we know, such comparative or manipulative studies have yet to be done for any ground-foraging bird guild.

Our findings of ecological segregation among the coexisting species, and especially the complementary patterns in how they search for and capture prey and in foods taken, generally support predictions of competition theory (MacArthur 1972). It is impossible, however, to tell whether past competition has been important in the evolution of these habitat preferences and foraging patterns. We have no evidence for interspecific aggression or other forms of ongoing competition among the species at Hubbard Brook, although these are difficult to detect. The observations of habitat shifts of thrushes in Maine (Morse 1971) and the expansion of the Veery into spruce forests in the southern Appalachians where its congeners are absent (Noon 1981) suggests that competition might be important in certain situations, although Wiens (1983) and James et al. (1984) have questioned Noon's conclusions.

As caveats to this discussion, it is important to note that other factors may also have important effects on the species composition and abundance of these ground-foraging birds. One is a matter of the scale at which these species and habitats are viewed. For instance, our study site at Hubbard Brook was in deciduous forest, but a few hundred meters in elevation above our plot, the forest grades into a boreal, coniferous forest where Swainson's Thrushes are more abundant (Sabo and Holmes 1983). Likewise, Wood Thrushes and Veeries are more common at lower elevations (see also Noon 1981). The presence of more preferred areas nearby might provide a source of birds that would settle in our study areas in years of high population density, and thus affect the relative abundance of species that we observed. Likewise, an examination of the abundance and resource use patterns of these species over such a habitat gradient might illustrate more clearly the habitat preferences, spacing patterns and foraging responses of these species. The present study was limited by analyses of only relatively few individuals occupying a single 10-ha section of forest and by not having information on the behavioral flexibility of these species in terms of their responses to different habitats or foraging opportunities. Such plasticity may differ among species, and play an important role in what habitats they occupy.

On an even larger scale is the influence on these species of events during migration or on their wintering grounds. The breeding densities of the four species of ground-foragers that winter in Central and South America (Wood and Swainson's thrushes, Veery, Ovenbird) remained relatively constant at Hubbard Brook during the five years of this study (Holmes et al. 1986). However, densities of the three species that winter primarily

in the subtemperate regions of North America (Hermit Thrush, Winter Wren, Dark-eyed Junco) fluctuated strongly and synchronously, coincident with the occurrence of severe winter weather (Holmes et al. 1986). In fact, following the winter of 1977–78, the breeding densities of these three species at Hubbard Brook and in the northeastern U.S. as a whole, declined significantly for several years (see Holmes et al. 1986). Thus, following the arguments of Fretwell (1972), it is possible that the breeding densities of at least some of these species are kept below carrying capacity by winter mortality.

Concluding comments.—Our results support Moermond's (1979) contention that the structure and characteristics of the habitat, including available food resources, will have a major influence in determining which species are present and how resources are used. The foraging tactics used by each species are in turn determined by their morphological and behavioral abilities (e.g., see Dilger 1956b for the thrushes considered here), which reflect selective pressures during their evolutionary history. Thus, foraging tactics, bird morphology, habitat structure, and historical events all interact in a complex way to determine which species will be present in a given location and thus determine guild and community structure.

Finally, on a methodological note, we found that the description of foraging behavior of these ground-foraging birds when based on initial foraging observations were often biased toward conspicuous maneuvers. Records from longer sequences provided a more complete description of the foraging repertoires of these species.

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