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Use of Invertebrates by Birds in Red Maple Forested Wetlands and Contiguous Forested Uplands in Southern Rhode Island

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USE OF INVERTEBRATES BY BIRDS IN RED MAPLE FORESTED WETLANDS AND CONTIGUOUS FORESTED UPLANDS IN SOUTHERN RHODE ISLAND

BY

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ABSTRACT

Successful management of wetland wildlife populations requires a basic understanding of invertebrate ecology and their availability as food to higher life forms. Community structure, abundance, and seasonal dynamics of litter invertebrates in red maple forested wetlands are unknown. Differences in these parameters may influence where wildlife species forage along a wetland-upland gradient. I studied invertebrate use by ground-foraging birds along moisture gradients from upland forests to red maple (Acer rubrum) forested wetlands at three sites in Washington County, Rhode Island from April through August 1991. I examined diets of ground-foraging birds by stomach-flushing birds with saline solution and immediately preserving stomach contents. The invertebrates within the stomach samples were identified at least to order. I collected invertebrates along the upland-wetland gradient at each site to determine the mean biomass of invertebrates available to ground-foraging birds. Additionally, I monitored water tables, sampled shrub density and identified microhabitat types along the gradient at each site to correlate with invertebrate biomass. The most common invertebrates found in ground litter were larval Diptera, larval Coleoptera, adult Hymenoptera (Formicidae), adult Coleoptera and Araneae. The mean biomass of the litter invertebrates was greater in the wetland habitats at all three sites ($P < 0.05$). The mean biomass of litter invertebrates differed significantly from month to month along the gradient at two sites

(*P* < 0.05). Adult Coleoptera, larval Lepidoptera, and Araneae were the most common invertebrates in bird diets. The target bird species did not eat invertebrates in proportion to their availability (*P* < 0.05). Veeries (*Catharus fuscescens*) selected adult Coleoptera, adult Diptera, and larval Lepidoptera; Northern Waterthrush (*Seiurus novaboracensis*) selected adult Coleoptera and adult Diptera; Canada Warblers (*Wilsonia canadensis*) selected adult Coleoptera, adult and larval Lepidoptera, adult Hemiptera, and Orthoptera; Gray Catbirds (*Dumetella carolinesis*) selected adult Coleoptera, adult Diptera, adult and larval Lepidoptera, adult Hemiptera, Trichoptera and Orthoptera; Ovenbirds (*Seiurus aurocapillus*) selected adult Coleoptera, larval Lepidoptera, and adult Hemiptera. Differences in mean biomass of those invertebrate taxa eaten by the target birds between upland and wetland zones were noted only at Arrow Swamp; mean biomass was greater in the wetland zones than in the upland zones for two bird species (*P* < 0.05). The mean biomass of those invertebrate taxa eaten by the target birds prey at each site tended to decrease from April to August.

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Heartfelt appreciation goes to my friends Duane Roberts, Debra Whitehead, Mary Salerno, Josef Gorres and Jennifer Brown for their words of wisdom and emotional support. Thanks to Michael and Rigby for their endless patience and love.

DEDICATION

This thesis is dedicated to my parents, grandfather and Sharkey, who instilled in me a love of wildlife, and to William Nutting, Ph.D. who reminded me this love was still there.

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I. INTRODUCTION

Food availability commonly limits wildlife populations and affects how wildlife select habitats (Martin 1987). Food type, food abundance, and the locations from which food is taken are of critical importance to the survival of any animal (Morrison et al. 1992). Undisturbed upland habitat surrounding wetlands may be necessary for survival of many wetland species because of the food resources it provides to these species.

Managing wetland wildlife populations requires a basic understanding of invertebrate ecology and availability of invertebrates for higher life forms. Invertebrates in forest litter are of particular interest because several vertebrates (e.g., birds, small mammals, reptiles, and amphibians) depend on invertebrates for food (Martin 1987). Community structure, abundance, and seasonal dynamics of litter invertebrates in red maple forested wetlands and adjacent upland forests are unknown. Differences in these parameters may influence where upland or wetland wildlife species forage along this wetland-upland gradient. Knowledge of wildlife foraging patterns will aid wetland managers in determining biologically significant widths of protected upland habitat (buffer zones) around red maple forested wetlands.

Birds are an appropriate taxon for studying the importance of invertebrate communities along the wetland-upland gradient because they are conspicuous consumers of invertebrates. Birds can choose foraging sites along the moisture gradient because they are highly mobile. Also, there are reliable methods for determining invertebrate use by birds (Rosenberg and Cooper 1990).

Ground-foraging insectivorous birds tend to track temporal variation in resource availability more precisely than do other bird species; positive correlations between bird capture rates and abundances of litter arthropods were stronger for ground insectivores (Karr and Brawn 1990). Therefore, measuring abundances of arthropods in litter is a good way of determining the relative value of potential foraging areas for ground-foraging birds along a moisture gradient.

In Rhode Island, red maple forested wetlands comprise 77% of all palustrine wetlands (Golet et al., In press.). Several species of birds are found in red maple forested wetlands during the breeding season (Swift 1980). Among the most common of these birds are the Gray Catbird (Dumetella carolinesis), Veery (Catharus fuscescens), and Ovenbirds (Seiurus aurocapillus). Gray Catbirds are believed to forage extensively on the ground (Bent 1958). Veeries and Ovenbirds direct >50% of their foraging attacks toward prey in the forest litter, on ground layer herbs, ferns, and low seedling foliage (Holmes and Robinson 1988).

Other species that are mainly ground foragers include Northern Waterthrush (Seiurus novaboracensis) (Bent 1953, Eaton 1957, Craig 1984) and Canada Warbler (Wilsonia canadensis) (Bent 1953). In red maple forested wetlands of southern New England, these latter two species tend to be wetland-dependent (Merrow 1990).

Insect availability is the abundance of potential prey in microhabitats used by an insectivore when searching for food (Wolda 1990). All the arthropods detected in abundance estimates are not potential prey items for birds; some may be unpalatable or require excessive time or energy for capture (Martin 1986, Wolda 1990). Use is a demonstrated presence of a particular prey item in an animal's diet (Morrison et al. 1992). Selection is use coupled with evidence that the frequency of occurrence in the diet (by number of prey items, biomass, etc.) is significantly greater statistically than the frequency in the animal's environment (Morrison et al. 1992).

Scientists studying ecological relationships of animals seldom attempt to quantify the occurrence of prey items in the diet. Rather, studies have concentrated on indirect measures of food use such as bird foraging locations (Hutto 1985; Rosenberg and Cooper 1990).

There are several benefits to measuring food use directly by obtaining diet samples from birds. In the field, researchers often do not have time to identify the prey item in the bird's mouth before the item is swallowed or the bird flies away.

When diet samples are brought back to the lab, researchers can more accurately identify the prey items because the invertebrates (whole or fragmented) may be placed under the microscope for detailed analysis and expert taxonomists can be consulted if necessary.

Comparatively few field experiments have tested the role of specific factors in regulating wetland invertebrate populations (Neckles et al. 1990). Shelford (1951) and Kendeigh (1979) emphasized that environmental factors regulated invertebrate populations. Two significant factors influencing avian community abundance in studies of red maple forested wetlands of southern Rhode Island were water regime and vegetation structure (Golet et al., In press.). Perhaps these factors also influence the insectivorous prey base of birds in red maple forested wetlands and contiguous forested uplands.

The extent of flooding, and its timing and duration determine the composition and productivity of plants and associated animal within wetland systems (Fredrickson and Reid 1986). In 8 Massachusetts shrub and forested wetlands, spanning a wide range of hydrologic, edaphic and structural conditions, wetter sites also had greater peat depths, denser shrub layers, and a larger, more diverse breeding bird community (Swift et al. 1984).

Shrub layer structure appeared to be most closely related to avian richness and abundance (Swift et al. 1984, Merrow 1990). Even though we may be able to measure structural features that correlate to the density of certain birds, the correlation alone does not tell us what it is about the structural variable that the bird responds to (e.g., does higher shrub density provide greater protection for birds, better nesting sites or better foraging sites?). Changes in shrub density within a habitat may influence the abundance and types of ground-dwelling invertebrates and ultimately determine foraging sites for some birds.

Lastly, the type of litter and litter moisture may influence types of invertebrates and their abundances found along a gradient from wetland to upland. Litter is a key element in the productivity of wetlands and eventually determines the value of a site for animal life (de la Cruz 1979, Nelson and Kadlec 1984, Batema et al. 1985, White 1985, Wylie 1985).

In this study, I obtained baseline data on the invertebrate food of birds associated with red maple forested wetland ecosystems. I identified invertebrates along the gradient from forested upland through forested wetland; determined differences in biomass of invertebrates among moisture zones and throughout the breeding season; determined use of prey by 5 target birds species; assessed food selection by comparing abundance of invertebrate taxa in bird diets to abundance of invertebrate taxa along the gradient, and determined the relationship among environmental variables and invertebrate biomass.

II. METHODS

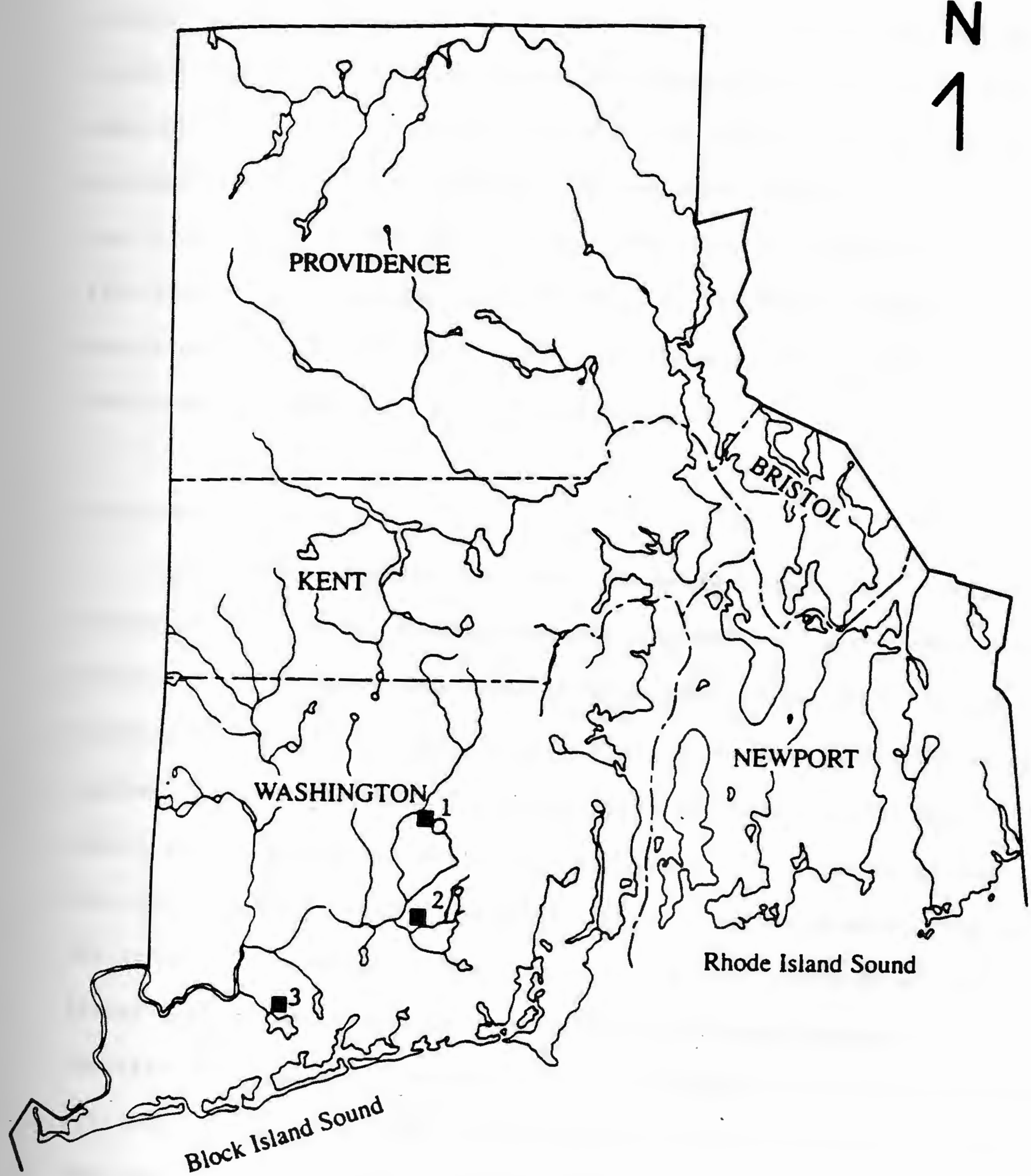
Site Description

I selected three study sites by examining aerial photographs (scale=1:9600) and by ground truthing. Each site was ≥30 ha and included contiguous tracts of mature red maple forested wetlands and broad-leaved deciduous upland forest (Society of American Foresters 1980). The criteria for site selection included: 1) predominance of very poorly drained soils in the wetland and an obvious gradient toward moderately well to well drained soils in the upland (See Wright and Sautter [1979] for drainage class definitions), 2) average canopy height ≥15 m, 3) tree canopy closure ≥75%, 4) lack of significant land use impacts during the last 40 years, and 5) <15% of canopy dominated by conifers.

All three sites were in Washington County, Rhode Island (Fig. 1) and elevations ranged from 12 to 73 m above sea level. The closest sites were 8 km apart. The study sites had 60 ha (Arrow Swamp); 402 ha (Burlingame State Park) and 1,483 ha (Great Swamp Wildlife Management Area) of red maple forested wetlands, respectively.

Both Arrow Swamp and Burlingame State Park had upland habitat with well drained soils (Canton-Charlton series) overlying friable till material, and wetlands with predominantly very poorly drained soils (mostly Adrian series and some Carlisle) overlying glaciofluvial material (Rector 1981). Great Swamp had upland forest with moderately well drained Woodbridge soils overlying compact glacial till, which caused perching of the water table. The wetland at Great Swamp had very poorly drained soils (Adrian and Carlisle series) overlying a combination of glacio-fluvial and glacio-lacustrine material.

Figure 1. Location of sites in Washington County, Rhode Island



Scale: 1:250,000

Legend:

■ Location of sites
1-Arrow Swamp
2-Great Swamp
3-Burlingame State Park

I divided each site into 4 zones based on soil moisture and distance from the wetland-upland edge. I defined the wetland-upland edge as the upslope boundary of the very poorly drained soil drainage class. I established 2 zones on each side of the wetland-upland edge (zone A-farthest into upland, zone B-contiguous with upland-wetland edge on upland side, zone C-contiguous with wetland-upland edge on the wetland side and zone D-farthest into wetland). The centers of zones B and C were 30-45 m from the boundary. The centers of zones A and D lay 120-135 m from the upland-wetland boundary. I placed 3 sample plots in each zone with the centers of each plot $\geq$90 m apart to insure independence. Each plot was 60 m in diameter.

Invertebrate Sampling

Invertebrate sampling was conducted every 2 weeks from April through August, 1991. During each sampling session, sites were sampled within 5 days of each other. All samples at a site were collected within a 3-hour period. Within each plot, I sampled invertebrates at 3 randomly located points at least 5 m apart to insure independence. One sample was collected per point. At each point, I collected litter containing invertebrates by placing a 30 cm diameter plastic ring on the ground and scraping to the root mass. A total of 0.64 m^2 of litter was collected in each zone during each sample period. To identify the type of microhabitat for each sample, we categorized the collected litter by percent cover type (e.g., 100% loose dry leaves; 90% sphagnum moss, 10% wet compact leaves).

I extracted invertebrates from litter using Tungren funnels with 1-mm mesh size. I placed them under 100-watt lights for 48 hours

(Steyskal et al. 1986). I determined 48 hours was the minimum amount of time needed to extract the maximum number of invertebrates in an earlier pilot study. I categorized invertebrates by taxon (at least to order) and total body length (mm). Length categories included: 1-5 mm, 6-10 mm, 11-15 mm, and ≥16 mm. The number of individuals in each taxon was counted for each sample.

I determined the total number of individuals for each taxon in each zone by order and length class. I determined mean biomass of invertebrates for each zone using previously established models of length-weight relationships (Rogers et al. 1977). I compared mean biomass of invertebrates among zones using Wilcoxon signed-rank tests (SAS Institute, Inc. 1989). I compared mean biomass of invertebrates among microhabitat types zones using Wilcoxon signed-rank tests (SAS Institute, Inc. 1989).

I divided the summer season by months 13 April-30 April; 1 May-30 May; 31 May-30 June; 1 July-30 July; 31 July-28 August. I compared mean biomass of invertebrates through the summer season using Wilcoxon signed-rank tests (SAS Institute, Inc. 1989).

Diet Sampling

To sample bird diets, I mist-netted 5 bird species, including Ovenbird, Northern Waterthrush, Veery, Gray Catbird, and Canada Warbler 2 times/week at each site and zone from May through August, 1991. I stomach-flushed the birds with lukewarm water (Forde et al. 1982) and banded them with a U.S. Fish and Wildlife Service aluminum leg band (20 Gray Catbird, 13 Ovenbird, and 14 Veery, 7 Northern Waterthrush, 8 Canada Warbler). I immediately stored the stomach contents in a 70%

ethanol, 29% water, and 1% glycerol solution. I examined 181 ingested invertebrates to obtain diet information. I compared invertebrate taxa from the diet samples to the invertebrate availability samples to determine diet selection for the 5 bird species using Chi-square tests (SAS Institute, Inc. 1989). Invertebrates absent from the diets of each bird species were omitted, and, for each species, mean biomass of invertebrates in the diets was compared among zones and compared among months throughout the summer (April-August).

Measuring Water Tables

I placed water table wells in the center of each plot at least 1 m into the ground to measure water table depth. I measured water tables semi-monthly. Mean biomass of invertebrates pooled over the summer at each wetland plot was correlated with average depth of the water table throughout the summer at each wetland plot using Spearman's rank-order correlation (SAS Institute, Inc. 1989). I was not able to correlate mean biomass of invertebrates at upland plots with upland water tables because the water tables at most upland plots were too deep to be easily measured.

Shrub Density Sampling

I sampled shrub density within each plot by counting the number of stems in four 0.6 x 27-m plots for a total of 64.8 m^2 sampled per plot. Shrubs included all woody plants <6 m tall and < 7.6 cm dbh. Mean biomass of invertebrates throughout the summer at each plot was correlated with mean shrub density at each plot using Spearman's rank-order correlation (SAS Institute, Inc. 1989).

III. RESULTS

Invertebrate Community

I identified 9,996 invertebrates from 1,769 detritus samples. Sixty families, 23 orders, 7 classes, and 2 phyla were recorded in the samples (Appendix A). The most common invertebrates in the detritus samples included larval Diptera (22.5% of all individuals counted), Araneae (16.3%), adult Hymenoptera (12.3%), larval Coleoptera (9.8%), and adult Coleoptera (9.8%) (Appendix A).

Invertebrate Use by Birds

Adult Coleoptera (59.0% of all prey), larval Lepidoptera (13.7%), and Araneae (9.6%) were the most common invertebrates in avian diet samples (Table 1). The target bird species did not eat invertebrates in proportion to their availability (Table 2). Veeries selected adult Coleoptera, adult Diptera, and larval Lepidoptera; Northern Waterthrush selected adult Coleoptera, Araneae, and adult Diptera; Canada Warblers selected adult Coleoptera, adult and larval Lepidoptera, adult Hemiptera, and Orthoptera; Gray Catbirds selected adult Coleoptera, adult Diptera, adult and larval Lepidoptera, adult Hemiptera, Trichoptera and Orthoptera; Ovenbirds selected adult Coleoptera and larval Lepidoptera.

Biomass by Moisture Zone

The biomass of litter invertebrates was usually greater in wetland habitats. At Arrow Swamp and Burlingame State Park, the mean biomass of invertebrates was significantly greater in zones C and D vs zones A and B ($\underline{P} < 0.001$) (Table 3). This difference was similar at Great

Table 1. Percent of invertebrate prey found in bird diet samples captured along a soil-moisture gradient from forested upland to forested red maple wetland at three sites in Washington County, Rhode Island, May-August 1991.

		Bird species					
Taxon		All bird species (n=62)	Veery (n=14)	Northern Waterthrush (n=7)	Canada Warbler (n=8)	Gray Catbird (n=20)	Ovenbird (n=13)
Coleoptera	(a)[a]	59.0	64	74.3	33.3	56.1	56
Coleoptera	(1)	3.2	5.3	2.9	4.8	1.5	1.9
Araneae	-	9.6	12	11.4	14.3	6.1	7.7
Diptera	(a)	2.8	2.7	5.7	-	3.0	1.9

Table 1. Continued.

	Bird species					
	All bird species (n=62)	Veery (n=14)	Northern Waterthrush (n=7)	Canada Warbler (n=8)	Gray Catbird (n=20)	Ovenbird (n=13)
Taxon						
Diptera (1)	1.6	-	-	9.5	3.0	-
Diplopoda -	.4	-	-	-	-	1.9
Lepidoptera (a)[a]	3.6	1.3	-	9.5	7.6	1.9
Lepidoptera (1)	13.7	12	5.7	14.3	15.2	19.2

Table 1. Continued.

	Bird species					
	All bird species (n=62)	Veery (n=14)	Northern Waterthrush (n=7)	Canada Warbler (n=8)	Gray Catbird (n=20)	Ovenbird (n=13)
Taxon						
Hymenoptera (a)	2.4	2.7	-	-	1.5	5.8
Hemiptera (a)	2.4	-	-	9.5	3.0	3.8
Trichoptera (l)	.4	-	-	-	1.5	-
Orthoptera -	.8	-	-	4.8	1.5	-
Total %	100	100	100	100	100	100

[a] a=adult, l=larva.

Table 2. Litter invertebrate numbers in stomach samples of breeding birds along a forested upland to forested red maple wetland gradient, April-August 1991.

Taxon		Available	Bird species				
			Veery (n=14)	Northern Waterthrush (n=7)	Canada Warbler (n=8)	Gray Catbird (n=20)	Ovenbird (n=13)
Coleoptera	(a)[a]	998	48(+)[b]	26(+)	7(+)	37(+)	29(+)
Coleoptera	(1)	896	4(-)	1(-)	1(-)	1(-)	1(-)
Aranae		1442	9(-)	4(+)	3(-)	4(-)	4(-)
Diptera	(a)	114	2(+)	2(+)		2(+)	1

Table 2. Continued.

Taxon	Available	Bird species: Veery (n=14)	Northern Waterthrush (n=7)	Canada Warbler (n=8)	Gray Catbird (n=20)	Ovenbird (n=13)
Diptera (1)	1990			2(-)	2(-)	
Diplopoda	330					1(-)
Lepidoptera (a)	562	1(-)		2(+)	5(+)	1(-)
Lepidoptera (1)	224	9(+)	2(-)	3(+)	10(+)	10(+)

Table 2. Continued.

Taxon	Available	Bird species				
		Veery	Northern Waterthrush	Canada Warbler	Gray Catbird	Ovenbird
		($\underline{n}$=14)	($\underline{n}$=7)	($\underline{n}$=8)	($\underline{n}$=20)	($\underline{n}$=13)
Hymenoptera (a)	1087	2(-)			1(-)	3(-)
Hemiptera (a)	135			2(+)	2(+)	2(-)
Trichoptera (l)	39				1(+)	
Orthoptera	87			1(+)	1(+)	

[a] a=adult, l=larva.
[b] Symbols indicate invertebrate selection (+), and avoidance (-) using Chi-Square analysis ($\underline{P}$ < 0.05).

Table 3. Biomass (mg/m^2) of litter invertebrates collected along a soil moisture gradient from forested upland to red maple forested wetland in Washington County, Rhode Island, April-August, 1991.

	Arrow Swamp			Burlingame			Great Swamp		
Zone[a]	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N
A	16.1	20.1A[b]	80	16.6	21.2A	70	15.3	16.1A	72
B	10.9	14.8A	77	16.1	24.6A	70	22.7	20.4B	71
C	28.1	27.7B	81	21.6	21.8B	66	26.0	23.9B	74
D	26.6	25.1B	78	25.3	25.8B	67	23.4	23.3B	74

[a]Zones were based on soil moisture and distance from the wetland-upland edge. Zone A (furthest upland zone from wetland-upland edge), Zone B (closest upland zone to upland-wetland edge), Zone C (closest wetland zone to upland-wetland edge), Zone D (furthest wetland zone from wetland-upland edge).

[b]Means within a column followed by the same letter do not differ (Wilcoxon signed-rank test) ($\underline{P} < 0.03$).

Swamp, where invertebrate biomass was greater in zones B, C, and D ($P < 0.027$) (Table 3).

Differences in mean biomass of invertebrate taxa selected as prey were noted between upland and wetland zones only at Arrow Swamp. Mean biomass of prey taxa was greater in the wetland zones than in the upland zones for Canada Warblers and Northern Waterthrush ($P < 0.01$) (Table 4). No significant differences in mean biomass of prey taxa among zones were noted for any target bird species at Burlingame State Park or Great Swamp (Table 5). However, the biomass of prey taxa for Veeries, Northern Waterthrush, Canada Warblers, and Gray Catbirds was consistently higher in the wetland at Great Swamp (Table 6).

Monthly Differences in Biomass

The mean biomass of litter invertebrates at Arrow Swamp was significantly different from month to month in zones A, C, and D ($P < 0.04$) although there was no clear pattern in how the biomass changed (Table 7). The mean biomass of litter invertebrates at Burlingame State Park decreased significantly from May to June and June to July in zone C ($P < 0.0001$) (Table 3). The mean biomass of invertebrates decreased significantly from June to July in zone D ($P < 0.002$) (Table 8). There were no differences in mean biomass of invertebrates among the months in any zone at Great Swamp (Table 9).

The biomass of prey taxa at all sites tended to decrease in abundance from April to August for all target birds (Tables 10,11, 12). Significant decreases in the biomass for prey taxa of Veeries and Canada Warblers were found from May to June at Burlingame State Park ($P < 0.03$) (Table 11). Significant differences in the biomass of prey

Table 4. Biomass (mg/m^2) of prey taxa by soil-moisture zone along a forested upland to red maple forested wetland gradient at Arrow Swamp, Washington County, Rhode Island, April-August, 1991.

	Bird species														
	Veery			Northern Waterthrush			Canada Warbler			Gray Catbird			Ovenbird		
Zone[a]	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
A	8.4	12.5A[b]	63	7.2	10.8A	57	7.3	10.7A	57	10.8	17.0A	60	11.9	16.1A	60
B	8.6	12.5A	48	7.5	11:1A	46	7.5	11.1A	47	8.8	12.3A	50	9.5	11.4A	47

Table 4. Continued.

	Bird species														
	Veery			Northern Waterthrush			Canada Warbler			Gray Catbird			Ovenbird		
Zone[a]	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
C	11.9	16.1A	69	12.5	16.4B	63	12.6	16.3B	65	11.7	16.1A	71	12.5	16.6A	64
D	11.9	19.5A	56	11.6	18.8B	53	11.7	18.8B	52	11.8	19.5A	59	11.8	19.7A	52

[a] Zones were based on soil moisture and distance from the wetland-upland edge. Zone A (furthest upland zone from wetland-upland edge), Zone B (closest upland zone to upland-wetland edge), Zone C (closest wetland zone to upland-wetland edge), Zone D (furthest wetland zone from wetland-upland edge).

[b] Means within a column followed by the same letter do not differ (Wilcoxon signed-rank test) ($\underline{P} < 0.05$).

Table 5. Biomass (mg/m^2) of prey taxa soil-moisture by zone along a forested upland to red maple forested wetland gradient at Burlingame State Park, Washington County, Rhode Island, May-August, 1991. No Northern Waterthrush were captured at this site.

	Bird species											
	Veery			Canada Warbler			Gray Catbird			Ovenbird		
Zone[a]	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
A	9.8	16.6A[b]	48	8.8	14.7A	48	9.8	16.3A	48	11.9	15.0A	52
B	10.0	16.4A	47	9.1	16.4A	45	11.6	17.8A	49	15.5	19.1A	45

Table 5. Continued.

	Bird species											
	Veery			Canada Warbler			Gray Catbird			Ovenbird		
Zone[a]	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n
C	8.3	10.3A	51	7.9	8.5A	50	8.3	11.3A	53	9.2	10.6A	46
D	8.9	12.2A	43	9.2	12.1A	42	8.1	11.9A	47	9.5	12.3A	40

[a]Zones were based on soil moisture and distance from the wetland-upland edge. Zone A (furthest upland zone from wetland-upland edge), Zone B (closest upland zone to upland-wetland edge), Zone C (closest wetland zone to upland-wetland edge), Zone D (furthest wetland zone from wetland-upland edge).

[b]Means within a column followed by the same letter do not differ (Wilcoxon signed-rank test) ($P < 0.05$).

Table 6. Biomass (mg/m^2) of prey taxa by soil-moisture zone along a forested upland to red maple forested wetland gradient at Great Swamp, Washington County, Rhode Island, April-August, 1991.

	Bird species														
	Veery			Northern Waterthrush			Canada Warbler			Gray Catbird			Ovenbirds		
Zone[a]	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
A	9.4	12.5A[b]	55	8.8	12.3A	55	8.7	12.3A	56	9.4	12.3A	55	11.9	14.5A	54
B	9.8	11.6A	55	9.1	10.3A	51	9.1	10.2A	51	10.2	11.9A	55	13.6	11.3A	56

Table 6. Continued.

	Bird species														
	Veery			Northern Waterthrush			Canada Warbler			Gray Catbird			Ovenbirds		
Zone[a]	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n
C	13.0	17.8A	61	12.7	17.8A	61	12.8	17.9A	61	13.1	17.7A	63	14.2	17.8A	58
D	13.0	18.4A	53	13.4	18.4A	50	13.2	18.3A	51	12.3	17.3A	54	12.0	17.5A	51

[a]Zones were based on soil moisture and distance from the wetland-upland edge. Zone A (furthest upland zone from wetland-upland edge), Zone B (closest upland zone to upland-wetland edge), Zone C (closest wetland zone to upland-wetland edge), Zone D (furthest wetland zone from wetland-upland edge).

[b]Means within a column followed by the same letter do not differ (Wilcoxon signed-rank test) ($P < 0.05$).

Table 7. Litter invertebrate biomass (mg/m^2) by month along a soil-moisture gradient from forested upland to red maple forested wetland at Arrow Swamp, Washington County, Rhode Island, April-August, 1991.

	Zone[a]											
	A			B			C			D		
Month	X	SD	n	X	SD	n	X	SD	n	X	SD	n
April	8.2	7.6ABC[b]	9	9.0	8.6A	8	30.0	41.0A	9	41.5	37.3ABC	9
May	3.3	25.9BD	17	11.4	19.9A	16	34.2	28.2AB	18	27.7	21.4A	17
June	20.2	18.4AD	18	14.0	13.4A	18	27.4	28.1ABCD	18	24.9	23.3B	16

Table 7. Continued.

	Zone[a]											
	A			B			C			D		
Month	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
July	21.8	20.4C	18	11.0	16.2A	18	16.2	14.8BC	18	17.7	25.6C	19
August	13.0	18.8ABD	18	7.7	11.2A	17	33.5	28.1ABD	18	29.3	19.6A	17

[a]Zones were based on soil moisture and distance from the wetland-upland edge. Zone A (furthest upland zone from wetland-upland edge), Zone B (closest upland zone to upland-wetland edge), Zone C (closest wetland zone to upland-wetland edge), Zone D (furthest wetland zone from wetland-upland edge).

[b]Means within a column followed by the same letter do not differ (Wilcoxon signed-rank test) ($P \leq 0.05$).

Table 8. Litter invertebrate biomass (mg/m^2) by month along a soil-moisture gradient from forested upland to red maple forested wetland at Burlingame State Park, Washington County, Rhode Island, April-August 1991.

	Zone[a]											
	A			B			C			D		
Month	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
May	8.5	24.5A[b]	17	29.8	39.2A	16	44.2	24.4A	18	33.4	19.5A	17
June	20.6	23.7A	18	11.1	13.4A	18	22.6	16.9B	18	36.7	38.1A	16

Table 8. Continued.

	Zone[a]											
	A			B			C			D		
Month	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
July	13.6	14.1A	17	13.2	22.0A	17	13.8	21.0C	17	12.3	20.4B	16
August	14.4	21.6A	18	10.9	10.9A	18	10.3	8.4C	18	19.0	11.3B	18

[a]Zones were based on soil moisture and distance from the wetland-upland edge. Zone A (furthest upland zone from wetland-upland edge), Zone B (closest upland zone to upland-wetland edge), Zone C (closest wetland zone to upland-wetland edge), Zone D (furthest wetland zone from wetland-upland edge).

[b]Means within a column followed by the same letter do not differ (Wilcoxon signed-rank test) ($P \leq 0.05$).

Table 9. Litter invertebrate biomass (mg/m^2) by month along a soil-moisture gradient from forested upland to red maple forested wetland at Great Swamp, Washington County, Rhode Island, April-August 1991.

	Zone[a]											
	A			B			C			D		
Month	$\bar{X}$	SD	*n*	$\bar{X}$	SD	*n*	$\bar{X}$	SD	*n*	$\bar{X}$	SD	*n*
April	18.4	17.2A[b]	8	8.2	11.7A	6	27.2	37.6A	9	22.5	25.1A	9
May	13.8	17.8A	14	22.9	24.5A	14	34.6	31.3A	14	26.5	20.7A	15
June	13.4	10.4A	15	27.5	18.7A	17	21.1	16.9A	15	33.8	26.7A	17

Table 9. Continued.

	Zone[a]											
	A			B			C			D		
Month	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
July	11.5	14.3A	17	26.1	23.8A	17	23.2	17.0A	18	15.4	16.5A	15
August	20.3	19.6A	18	19.4	15.6A	17	25.6	20.3A	18	18.0	24.0A	18

[a]Zones were based on soil moisture and distance from the wetland-upland edge. Zone A (furthest upland zone from wetland-upland edge), Zone B (closest upland zone to upland-wetland edge), Zone C (closest wetland zone to upland-wetland edge), Zone D (furthest wetland zone from wetland-upland edge).

[b]Means within a column followed by the same letter do not differ (Wilcoxon signed-rank test) ($P < 0.05$).

Table 10. Biomass (mg/m^2) of prey taxa by month for all zones at Arrow Swamp, Washington County, Rhode Island, April-August 1991.

	Bird species														
	Veery prey			Northern Waterthrush prey			Canada Warbler prey			Gray Catbird prey			Ovenbird prey		
Month	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
April	12.5	19.7A[a]	29	13.1	20.3A	27	13.2	20.3A	27	13.0	20.5A	28	15.3	20.8A	24
May	11.9	18.1A	48	11.7	18.0A	45	11.6	17.8A	46	14.5	22.5A	49	15.2	22.0A	45
June	10.6	13.4A	58	10.2	12.7A	56	10.3	12.9A	55	10.0	12.2A	60	10.9	12.3A	56

Table 10. Continued.

	Bird species														
	Veery prey			Northern Waterthrush prey			Canada Warbler prey			Gray Catbird prey			Ovenbird prey		
Month	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n
July	10.0	17.5A	52	8.4	15.6A	45	8.6	15.6A	46	10.5	17.5A	51	9.7	16.6A	47
August	7.3	8.0A	49	7.3	8.0A	46	7.2	7.9A	47	8.0	8.6A	52	8.8	9.7A	51

[a]Means within a column followed by the same letter do not differ (Wilcoxon signed-rank test) ($P < 0.05$).

Table 11. Biomass (mg/m^2) of prey taxa by month for all zones at Burlingame State Park, Washington County, Rhode Island, May-August 1991. No Northern Waterthrush were captured at this site.

	Bird species											
	Veery prey			Canada Warbler prey			Gray Catbird prey			Ovenbird prey		
Month	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
May	16.2	20.9A	54	14.5	19.0A	54	15.3	20.0A	58	17.7	19.2A	53
June	7.0	10.2B	41	6.7	10.3B	40	6.6	8.9A	40	9.7	10.9A	38

Table 11. Continued.

	Bird species											
	Veery prey			Canada Warbler prey			Gray Catbird prey			Ovenbird prey		
Month	$\bar{X}$	SD	*n*	$\bar{X}$	SD	*n*	$\bar{X}$	SD	*n*	$\bar{X}$	SD	*n*
July	6.1	5.6B	40	5.6	5.4B	39	7.7	12.7A	43	9.8	14.5A	40
August	6.5	9.4B	54	6.6	9.5B	52	6.9	10.2A	56	8.0	18.1A	52

[a]Means within a column followed by the same letter do not differ (Wilcoxon signed-rank test) ($P < 0.05$).

taxa of Veeries, Canada Warblers, Northern Waterthrush, and Gray Catbird were found between several months at Great Swamp ($\underline{P} < 0.002$) (Table 12).

Influence of Environmental Factors

At Arrow Swamp, the average water table depth was inversely correlated to invertebrate biomass ($\underline{r}$=-0.77,$\underline{P}$=0.07,N=6). At Burlingame State Park, the average water table depth was positively correlated to invertebrate biomass ($\underline{r}$=0.77,$\underline{P}$=0.07,N=6). At Great Swamp, no correlation was found between the average water table and invertebrate biomass. For all three sites, invertebrate biomass was not correlated with shrub density.

The dominant microhabitat types at all three sites included >70% loose-dry leaves; >70% sphagnum moss; >70% loose-moist leaves, and >70% compact-wet leaves. At Arrow Swamp, loose-dry leaves comprised 45% of all samples, compact-wet leaves comprised 17% of all samples, loose-moist leaves comprised 15% of all samples and sphagnum moss comprised 11% of all samples. At Burlingame State Park, loose-dry leaves comprised 38% of all samples, loose-moist leaves comprised 23% of all samples, compact-wet leaves comprised 22% of all samples and sphagnum moss comprised 5% of all samples. At Great Swamp, loose-dry leaves comprised 35% of all samples, loose-moist leaves comprised 29% of all samples, compact-wet leaves comprised 9% of all samples and sphagnum moss comprised 9% of all samples.

At all three sites, the highest invertebrate biomass tended to be found in wet microhabitat types such as sphagnum and compact-wet leaves. Loose-dry microhabitat types tended to have the lowest invertebrate biomass (Table 13).

Table 12. Biomass (mg/m^2) of prey taxa by month for all zones at Great Swamp, Washington County, Rhode Island, April-August 1991.

	Bird species														
	Veery prey			Northern Waterthrush prey			Canada Warbler prey			Gray Catbird prey			Ovenbird prey		
Month	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n
April	23.1	24.8A	25	23.4	24.5A	22	23.5	24.5A	24	21.6	23.1A	26	21.9	23.8A	24
May	15.3	16.3AB	44	14.8	16.4AB	45	9.1	16.4AB	44	14.1	16.1AB	46	14.8	16.9A	43
June	9.4	15.6CD	54	9.2	15.8CD	52	14.7	15.7CD	53	9.4	15.6C	56	11.4	15.3A	56

Table 12. Continued.

	Bird species														
	Veery prey			Northern Waterthrush prey			Canada Warbler prey			Gray Catbird prey			Ovenbird prey		
Month	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n
July	9.5	9.8BC	47	8.6	7.7BC	45	8.7	7.6BC	45	10.5	10.5ABD	47	11.1	8.8A	49
August	6.1	8.4D	54	6.1	8.4D	53	2.5	8.4D	53	6.7	8.8CD	52	10.8	12.8A	47

[a] Means within a column followed by the same letter do not differ (Wilcoxon signed-rank test) ($P < 0.05$).

Table 13. Biomass (mg/m^2) of invertebrates in 7 microhabitat types at 3 sites in Washington County, Rhode Island, April-August 1991.

	Sites								
	Arrow Swamp			Burlingame			Great Swamp		
Microhabitat type[a]	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
Loose-Dry	9.3	11.0	145	11.6	14.8	110	12.0	12.5	113
Sphagnum	16.0	17.1	37	16.1	22.5	13	18.9	18.8	30
Loose-Moist	17.0	20.5	49	8.4	10.6	67	13.8	11.2	92
Compact-Wet	17.2	16.1	56	16.9	15.0	64	14.8	13.9	30
Compact-Moist	19.0	16.1	7	-	-	-	-	-	-
Cmwt/Sphg	14.3	9.5	7	15.0	15.0	8	-	-	-
Lsmo/Sphg	-	-	-	-	-	-	16.4	13.4	7

[a] Cmwt/Sphg=50% Compact-wet leaves, 50% sphagnum moss, Cmmo/Sphg=50% Compact-moist leaves, 50% sphagnum moss.

IV. DISCUSSION

Invertebrate Community

Thirty-eight percent of all the invertebrates I found in zone C and 23% of all the invertebrates I found in zone D were larval Diptera. It is not surprising that larval Diptera were the most common individuals found in the litter layer of these zones because many larval Diptera live in a variety of microhabitats; e.g., water, soil, under bark or stones, or on vegetation (Borror et al. 1989) typically found in red maple forested wetlands. Studies of invertebrates from seasonally flooded freshwater wetlands reveal remarkable similarities in community structure (Neckles 1990). Depressions which are flooded for only short periods during the year are characterized by very high densities of aquatic invertebrates with low taxonomic diversities (Wiggins et al. 1980).

The order Araneae is a large and widespread group. They occur in many types of habitats and are often very abundant (Borror et al. 1989). In my study, this group appeared to be evenly distributed across all zones at all sites. From my diet samples, only Veeries selected this group. All other bird species avoided Araneae as a prey item.

Coleoptera are also a large and widespread group found in a variety of habitats. In my study, the Elateridae, Hydrophilidae, Staphylinidae and Carabidae families were most abundant. Most families appeared evenly distributed across all moisture zones except the larval and adult stages of Hydrophilidae and Staphylinidae and larval Carabidae. These groups were the most abundant in zones C and D. Hydrophilidae and Staphylinidae are families which have species that inhabit aquatic ecosystems such as the forested wetlands that I studied. Larval Elateridae and adult Cantharidae were most abundant in zones A and B. In a similiar study, Holmes and Robinson (1988), noted the Coleoptera families Elateridae, Cantharidae, and Carabidae were commonly found in diet samples of ground-foraging birds in a deciduous upland forest in New Hampshire.

Many Hymenoptera families, particularly Formicidae which were commonly found in my samples, are non-flying and build nests in the ground. I found the highest numbers of adult Formicidae in both zones A and B. Most of these were of the subfamily Mermicinae.

Invertebrate Use by Birds

I did not find Veeries selecting adult Diptera. Instead they selected adult Coleoptera, larval Lepidoptera, and adult Hemiptera. These results may reflect the bias of finding hard-bodied invertebrates, which are more difficult for birds to digest, more frequently in diet samples. Bent (1953) found Veeries principally ate ground beetles, ants, caterpillar and grasshoppers. Holmes and Robinson (1988) found Veeries foraged more on the ground than other Catharus spp. in hardwood forests and took a large proportion of Diptera, especially adult tipulids, which are often on the litter surface.

I found Northern Waterthrush selected adult Coleoptera, Araneae, adult Diptera, adult Hemiptera and Orthoptera. Craig (1984) found aquatic invertebrates such as nymphal Ephemeroptera and larval Chironomid predominated in the habitats frequented by Northern Waterthrush. The few invertebrates he saw eaten by Northern

Waterthrush included larval Diptera and caterpillar. Although I only collected 7 diet samples, these are probably more accurate than Craig's limited observations.

I found Canada Warblers selecting adult Coleoptera, adult and larval Lepidoptera, adult and larval Hemiptera, and Orthoptera. Similarly, Bent (1953) summarized a few accounts of Canada Warbler foraging bouts. He found Canada Warblers ate moths, flies, beetles larvae, hairless caterpillars, eggs of insects, spiders and mosquitoes. Also, he found diet samples of juvenile Canada Warblers included locusts.

I found Gray Catbirds selected adult Coleoptera, adult Diptera adult and larval Lepidoptera, adult Hemiptera larval Tricoptera and Orthoptera. Wings of adult Lepidoptera were frequently found in the stomachs of Gray Catbirds. This suggests that Gray Catbirds may forage in vegetative strata above litter more than the other target bird species. Martin (1951) reported that three-quarters of the Gray Catbirds diet consists of ants, beetles, caterpillar and grasshoppers; the remainder being made up of bugs, miscellaneous insects, and spiders.

Holmes and Robinson (1988) noted the Ovenbird's rapid, striking gleans and long, pointed beak resulted in the capture of highly mobile prey such as adult Diptera and other active prey such as Arachnida, adult Coleoptera, and Hymenoptera. Stenger (1958) found adult Coleoptera, unidentified larva and Hymenoptera were the most common constituents of the Ovenbird diet. These observations were consistent with my diet samples of Ovenbirds in red maple forested wetlands and contiguous uplands.

There are biases associated with analyzing diet samples (Rosenberg and Cooper 1990). Coleoptera, most of which were adults, were the most frequently found item in all diet samples. However, these results may be biased because Coleoptera body parts, especially elytra, probably persist longer in the stomachs than those of other types of prey (Robinson and Holmes 1982).

Like other researchers, I found it difficult to identify and quantify small and/or fragmented food items. I used whole invertebrates that I had collected in litter and keys from previous diet studies to help me identify these fragments or small parts.

Although I usually obtained more than one prey item per sample, the number of samples need to be increased in future studies to be confident about which invertebrates the birds are selecting. There is a need to continue to sample available invertebrates and identify the species of invertebrates selected and where they are most common. If the invertebrates that birds are selecting are most abundant at the wetland edge or in the wetland (such as I found with Northern Waterthrush and Canada Warblers), then buffer zones adjacent to red maple forested wetlands would be necassary as foraging areas or protectors of foraging areas for these birds.

Biomass by Moisture Zone

Invertebrate biomass tended to be higher in wetland zones at all three sites. I found that the Great Swamp has a more gradual slope and a perched water table; the soils are moister in zones A and B than in zones A and B at Arrow Swamp or Burlingame. At the Great Swamp, zones

B, C, and D had significantly higher biomass than zone A. This finding was consistent with invertebrate biomass being higher in wetter zones.

The difference in invertebrate biomass among zones B and C at Arrow Swamp and Burlingame may indicate an edge between wetland and upland habitat for invertebrates. This edge coincides with the wetland-upland edge we determined using known vegetation types and soil moisture at Arrow Swamp and Burlingame and also coincided with the perched areas at Great Swamp.

In general, the biomass of invertebrates eaten by the target birds was not significantly different among zones. However, the biomass of invertebrates eaten by Canada Warblers and Northern Waterthrush at Arrow Swamp was greater in the wetland zones. There was also a tendency for the biomass of invertebrates eaten by Canada Warblers and Northern Waterthrush to be greater in the wetland zones at Great Swamp.

In red maple forested wetlands, Canada Warblers and Northern Waterthrush are wetland dependent species (Merrow 1990). This suggests food may be a factor involved in habitat selection for Canada Warblers and Northern Waterthrush. Food may restrict bird species such as the Canada Warbler and Northern Waterthrush moving between upland and wetland habitats or it may attract birds from the uplands to forage where there is higher invertebrate biomass. This finding is consistent with Robinson and Holmes's (1982) hypothesis that food influences the pattern of bird habitat selection and community structure.

Studies of foraging behavior of ground-insectivores and other foraging guilds will help guide availability sampling. How bird foraging tactics change over the breeding season and knowledge of optimal foraging locations for birds along the moisture gradient would help determine invertebrate sampling schemes.

Monthly Differences in Biomass

I found the biomass of prey taxa for all bird species decreased from April through August. This suggests food may be a limited resource to birds during the breeding season. Ground-foraging insectivores that arrive on-site early, may have greater nest success because litter invertebrates are more abundant earlier in the breeding season.

Similarly, Craig (1984) studied seasonal changes in invertebrate biomass in Waterthrush territories along a deciduous forested riparian system in northeastern Connecticut. He sampled three times between mid-May and late June. He found biomass was highest early in the season and declined afterwards.

When I analyzed prey taxa and non-prey taxa together, no pattern of biomass increase or decrease was noted over time or within zones, although significant differences in invertebrate biomass throughout the breeding season were found at all three sites. Perhaps I masked what was actually happening to the target bird's food resources during the breeding season by analyzing changes in invertebrate biomass using all the extracted invertebrates from our samples.

If invertebrate food resources are more limited late in the breeding season, birds that arrive on site early may have greater nest success. Evolution would favor the "early bird".

However, invertebrate taxa and abundance may vary from year to year (Stenger 1958). Therefore, invertebrate communities and abundances along wetland-upland gradients would have to be sampled for several years to be certain that food is a limited resource during the breeding season at these sites.

Biases in Biomass Estimates

Most techniques which sample food availability are biased because researchers lack the birds' perception and do not know their feeding constraints (Robinson and Holmes 1982, Heinrich and Collins 1983, Sherry 1984). What is present in the field may not be what is actually available to the bird. We do not know which prey items a bird ignores because of the prey's inaccessibility (Kantak 1979, Avery and Krebs 1984), difficulty of capture (Hespenheide 1973), mechanical defenses (Sherry and McDade 1982) or chemical defenses (Eisner 1970, Janzen 1980).

I had no previous data on food habits of birds in red maple forested wetlands and contiguous uplands. I felt collecting litter down to the root mass at each sample point was a comprehensive way of sampling all potential food items which birds feeding on the surface of the litter and in the litter would encounter.

Many types of arthropods have clumped distributions which can greatly inflate variance estimates (Southwood 1966, Cooper and Whitmore 1990). I suspect many of the invertebrate taxa I collected were patchily distributed because I found high variances among samples. This made it difficult to detect differences in abundances of invertebrates between zones and prevented me from pooling sites.

More detailed work with species identification of invertebrates needs to be done to help understand differences in abundance among moisture zones in red maple forested wetlands and contiguous uplands. I identified most individuals of the invertebrate community only to order or family level because of time constraints. Changes in biomass over time or space may be masked when data for invertebrates are pooled at these ordinal levels. Species often have different life cycles and are associated with different habitats (Borror et al. 1989). Therefore, changes in abundance in species are not necessarily representative of those in another (Hutto 1985).

Invertebrate communities and abundances along these upland/wetland gradients would have to be sampled for several years in order to be certain that food is a limited resource during the breeding season at our sites because invertebrate types and abundance may change from year to year (Stenger 1958). Also, other invertebrates communities along the moisture gradient need to be sampled to determine the invertebrate prey base in all the vegetative strata of these habitats.

Environmental Variables

I did not find fluctuations in the water table or that the density of shrubs as I measured them influenced changes in invertebrate biomass along the moisture gradient. However, there were significant differences in biomass of invertebrates for each type of litter identified. It is possible that litter type more closely reflected changes in soil moisture than our water table measurements.

Future studies which try to correlate environmental factors with invertebrate abundance should focus on the herbaceous layer. This layer can relect changes in water regime more readily than taller vegetative layers such as shrubs (Golet et al. In press.). Also, since invertebrate biomass was higher in wetter litter types, more work should be done with this variable. Perhaps a more precise method of measuring water moisture in each sample should be used (e.g., automated tensiometers which are mobile and can give quick measurements of litter moisture).

Appendix A. Taxonomic composition of the invertebrate community in litter samples collected from forested red maple wetlands and adjacent forested uplands in Washington County, Rhode Island, April-August 1991.

		Zones[a]							
		A		B		C		D	
Class	Order-Family	Total no.	%	Total no.	%	Total no.	%	Total no.	%
Arachnida									
	Araneae			311	13.9	257	16.5	448	14.6
	Attidae	1	0	0	0	0	0	0	0
	Thomisidae	3	0	4	0	0	0	4	0
	Pseudoscorpionida	108	5.8	105	6.7	54	1.8	64	2.0
Chilopoda		2	0	9	.6	1	0	0	0
	Geophilomorpha	33	1.4	57	3.7	14	.5	6	.2
	Lithobiomorpha	23	1.0	10	.6	0	0	0	0
	Scolopendromorpha	1	0	0	0	0	0	0	0
	Scutigeridae	1	0	0	0	0	0	0	0
Diplopoda		2	0	2	0	0	0	1	0
	Polydesmida	4	.2	7	.4	25	.8	3	.1
	Polyxenia	0	0	0	0	4	0	1	0
	Spirobila	54	2.4	85	5.5	88	2.9	54	1.7

Appendix A. Continued.

Class	Order-Family	Zones[a]							
		A		B		C		D	
		Total no.	%	Total no.	%	Total no.	%	Total no.	%
Insecta									
	Blatteria								
	Blattidae(A)	2	0	2	0	0	0	1	0
	Coleoptera								
	(L)	30	1.3	19	1.2	24	.8	47	1.5
	(A)	13	.6	11	.7	22	.7	42	1.3
	Byrrhidae								
	(A)	2	0	0	0	7	.2	5	.2
	Carabidae								
	(A)	6	.3	9	.6	34	1.1	19	.6
	(L)	27	1.2	24	1.5	80	2.6	92	2.9
	Cantharidae								
	(A)	35	1.6	24	1.5	1	0	0	0
	(L)	0	0	0	0	92	3.0	54	1.7
	Chrysomelidae								
	(L)	2	0	1	.1	0	0	0	0
	Curculionidae								
	(A)	4	.2	8	.5	4	.1	1	0

Appendix A. Continued.

Class	Order-Family	Zones[a] A Total no.	%	B Total no.	%	C Total no.	%	D Total no.	%
	Dermestidae								
	(A)	0	0	0	0	0	0	2	0
	Elateridae								
	(A)	4	.2	4	.3	1	0	0	0
	(L)	87	3.9	82	5.3	15	.5	12	.4
	Gyrinidae								
	(A)	0	0	0	0	1	0	2	0
	Helodidae								
	(A)	0	0	0	0	0	0	1	0
	(L)	1	0	0	0	19	.6	35	1.1
	Hydrophilidae								
	(A)	3	.1	2	.1	59	1.9	117	3.7
	(L)	0	0	0	0	12	.4	18	.6
	Lampyridae								
	(L)	3	.1	1	.1	4	.1	2	.1
	Languridae								
	(L)	0	0	1	0	0	0	1	0

Appendix A. Continued.

Class	Order-Family	Zones[a]							
		A		B		C		D	
		Total no.	%	Total no.	%	Total no.	%	Total no.	%
	Lycidae								
	(L)	3	.1	3	.2	17	.5	14	.4
	(A)	0	0	1	0	0	0	0	0
	Pselaphidae								
	(A)	8	.4	5	.3	9	.3	13	.4
	Scaphiedae								
	(A)	0	0	1	.1	3	.1	5	.2
	Scarabaeidae								
	(A)	0	0	6	.4	2	.1	1	0
	(L)	9	.4	1	.1	0	0	0	0
	Staphylinidae								
	(A)	26	1.2	24	1.5	248	8.1	184	5.9
	(L)	2	0	9	.6	27	.9	26	.8
	Tenebrionidae								
	(A)	0	0	13	.8	6	.2	0	0
	(L)	5	.2	0	0	0	0	4	.1

Appendix A. Continued.

Class	Order-Family	Zones[a]							
		A		B		C		D	
		Total no.	%	Total no.	%	Total no.	%	Total no.	%
	Diptera								
	Ceratopogonidae								
	(L)	0	0	.1	0	317	10.4	189	6.0
	Chironomidae								
	(A)	0	0	0	0	0	0	2	.1
	(L)	14	.6	23	1.5	559	18.3	250	7.9
	(P)	0	0	0	0	1	0	0	0
	Dolichopodidae								
	(L)	1	0	0	0	0	0	0	0
	Platypezidae								
	(L)	2	.1	1	.1	0	0	3	.1
	Tabanidae								
	(A)	0	0	0	0	0	0	2	.1
	(L)	8	.4	18	1.2	56	1.8	52	1.7
	Tipulidae								
	(A)	0	0	5	.3	0	0	9	.3
	(L)	23	1.0	0	0	160	5.2	171	5.4
	(P)	0	0	0	0	2	.1	1	0

Appendix A. Continued.

Class	Order-Family	Zones[a]							
		A		B		C		D	
		Total no.	%	Total no.	%	Total no.	%	Total no.	%
	Unidentified								
	(L)	3	.1	6	.4	70	2.3	63	2.0
	(A)	21	.9	14	.9	33	1.1	28	.9
	Hemiptera								
	Dipsocoridae								
	(A)	1	0	0	0	0	0	0	0
	(N)	2	.1	1	0	0	0	0	0
	Enicocephalidae								
	(A)	0	0	1	.1	5	.2	4	.1
	(N)	0	0	0	0	7	.2	5	.2
	Hebridae								
	(A)	0	0	0	0	0	0	1	0
	Lygaeidae								
	(A)	1	0	0	0	1	0	1	0
	(N)	0	0	0	0	0	0	1	0
	Mesovellidae								
	(A)	0	0	0	0	0	0	1	0

Appendix A. Continued.

Class	Order-Family	Zones[a] A Total no.	A %	B Total no.	B %	C Total no.	C %	D Total no.	D %
	Nabidae								
	(A)	0	0	1	.1	1	0	3	.1
	(N)	2	.1	1	.1	0	0	5	.2
	Schizopteridae								
	(N)	0	0	1	.1	1	0	2	.1
	Tineidae								
	(A)	1	0	0	0	7	.2	1	0
	(N)	0	0	0	0	1	0	0	0
	Unidentified								
	(A)	2	.1	9	.6	9	.3	20	.6
	(N)	4	.2	4	.3	6	.2	22	.7
	Homoptera								
	Membracidae								
	(A)	0	0	0	0	1	0	0	0
	(N)	1	0	6	.4	0	0	0	0
	Unidentified								
	(N)	2	.1	0	0	2	1	0	0

Appendix A. Continued.

Class	Order-Family	A Total no.	A %	B Total no.	B %	C Total no.	C %	D Total no.	D %
	Hymenoptera								
	Unidentified								
	(A)	44	2.0	18	1.2	13	.4	22	.7
	Braconidae								
	(A)	1	0	0	0	0	0	0	0
	Formicidae								
	(A)	429	19.2	410	26.3	52	1.7	88	2.8
	Sphecidae								
	(A)	0	0	0	0	6	.2	4	.1
	Lepidoptera								
	Unidentified								
	(L)	59	2.6	77	4.9	43	1.4	18	.6
	(A)	5	.2	1	.1	7	.2	33	1.0
	(P)	0	0	3	.2	0	0	0	0
	Arctiidae								
	(A)	1	0	0	0	2	.1	0	0
	(L)	2	.1	4	.3	0	0	3	.1

Zones[a]

Appendix A. Continued.

Class	Order-Family	Zones[a]							
		A		B		C		D	
		Total no.	%	Total no.	%	Total no.	%	Total no.	%
	Gelechidae								
	(L)	2	.1	1	.1	0	0	0	0
	Noctuidae								
	(A)	131	5.9	78	5.0	178	5.8	126	4.0
	(L)	1	0	2	.1	1	0	2	.1
	Oecophoridae								
	(L)	1	0	0	0	0	0	0	0
	Psychidae								
	(L)	1	0	0	0	0	0	0	0
	Pterophoridae								
	(L)	1	0	2	.1	0	0	0	0
	Tineidae								
	(L)	0	0	2	.1	1	0	1	0
	Megaloptera								
	(L)	0	0	0	0	4	.1	1	0
	Corydalidae								
	(L)	0	0	1	.1	3	.1	13	.4

Appendix A. Continued.

Class	Order-Family	Zones[a]							
		A		B		C		D	
		Total no.	%	Total no.	%	Total no.	%	Total no.	%
	Orthoptera								
	Unidentified								
	(A)	2	0	0	0	0	0	1	0
	(N)	11	.5	10	.6	4	.1	1	0
	Acrididae								
	(N)	1	0	0	0	0	0	0	0
	Gryllidae								
	(A)	9	.4	6	.4	3	.1	2	.1
	(N)	29	1.3	4	.3	1	0	3	.1
	Siphonoptera	0	0	0	0	3	.1	0	0
	Tricoptera								
	(L)	0	0	0	0	5	.2	5	.2
	Brachycentridae								
	(L)	0	0	0	0	0	0	2	.1
	Polycentripodidae								
	(L)	0	0	0	0	11	3	16	.4
Isopoda	(L)	1	0	3	.2	0	0	0	0

Appendix A. Continued.

Class	Order-Family	Zones[a] A Total no.	A %	B Total no.	B %	C Total no.	C %	D Total no.	D %
Malacostraca									
	Amphipod	0	0	1	.1	4	.1	25	.8
Oligocheate(Phylum: Annelida)		3	0	9	.6	30	.9	25	.8
Unknown Order									
	(A)	5	.2	1	.1	9	.3	16	.5
	(L)	43	1.9	38	2.4	86	2.8	125	4.1
	(P)	3	0	2	.2	18	.6	22	.7
	(N)	0	0	0	0	1	0	1	0
	Total	2235	100	1556	100	3060	100	3145	100

[a]Zones were based on soil moisture and distance from the wetland-upland edge. Zone A (furthest upland zone from wetland-upland edge), Zone B (closest upland zone to upland-wetland edge), Zone C (closest wetland zone to upland-wetland edge), Zone D (furthest wetland zone from wetland-upland edge).

Appendix B. Numbers of birds captured by zone at each site along a gradient from forested upland to red maple forested wetland, May-August, 1991.

	Bird species																			
	Veery (n=14)				Northern Waterthrush (n=7)				Canada Warbler (n=8)				Gray Catbird (n=20)				Ovenbird (n=13)			
Zone[a]	AS[b]	BU	GS	TOT[c]	AS	BU	GS	TOT	AS	BU	GS	TOT	AS	BU	GS	TOT	AS	BU	GS	TOT
A	-	1	3	4	-	-	-	0	-	1	-	1	2	5	2	9	1	-	3	4
B	1	1	3	5	-	-	-	0	-	-	-	0	-	1	2	3	-	4	1	5

Appendix 2. Continued.

	Bird species																			
	Veery (n=14)				Northern Waterthrush (n=7)				Canada Warbler (n=8)				Gray Catbird (n=20)				Ovenbird (n=13)			
Zone[a]	AS[b]	BU	GS	TOT[c]	AS	BU	GS	TOT	AS	BU	GS	TOT	AS	BU	GS	TOT	AS	BU	GS	TOT
C	2	-	1	3	2	-	1	3	-	1	-	1	2	2	2	6	1	1	-	2
D	-	-	2	2	2	-	2	4	1	-	5	6	-	1	1	2	-	-	2	2

[a]Zones were based on soil moisture and distance from the wetland-upland edge. Zone A (furthest upland zone from wetland-upland edge), Zone B (closest upland zone to upland-wetland edge), Zone C (closest wetland zone to upland-wetland edge), Zone D (furthest wetland zone from wetland-upland edge).

[b]AS=Arrow Swamp, BU=Burlingame State Park, GS=Great Swamp Management Area.

[c]TOT=Total number of birds captured at all three sites.

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