

Habitat Relationships of Migratory Songbirds in North-Central Wisconsin

We studied songbird habitat relationships over four spring and four fall migration seasons in Price County, Wisconsin. We found that songbirds used a mosaic of 15 habitats during migration, but that wetland habitats attracted more individuals and species than all other habitats combined. Given the diversity of species using these habitats, including many neotropical migrants and species of management concern, we feel it prudent to conserve, restore, or develop a mosaic of communities to serve as songbird refuges during migration.

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Songbird declines have been attributed to destruction of wintering grounds in the tropics and to fragmentation of breeding grounds. More recently, concern has developed about the places in between—the pockets of forest that provide essential food, water, and shelter during migration, and the landscape corridors that provide vital life links between wintering and breeding grounds (Moore and Simons 1992, Moore et al. 1993).

Moore et al. (1993) state that habitat use during migration has profound consequences on birds' abilities to satisfy energy requirements, their vulnerability to predators, and their exposure to environmental stress. How migrants

respond to contingencies that arise during migration affects their survival and reproductive success. Thus, there is a need to develop methods to monitor songbirds and their migration habitats if we are to understand the ecological consequences of habitat loss to migratory songbird populations.

Many songbird migration studies have been conducted in areas where birds congregate or funnel through, such as islands, along river corridors, peninsulas, or large ecological barriers such as mountains, ocean coastlines, the Great Lakes, or the Gulf of Mexico, to mention a few. However, fewer studies have been done in large, contiguous forest tracts to determine what

habitats are used by birds as refueling and resting stops during spring and fall migration.

Little is known about critical community and habitat relationships of many songbird species during migration: what kinds of habitats are important to them, where conservation of migration habitat is needed to minimize migratory stress, and how much songbird migratory habitat is being lost and where. To help address part of this problem, we designed a study to obtain information on community and habitat relationships of songbirds in a contiguous forested landscape in north-central Wisconsin during eight migration seasons from 1989 to 1992.

STUDY AREA

Study Site—Our study site was located 0.25 miles west of Fifield, Price County, Wisconsin (45° 52' 24" N, 90° 25' 49" W), on about 100 acres of private forest land that had not been logged for over 50 years (Figure 1). Logging done previous to that time was done selectively, so artificial habitat fragmentation due to logging was minimal.

This area is part of the glaciated Northern Highlands Physiographic Region, and consists of level to gently rolling topography of relatively low relief with an elevation of about 1,450 feet. Due to its glacial history, the forest is naturally fragmented and contains a rich variety of patchy habitats characteristic of the Northern Highlands. Our study area falls within Partners in Flight (PIF) Physiographic Area 20 (boreal and hardwood forest transition) and The Nature Conservancy's Superior Mixed Forest Ecoregion. The study area contains a mosaic of com-

munities and habitats made up of mixed deciduous and coniferous trees and distinct stands of mixed sugar and red maples, paper birch, quaking and big-tooth aspen, red pine, tamarack, white pine, black spruce, hemlock, and shrubby wetlands. Eleven acres of grasslands border the eastern edge of the study area.

Community and Habitat Descriptions—

The main study area was 100 acres in size and contained five general community types (Figure 1) with 15 easily identifiable habitats named for their dominant tree species. The vegetation in each habitat was quantitatively measured using the method of James and Shugart (1970). Scientific and common names of trees and plants mentioned in this article are provided in Appendix 1. The five general community types are described below; for detailed descriptions of the associated habitats in which mist nets were placed, see Appendix 2.

Upland Deciduous Community. The upland deciduous community was the largest community type, with 47.5 acres containing four habitat types: Aspen, Aspen Road, Northern Hardwoods, and Paper Birch. These four mesic forest stands contained pole- and saw-timber-sized deciduous canopy trees and a mixed deciduous and coniferous understory, or shrub layer. This community type was structurally complex, with all forest vegetation layers well developed. The ground flora was typical of northern dry-mesic forests (sensu Curtis 1959).

Lowland Conifer Community. The lowland conifer community was the second largest community type, at nearly 26 acres. It was composed of four habitat types: Black Spruce, Tamarack,

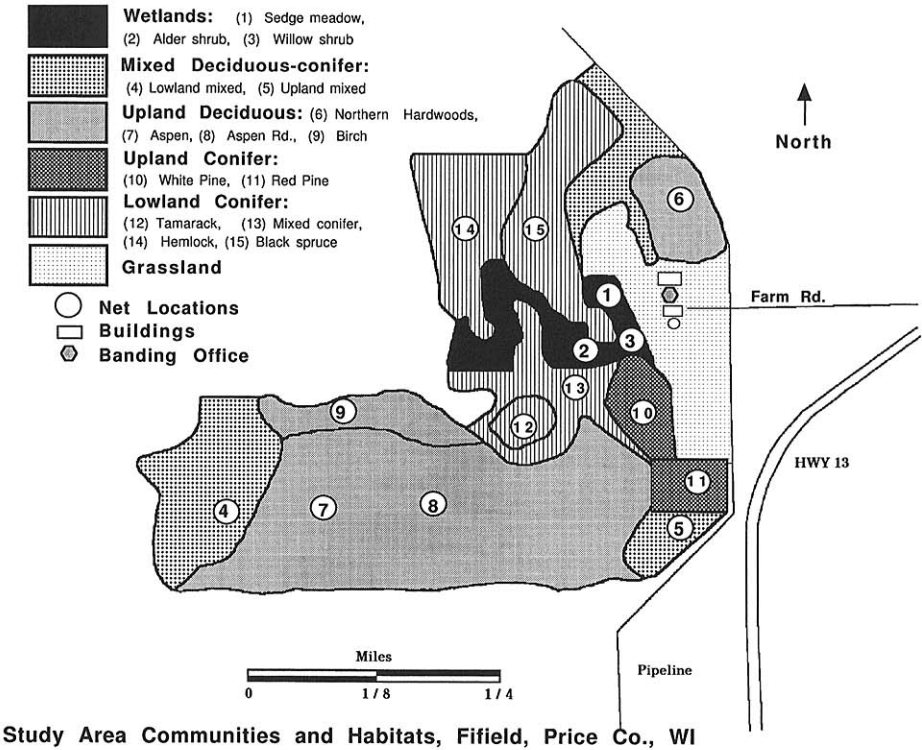


Figure 1. Fifield bird study area, net locations, and communities, 1989–1992, Price County, Wisconsin.

Hemlock, and Mixed Conifer. The black spruce and tamarack stands were growing on sphagnum moss where the soil was saturated most of the year. The hemlock and mixed conifer stands were on slightly drier ground where the soil was saturated during snow melt and generally after heavy rains. Except for low shrubs like Labrador-tea and leatherleaf, there was very little understory and structural diversity.

Mixed Deciduous-Conifer Community. The mixed deciduous-conifer community (13.5 acres) occurred on both lowlands and uplands, and included two habitat types: Lowland Mixed Deciduous-Conifer and Upland Mixed Deciduous-Conifer. The species com-

position of the canopy was diverse. Dead standing and downed trees and a dense shrub layer contributed to the structural complexity.

Wetland Community. The wetland community (Figure 2) was 7 acres in size and contained three habitat types: Alder Shrub, Willow Shrub, and Sedge Meadow. These habitats were composed of dense, scrubby shrubs with scattered pockets of small conifer and deciduous trees, or, in the case of Sedge Meadow, an open-canopy wet meadow. Soils were usually saturated, and standing water was present during and after snow melt and heavy rains.

Upland Conifer Community. The upland conifer community consisted of 7



Figure 2. This shrubby wetland community was used by the greatest number of species, more long-distance neotropical migrant species, and largest number of individuals, 1989–1992, Price County, Wisconsin.

acres in two habitat types: White Pine and Red Pine (Figure 3). Both stands consisted of dense, pole-sized trees, with little structural and tree species diversity.

METHODS

Mist netting, Banding, and Biological Data—From 1989 through 1992, birds were trapped during the spring (about mid-April to the end of May) and fall (about mid-August to the end of September) migration periods. We used up to 45 standard mist nets (12 meters $\times$ 2.6 meters of 36 millimeter mesh) totaling 504 meters (1,800 feet) in the 15 different habitats to monitor species movement, habitat relationships, and condition of resident and migrant birds as they used the forest.

Three mist nets were placed in a row at the same location within each habitat and were monitored throughout the course of the study. Nets were opened from dawn to dusk during favorable weather, and were checked for birds every hour or less. All mist net capture data were converted to birds per 1,000 net hours of operation to standardize sample effort among habitats for comparative purposes. Our sample unit was the “net hour”: one 12 meter $\times$ 2.6 meter mist net open for 1 hour. Birds were removed from mist nets, placed in cloth bird bags, and transported to an on-site banding office for processing. We recorded the time of capture and habitat type in which each bird was captured.

Once in the banding office, the following data from each bird were en-



Figure 3. This red pine plantation was the least used by bird species and individuals of all 15 habitats studied due to its lack of vegetative and structural diversity, 1989–1992, Price County, Wisconsin.

tered directly into a computer: date, time, habitat location, band number, and biological data such as age, sex, weight, and wing length. After being checked for ticks and banded with an official U.S. Fish and Wildlife Service numbered band, each bird was released from the banding office. Ticks removed from birds were put in vials with a small piece of moist filter paper and refrigerated until examined. Some birds ($N=106$) were released unprocessed, except for identification, when there was a high volume of birds that could not all be kept long enough and processed safely without causing them undue stress.

Migratory Bird Classification—We classified migrant species according to

Partners in Flight Research Working Group (1992) lists. The PIF “A” list refers to neotropical species that breed in North America and spend their non-breeding period primarily south of the United States, and are referred to in our study as “long-distance neotropical migrants.” Species on PIF’s “B” list breed and winter extensively in North America, but some populations winter south of the United States, and are referred to in our study as “short-distance migrants.” We classified permanent residents and questionable species as “O” (other). Scientific and common names and migratory status of birds we studied are provided in Table 1.

Versatility Rating—A versatility rating is a good measure of how adaptable a

Table 1. Species, migratory class, and number of birds trapped, spring and fall combined, 1989–1992, Price Co., Wisconsin.

Common Name	Latin Name	Migratory Class ¹	No. Birds
Sharp-shinned Hawk	<i>Accipiter striatus</i>	A	26
Broad-winged Hawk	<i>Buteo platypterus</i>	A	2
Ruffed Grouse	<i>Bonasa umbellus</i>	O	2
American Woodcock	<i>Scolopax minor</i>	O	5
Black-billed Cuckoo*	<i>Coccyzus erythrophthalmus</i>	A	2
Northern Saw-whet Owl	<i>Aegolius acadicus</i>	B	8
Whip-poor-will*	<i>Caprimulgus vociferus</i>	A	2
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	A	3
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	B	25
Downy Woodpecker	<i>Picoides pubescens</i>	O	18
Hairy Woodpecker	<i>Picoides villosus</i>	O	23
Black-backed Woodpecker	<i>Picoides arcticus</i>	O	1
Northern Flicker	<i>Colaptes auratus</i>	B	13
Pileated Woodpecker	<i>Dryocopus pileatus</i>	O	3
Olive-sided Flycatcher*	<i>Contopus borealis</i>	A	1
Eastern Wood-Pewee*	<i>Contopus virens</i>	A	2
Yellow-bellied Flycatcher	<i>Epidonax flaviventris</i>	A	1
Alder Flycatcher	<i>Epidonax alnorum</i>	A	8
Least Flycatcher	<i>Epidonax minimus</i>	A	23
Eastern Phoebe	<i>Sayornis phoebe</i>	B	1
Great-crested Flycatcher*	<i>Myiarchus crinitus</i>	A	3
Blue-headed Vireo	<i>Vireo solitarius</i>	A	7
Philadelphia Vireo*	<i>Vireo philadelphicus</i>	A	1
Red-eyed Vireo	<i>Vireo olivaceus</i>	A	55
Gray Jay	<i>Perisoreus canadensis</i>	O	10
Blue Jay	<i>Cyanocitta cristata</i>	O	37
Tree Swallow	<i>Tachycineta bicolor</i>	B	19
Black-capped Chickadee	<i>Poecile atricapillus</i>	O	289
Red-breasted Nuthatch	<i>Sitta canadensis</i>	O	43
White-breasted Nuthatch	<i>Sitta carolinensis</i>	O	7
Brown Creeper	<i>Certhia americana</i>	B	89
House Wren	<i>Troglodytes aedon</i>	A	1
Winter Wren	<i>Troglodytes troglodytes</i>	B	1
Golden-crowned Kinglet	<i>Regulus satrapa</i>	B	44
Ruby-crowned Kinglet	<i>Regulus calendula</i>	B	42
Eastern Bluebird	<i>Sialia sialis</i>	B	25
Veery*	<i>Catharus fuscescens</i>	A	9
Gray-checked Thrush	<i>Catharus minimus</i>	A	44
Swainson's Thrush	<i>Catharus ustulatus</i>	A	303
Hermit Thrush	<i>Catharus guttatus</i>	B	366
Wood Thrush*	<i>Hylocichla mustelina</i>	A	2
American Robin	<i>Turdus migratorius</i>	B	38
Gray Catbird	<i>Dumetella carolinensis</i>	A	6
Brown Thrasher	<i>Toxostoma rufum</i>	B	1
Cedar Waxwing	<i>Bombycilla cedrorum</i>	B	3
Tennessee Warbler*	<i>Vermivora peregrina</i>	A	236
Orange-crowned Warbler	<i>Vermivora celata</i>	A	1
Nashville Warbler*	<i>Vermivora ruficapilla</i>	A	202
Northern Parula	<i>Parula americana</i>	A	1
Chestnut-sided Warbler*	<i>Dendroica pensylvanica</i>	A	20
Magnolia Warbler*	<i>Dendroica magnolia</i>	A	126

(continued)

Table 1. (continued)

Common Name	Latin Name	Migratory Class ¹	No. Birds
Cape May Warbler*	Dendroica tigrina	A	22
Black-throated Blue Warbler	Dendroica caerulescens	A	1
Yellow-rumped Warbler	Dendroica coronata	B	284
Black-throated Green Warbler*	Dendroica virens	A	56
Blackburnian Warbler*	Dendroica fusca	A	8
Palm Warbler	Dendroica palmarum	A	97
Bay-breasted Warbler*	Dendroica castanea	A	34
Blackpoll Warbler	Dendroica striata	A	61
Black-and-white Warbler	Mniotilta varia	A	31
American Redstart*	Setophaga ruticilla	A	49
Ovenbird*	Seiurus aurocapillus	A	355
Northern Waterthrush	Seiurus noveboracensis	A	11
Mourning Warbler*	Oporornis philadelphia	A	7
Common Yellowthroat*	Geothlypis trichas	A	39
Wilson's Warbler	Wilsonia pusilla	A	4
Canada Warbler*	Wilsonia canadensis	A	5
Scarlet Tanager*	Piranga olivacea	A	3
Chipping Sparrow	Spizella passerina	A	30
Savannah Sparrow	Passerculus sandwichensis	B	2
Fox Sparrow	Passerella iliaca	B	9
Song Sparrow	Melospiza melodia	B	26
Lincoln's Sparrow	Melospiza lincolni	A	47
Swamp Sparrow	Melospiza georgiana	B	6
White-throated Sparrow	Zonotrichia albicollis	B	378
Harris's Sparrow	Zonotrichia querula	B	1
White-crowned Sparrow	Zonotrichia leucophrys	B	2
Dark-eyed Junco	Junco hyemalis	B	136
Northern Cardinal	Cardinalis cardinalis	O	2
Rose-Breasted Grosbeak*	Pheucticus ludovicianus	A	11
Indigo Bunting*	Passerina cyanea	A	2
Common Grackle	Quiscalus quiscula	B	5
Brown-Headed Cowbird	Molothrus ater	B	2
Purple Finch	Carpodacus purpureus	B	40
White-winged Crossbill	Loxia leucoptera	O	1
Common Redpoll	Carduelis flammea	O	2
Pine Siskin	Carduelis pinus	B	45
American Goldfinch	Carduelis tristis	B	13
Evening Grosbeak	Coccothraustes vespertinus	O	4

*Species declining or of management concern (Partners In Flight scores of 3 or greater) in the Midwest (Thompson et al. 1993)

¹A = Long distance Migrant, B = Short distance Migrant, and O = Other (Partners in Flight Research Working Group 1992)

species is to habitat change or loss. The more habitats a species uses, the more versatile it is; the fewer habitats it uses, the less versatile it is (Benyus et al. 1992). In this study, our 15 habitat types were aggregated into five community types and our measure of versatility was based on those five

community types. Bird species were divided into three groups based on the number of communities they used on the study area; low (1–2 communities used), intermediate (3–4 communities used), and high (all 5 communities used). Only those species (36 out of 89 total) for which more than 20

individuals were captured were included in the analysis. Restricting the analysis to these 36 species means that, for example, the chance of assigning a 'high' species to the 'intermediate' category is less than 5%.

RESULTS

Bird Capture and Tick Data—Mist nets were operated for 186 days in up to 15 habitats for a total of 58,856 net hours over eight migration seasons from 1989 to 1992 (Table 2). We trapped and banded 4,031 individual birds of 89 species (Table 2) and had 1,315 recaptures of our own previously banded birds.

More individuals (2,874) and species (75) were captured during fall migration than in spring (1,157 individuals; 70 species). Capture rates (birds trapped per 1,000 net hours) for all communities and years combined were also higher in fall (102.6) than in spring (37.5). Fifty-six species (63%) were common to both spring and fall, whereas 13 species were captured only in spring and 20 only in fall. The following six species (listed in order of abundance) made up 50% of the spring captures: Hermit Thrush, White-

throated Sparrow, Ovenbird, Black-capped Chickadee, Nashville Warbler, and Pine Siskin. The following seven species made up 50% of the fall captures: Swainson's Thrush, White-throated Sparrow, Tennessee Warbler, Ovenbird, Black-capped Chickadee, Hermit Thrush, and Magnolia Warbler.

Of 1,184 ticks removed from 335 birds of 26 species, 60 rabbit ticks (*Hae-maphysalis leporispalustris*) from eight species of birds were found to be infected with the Lyme disease spirochete, *Borrelia burgdorferi* (Nicholls and Callister 1996).

Bird Community/Habitat Relationships—All community types were used by a wide variety of species, but some were used much more than others (Table 3). The highest capture rate occurred in the wetland community type (170 birds per 1,000 net hours) (Figure 4c). Comprising only 7% of the study area, this community was used by migrating birds far in excess of its acreage proportion (Figure 4c). More individuals were netted in the Wetland community (54% of all new captures) than in the other four community types combined.

Table 2. Mist net trapping summary for eight migration seasons, spring and fall, 1989–1992, Price Co., Wisconsin.

Year	Trapping Period	Days Nets Open	Net Hours	New Birds	Retrap Birds	Total Birds
1989	4/21–5/26	28	9165	311	165	476
	8/24–10/6	24	6609	574	122	696
1990	4/25–6/1	23	6883	254	151	405
	8/21–9/27	29	9773	717	204	921
1991	4/22–5/30	23	7556	181	158	339
	8/27–10/3	27	6074	800	173	973
1992	4/28–5/21	17	7241	411	192	603
	8/26–9/17	15	5555	783	150	933
Totals		186	58856	4031	1315	5346

The Wetland community also had the highest species richness, with 77 out of the 89 total species captured (Figure 5); over half (54.5%) of those species are classified as long-distance neotropical migrants (Figure 5). The Upland Deciduous community had the second highest species richness (46), with over half (54.4%) of those species classified as long-distance neotropical migrants. The Lowland Conifer (45 species) and Mixed Deciduous-Conifer communities (41 species) followed, with long-distance neotropical migrants comprising 48.9% and 46.3%, respectively. The Upland Conifer community had the least number of species (16), of which 43.8% were long-distance neotropical migrants. Generally, more species were captured (Figure 6), and higher capture rates of long-distance neotropical migrants occurred (Figure 4a and b), in fall rather than in spring.

All three wetland habitats—Alder Shrub, Willow Shrub, and Sedge Meadow—contributed to the high capture rate within the Wetland community. These three habitats each attracted more individual birds (Figure 7) and more species (Figure 5) than any of the other 12 habitats.

Versatility Rating—Our quantification of the number of communities a bird species used represents the adaptability of that species to community change or loss. Eight species fell in the low versatility group that used only one to two communities, 14 fell in the intermediate group using three to four communities, and 14 fell in the high group using all five communities. These results indicate that while some of the species in the study area tended to specialize in a few communities

rather than many, most species seemed to be habitat generalists during migration.

Migratory Bird Classification—Of the 89 species captured, most are classified as long-distance neotropical migrants (46), followed by short-distance migrants (28) and other birds (15). We found species from all three migration categories in every habitat type.

Of the 4,031 individuals captured, most were long-distance neotropical migrants (48.6%), followed by short-distance migrants (40.3%) and other birds (11.1%). More individuals of long-distance neotropical migrants (55.7%) than short-distance migrants (33.7%) were captured in fall, whereas the opposite was true in spring when more short-distance (56.6%) than long-distance neotropical migrants (31%) were captured. The percentage of other birds was slightly higher in spring (12.4%) than in fall (10.6%).

DISCUSSION

Methods Used—Small birds in dense vegetation are usually difficult to census, especially outside of the breeding season when few individuals are singing. Mist netting, one of the most efficient methods of censusing birds, can be used to assess habitat use of small bird species, with certain reservations related to net mesh size, bird size, degree of shading, vegetation height, and time of day (Jenni and Leuenberger 1996). Our mist nets, open from dawn to dusk, could not cover the entire vegetation height in most habitats because many trees were up to 80 feet tall. As a result, we undoubtedly missed some birds that prefer higher vegetation strata. Point counts (Hutto et al. 1986)

Table 3. Species presence or absence by community type, spring and fall, 1989–1992, Price County, Wisconsin

Species	Wetland		Upland Deciduous		Mixed Decid. Conifer		Upland Conifer		Lowland Conifer	
	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
American Woodcock	X	X			X					
Sharp-shinned Hawk	X	X	X	X	X	X			X	X
Broad-winged Hawk					X					
Ruffed Grouse			X							X
Black-billed Cuckoo*		X								
Northern Saw-whet Owl	X	X			X				X	X
Whip-poor-will*	X		X							
Ruby-throated Hummingbird	X	X								
Black-backed Woodpecker										X
Downy Woodpecker		X		X	X	X				
Hairy Woodpecker	X	X	X	X		X		X	X	X
Pileated Woodpecker						X			X	
Yellow-bellied Sapsucker	X	X	X	X	X				X	X
Northern Flicker	X	X						X	X	X
Great-crested Flycatcher*			X			X				
Olive-sided Flycatcher*	X									
Eastern Wood-Pewee*			X							
Eastern Phoebe	X									
Least Flycatcher	X	X	X	X		X				X
Alder Flycatcher	X	X								X
Yellow-bellied Flycatcher		X								
Tree Swallow	X									
Blue Jay	X	X	X	X	X	X		X	X	
Gray Jay	X								X	X
Black-capped Chickadee	X	X	X	X	X	X		X	X	X
Brown Creeper	X	X	X	X	X	X			X	X
Red-breasted Nuthatch	X	X	X	X	X	X		X	X	X
White-breasted Nuthatch			X	X						X
House Wren		X								
Winter Wren						X				
Golden-crowned Kinglet		X	X	X	X	X			X	X
Ruby-crowned Kinglet	X	X	X	X	X				X	
Eastern Bluebird								X		
Wood Thrush*									X	
Veery*	X	X	X		X				X	
Swainson's Thrush	X	X	X	X	X	X		X	X	X
Gray-checked Thrush	X	X	X	X		X		X	X	X
Hermit Thrush	X	X	X	X	X	X	X	X	X	X
American Robin	X	X	X	X	X	X		X	X	X
Gray Catbird	X	X								
Brown Thrasher		X								
Cedar Waxwing		X								
Solitary Vireo		X			X				X	
Red-eyed Vireo		X	X	X		X				
Philadelphia Vireo*		X								
Tennessee Warbler*	X	X		X	X	X				X

(continued)

Table 3. (continued)

Species	Wetland		Upland Deciduous		Mixed Decid. Conifer		Upland Conifer		Lowland Conifer	
	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
Orange-crowned Warbler		X								
Nashville Warbler*	X	X	X	X	X	X			X	X
Northern Parula		X								
Black-and-white Warbler	X	X	X	X		X			X	X
Black-throated Blue Warbler		X								
Black-throated Green Warbler*	X	X	X	X	X	X	X		X	X
Blackburnian Warbler*	X	X								X
Chestnut-sided Warbler*	X	X		X	X	X				
Cape May Warbler*		X								X
Magnolia Warbler*	X	X	X	X	X	X	X	X		X
Yellow-rumped Warbler	X	X	X	X	X	X		X	X	X
Bay-breasted Warbler*		X		X		X		X		X
Palm Warbler	X	X							X	X
Mourning Warbler*		X		X						
Canada Warbler*	X	X	X							
Wilson's Warbler	X	X								
Ovenbird*	X	X	X	X	X	X	X	X	X	X
Northern Waterthrush	X	X	X						X	
Common Yellowthroat*	X	X	X							
Blackpoll Warbler		X		X						X
American Redstart*	X	X	X	X		X		X		X
Rose-breasted Grosbeak*	X	X								
Northern Cardinal	X				X					
Indigo Bunting*		X			X					
Savannah Sparrow		X								
Song Sparrow	X	X	X							
Chipping Sparrow	X	X							X	
Dark-eyed Junco	X	X	X	X		X			X	X
Harris' Sparrow		X								
White-throated Sparrow	X	X	X	X	X	X			X	X
White-crowned Sparrow	X									
Fox Sparrow	X	X		X						X
Lincoln's Sparrow	X	X		X						
Swamp Sparrow	X	X								
Brown-headed Cowbird			X		X					
Common Grackle		X		X		X				
Scarlet Tanager*		X	X							
Pine Siskin	X								X	
American Goldfinch	X	X								
White-winged Crossbill									X	
Common Redpoll	X									
Purple Finch	X	X	X		X					
Evening Grosbeak	X									
Total Number of Species	55	67	37	34	29	30	4	15	32	35

*Species declining or of management concern (scores 3 or greater) in the Midwest (Thompson et al. 1993)

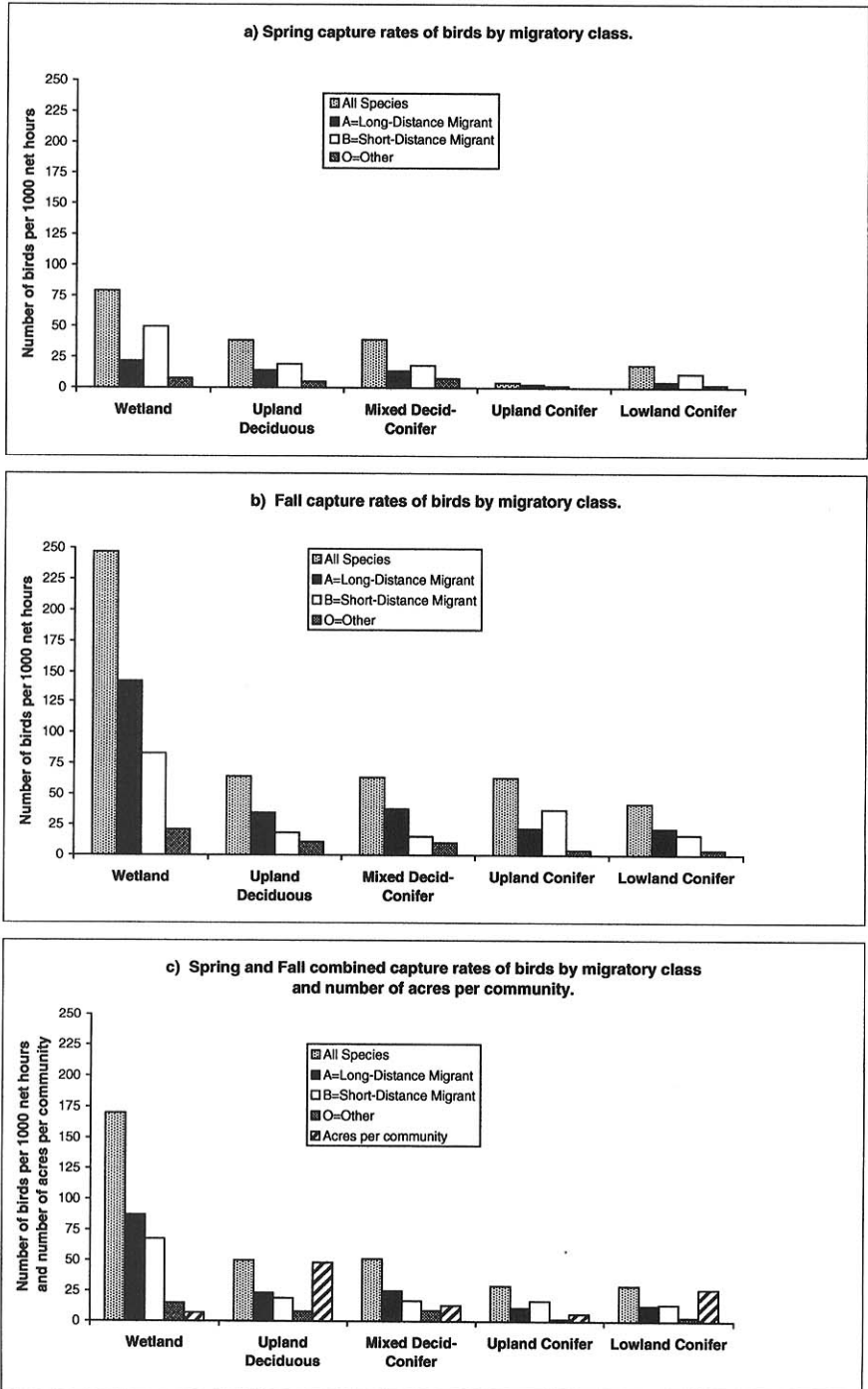


Figure 4. Capture rates of individual birds (N = 4031) by community type, season, migratory status, and acres available, 1989–1992, Price County, Wisconsin.

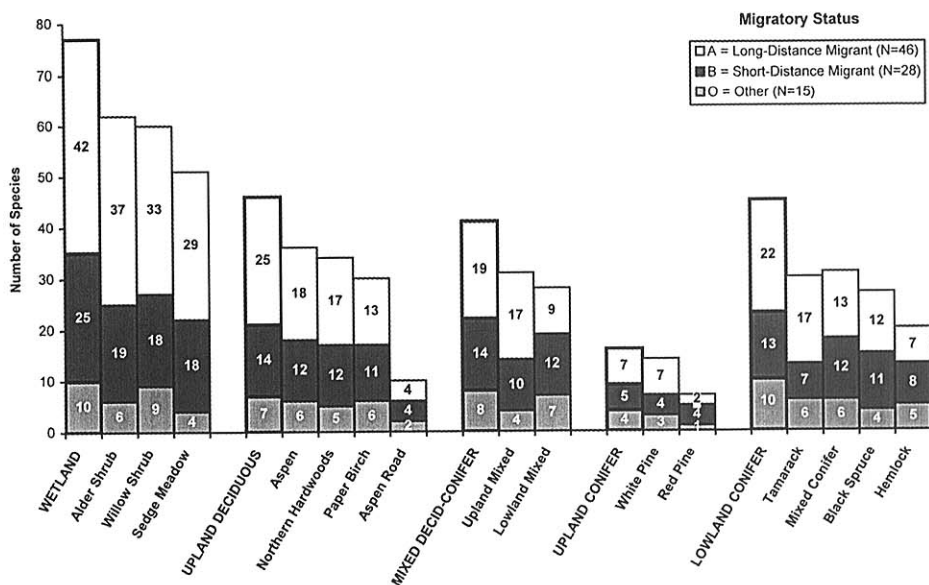


Figure 5. Total number of bird species (N=89) captured by community and habitat type and migratory status, 1989–1992, Price County, Wisconsin.

that record all birds seen or heard during the count period in spring, in combination with mist netting, would provide a more complete census of birds using an area during migration. We, in fact, tested this idea in spring (unpub. data) and found that we detected some birds with mist nets that we did not detect with point counts, and vice versa. Point counts used in combination with mist netting to census fall birds would be much less useful because most point-count birds are heard rather than seen and fewer birds are singing in the fall.

Mixed Species Flocks—Migratory songbirds form mixed species flocks together with resident birds while at migration stopovers. It was not unusual for us to capture some of these mixed species flocks in mist nets as they moved about the habitats while feeding, especially in the Wetland com-

munity. In fact, we once caught 11 species of birds in one mist net. Mixed species flocks confer the advantage of more predator-detecting eyes and ears looking and listening for predators. And, if migrating songbirds that stop to refuel join resident birds—such as Black-capped Chickadees and Red-breasted Nuthatches—who know local food sources, habitats, and potential predators in the area, their feeding is likely more efficient and safer even though there may be more competition for food resources.

Importance of Wetlands—Based upon our mist net results, the Wetland community (Figure 2) was by far the most used community in our study area, and was characterized by having the greatest number of species, more long-distance neotropical migrant species, and the largest number of individuals. A preliminary analysis of our spring

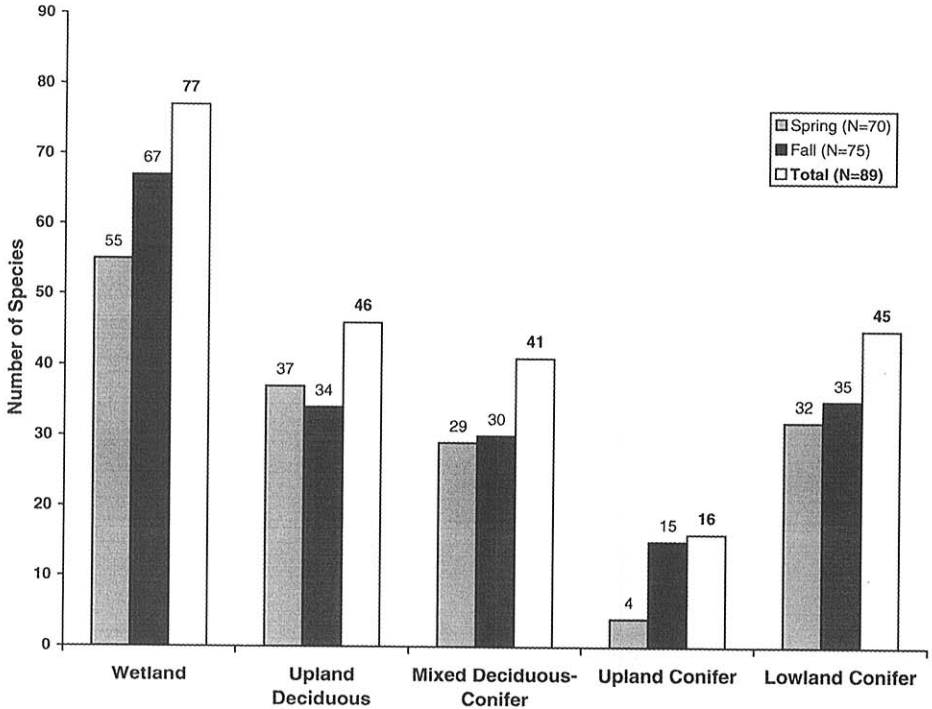


Figure 6. Number of bird species (N = 89) captured by community type and season, 1989–1992, Price County, Wisconsin.

point count data indicated a similar pattern, with a high number of migrant species and individuals found in the Wetland community (unpub. results).

Many of the birds normally found in the upper canopy, such as Red-eyed Vireos and Blackburnian Warblers, were frequently caught in wetland habitats, often in mixed species flocks. When frequent foggy conditions brought down migrants over a forest area, the wetlands attracted birds like a magnet, probably because there was an abundant food supply of insects and berries, accessible water, and dense vegetation that offered protection from bad weather and predators. Even the agile, bird-eating Sharp-shinned

Hawk had a difficult time penetrating the dense, shrubby wetland habitats (pers. obs.).

Although the value of wetlands to wildlife has sometimes been underestimated by land managers in the past, our study shows that wetlands play an extremely important role as en route refueling and resting sites for migratory songbirds. Fortunately, there are numerous scattered, shrubby wetlands in the forested landscape of northern Wisconsin that serve as important songbird migration refuges.

Wisconsin has already lost 47% of its original 10 million acres of wetlands since European settlement (Wisconsin Department of Natural Resources 1995), with greater loss in the southern

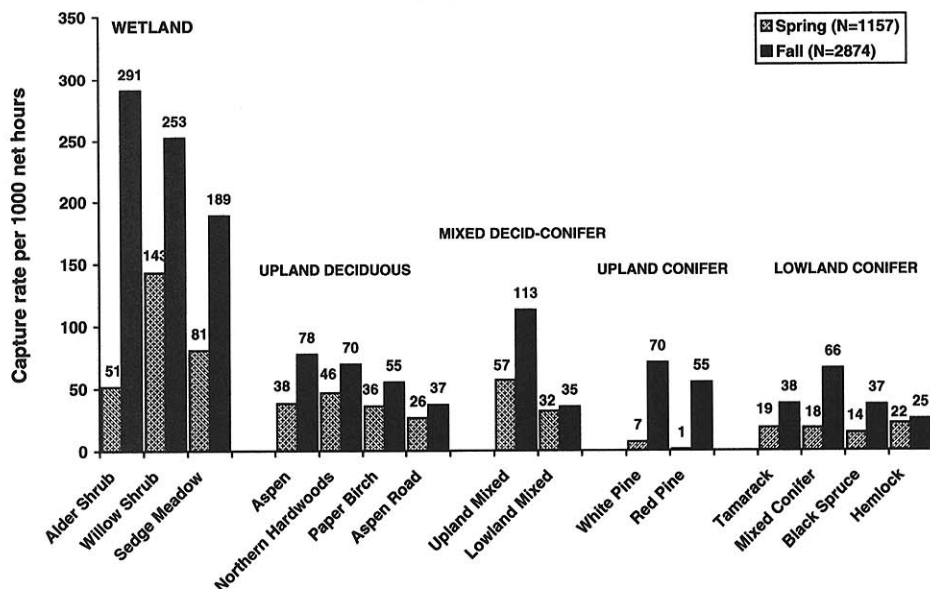


Figure 7. Seasonal capture rates of individual birds (N = 4031) by habitat type within each community, 1989–1992, Price County, Wisconsin.

than the northern part of the state due to development and drainage for agriculture. About 40% of Wisconsin's over 400 recorded bird species live in or use wetlands—no other habitat type comes close in terms of importance. The Wisconsin Department of Natural Resources plays the lead role in preventing wetland loss through an aggressive regulatory program involving local, state, and federal governments. Laws require that new wetlands be created to replace those being lost (wetland mitigation) through development, but the value of these mitigated wetlands to migratory songbirds remains unstudied. We feel it is important to study mitigated, as well as natural, wetlands to determine their value as songbird habitat and to protect and conserve remaining wetlands throughout Wisconsin so they may serve as songbird migration refuges as well as

habitat for a wide variety of other life forms.

Songbird Refuges—Conserving and managing songbird refuges can be more difficult than first meets the eye. Management of habitat is a first step for bird conservation, but species interactions and biogeographic factors inevitably complicate simple management prescriptions (Howe et al. 1996). Also, variable weather patterns influence the movement of migrants, so use of stopover sites can change dramatically from year to year and season to season (Moore et al. 1993). While songbird refuges that provide life-giving vital links to migratory birds may not be used every year or every season, key refuges must be conserved and protected in a variety of habitats and geographical areas along migratory

pathways so they are available when birds need them.

Migratory Status Comparison with Other Wisconsin Studies—Our study was just a snapshot in time and space. We recorded only a sample of the birds using the area, and only during spring and fall. If one were to multiply the number of birds we found using our 100-acre study area by the thousands of acres of similarly diverse habitat across northern Wisconsin, one could calculate how important these northern forest habitats must be to our neotropical migratory songbirds.

As examples, 51.7% of the 89 species and 48.6% of the 4,031 individuals in our study were neotropical migrants. Weisbrod et al. (1993), in a mist net study during spring and fall along the St. Croix River in Burnett County, about 120 miles west of our study area, found that neotropical migrants comprised 66% of the 118 species they captured and 72.7% of all individuals ($N = 16,527$). In a breeding bird point count study about 50 miles north of our study area in Ashland County, Elias (1997) observed 80 species, of which 47.5% were neotropical migrants, representing 68.8% of the total number ($N = 3,147$) of birds observed.

These studies show how important these northern habitats are to neotropical migrants. There is concern, however, that these habitats may become more fragmented though logging and development, resulting in a serious loss of habitat quality. If this does happen, we expect that competition for resources will increase, leading to more declines in bird populations that depend upon these resources.

Bird-Tick Diseases—While habitat loss of wintering grounds, breeding grounds, and resting and refueling habitats are thought to contribute to declines of some migratory bird populations, little is known about the impact zoonotic diseases (diseases transmitted between humans and animals) may have on declining bird populations.

Our bird-tick disease results confirm that birds are important disseminators of ticks carrying Lyme disease. If a tick feeds on an infected bird, it could carry the bacterium to another animal, including a human. An infected tick could also hitch a ride on a bird and then drop off somewhere along the migration route, possibly setting up a new infection center or contributing to a center already established. This may explain, in part, how this disease has been able to move rapidly throughout the United States and across short and long distances.

Birds may also be competent reservoir hosts for Lyme disease spirochetes. For example, Richter et al. (2000) recently found that captive American Robins infected with the Lyme bacterium become as infectious for vector ticks as do reservoir mice, but infectivity in robins wanes more rapidly. However, robins remain susceptible to reinfection, became infectious again, and permitted repeated feeding by vector ticks. Research is needed to determine whether robins and other birds are important disease reservoirs under natural conditions.

In a more recent study on our Fifield study site, Larson (2000) reported the first evidence of granulocytic ehrlichiosis (GE) infection of two Dark-eyed Juncos, one American Goldfinch, and 40 rabbit ticks removed from birds. His

results suggest that migratory birds may play a role in the geographic expansion of GE and that rabbit ticks may be important in maintaining enzootic cycles of GE in northern Wisconsin. We suggest that more work needs to be done on the role migratory birds play in the dissemination of tick-borne zoonotic diseases and the potential impact they may have on bird populations themselves.

Vegetation Structure—In general, we found that the more diverse a community or habitat was in plant species composition and physical and foliage structure, the more bird species and individuals we found using it. This was certainly true in our Wetland, Mixed Deciduous-Conifer, and Upland Deciduous communities, the complexity of which allowed many individual birds and species to utilize available resources to help meet their energetic requirements. This does not mean that less complex communities, such as our Lowland and Upland Conifers were unimportant, as they also served some species well, as illustrated by the Red Pine habitat.

Red Pine habitat (Figure 3) had by far the least vegetative diversity and structure of all of the 15 habitats and, as a result, we expected little use of that habitat. In fact, it was used very little except by flocks of migrating Eastern Bluebirds in the fall that were caught in the middle of the plantation while feeding on sawflies that were feeding on pine needles. One normally expects bluebirds to be feeding out in open grasslands with scattered shrubs and not in the middle of a dense conifer plantation. But the bluebirds were opportunistic and versatile enough to uti-

lize the sawfly outbreak to their refueling advantage.

Versatility—In songbird management, we must consider that species range from generalists to specialists. The less versatile a species is, the less the margin for errors in management. When managing habitats for migrating birds, it is important to provide all of the resources each species needs to refuel and to successfully complete its migratory journey. Given the diversity of migratory species, each with their own, often unique, resource requirements, it seems prudent to conserve, restore, or develop a mosaic of communities that accommodate the needs of all songbirds during migration.

Habitat Conservation—Stopover habitat conservation is important because, unless habitat requirements during migration are met, conservation measures that focus on temperate breeding grounds and neotropical wintering areas will be compromised (Dunne et al. 1989). Migratory songbirds have a three-part life cycle that includes time in their wintering area, their breeding area, and time spent in between these two areas (Craves 1997). They spend about 30% of their time on breeding grounds and the rest of their time on wintering grounds and in migration. Many neotropical migratory birds fly over 1,000 miles from wintering to breeding grounds. The energy used to make such a trip requires that birds stop to rest and refuel several times before they reach their destination. As more and more migration habitats are lost, birds must use extra energy to find suitable habitat for refueling; if they can't find quality habitat to refuel, they won't survive the trip. If they do make

it to their destination, they may arrive in such poor condition that they will be unable to set up territories, breed, nest, and raise young.

The rigors of migration often place birds close to their physiological limits in unfamiliar landscapes where they do not have the luxury of selecting alternative habitats (Moore et al. 1993). Migrant birds have to choose habitats repeatedly during migration, often finding themselves in different habitats day to day and year to year. Migration is something akin to Russian roulette: making the wrong choice can be disastrous, especially for inexperienced hatching-year birds migrating for the first time.

For many species, adults migrate at different times than young of the year, so the young often do not have the benefit of adult experience. Death during migration can take a heavy toll; it has been estimated that up to half of all migrants heading south in fall will not return to breed the following spring (Craves 1997). A comprehensive plan to reduce en route migration mortality and reproductive failure has been outlined by Moore et al. (1993, 1995). Their plan provides guidelines and recommendations for migratory bird habitat conservation and management according to geographical scale that can be used to plan much-needed migration habitat conservation efforts. Our study supports these efforts, having shown that protecting wetland habitats in northern Wisconsin, in particular, and a mosaic of habitats, in general, will be important to the conservation of songbirds during migration.

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Appendix 1. Common and scientific names of all plant species mentioned in the text. Scientific names are according to Voss (1972, 1985, and 1996) for monocots and dicots, and according to Morin (1993) for Pteridophytes and Gymnosperms.

Common Name	Scientific name
Balsam fir	<i>Abies balsamea</i>
Barren strawberry	<i>Waldsteinia fragarioides</i>
Beaked sedge	<i>Carex rostrata</i>
Bebb's willow	<i>Salix bebbiana</i>
Big-tooth aspen	<i>Populus grandidentata</i>
Black cherry	<i>Prunus serotina</i>
Black spruce	<i>Picea mariana</i>
Blue bead lily	<i>Clintonia borealis</i>
Blueberry	<i>Vaccinium angustifolium</i> , <i>V. myrtilloides</i>
Blue-joint grass	<i>Calamagrostis canadensis</i>
Bracken fern	<i>Pteridium aquilinum</i>
Bunchberry	<i>Cornus canadensis</i>
Canada mayflower	<i>Maianthemum canadense</i>
Chokecherry	<i>Prunus virginiana</i>
Small cranberry	<i>Vaccinium oxycoccus</i>
Creeping snowberry	<i>Gaultheria hispidula</i>
Dewberry	<i>Rubus hispidus</i>
Goldthread	<i>Coptis trifolia</i>
Hazlenut	<i>Corylus americana</i> , <i>C. cornuta</i>
Hemlock	<i>Tsuga canadensis</i>
Labrador tea	<i>Ledum groenlandicum</i>
Lady fern	<i>Athyrium filix-femina</i>
Large-leaved aster	<i>Aster macrophyllus</i>
Leatherleaf	<i>Chamaedaphne calyculata</i>
Leatherwood	<i>Dirca palustris</i>
Meadow willow	<i>Salix petiolaris</i>
Meadowsweet	<i>Spiraea alba</i>
Orange hawkweed	<i>Hieracium aurantiacum</i>
Paper birch	<i>Betula papyrifera</i>
Partridgeberry	<i>Mitchella repens</i>
Pennsylvania sedge	<i>Carex pensylvanica</i>
Pink lady's slipper	<i>Cypripedium acaule</i>
Princess pine	<i>Lycopodium obscurum</i>
Quaking aspen	<i>Populus tremuloides</i>
Red maple	<i>Acer rubrum</i>
Reed canary grass	<i>Phalaris arundinacea</i>
Round-lobed Hepatica	<i>Hepatica americana</i>
Running pine	<i>Lycopodium lagopus</i>
Soft rush	<i>Juncus effusus</i>
Speckled alder	<i>Alnus rugosa</i>
Sphagnum moss	<i>Sphagnum</i> spp.
Starflower	<i>Trientalis borealis</i>
Sugar maple	<i>Acer saccharum</i>
Tamarack	<i>Larix laricina</i>
Three-leaved Solomon's seal	<i>Smilacina trifolia</i>
Violet	<i>Viola</i> sp.
White cedar	<i>Thuja occidentalis</i>
White pine	<i>Pinus strobus</i>
White spruce	<i>Picea glauca</i>
Wild sarsaparilla	<i>Aralia nudicaulis</i>
Wintergreen	<i>Gaultheria procumbens</i>
Wood fern	<i>Dryopteris intermedia</i>
Wool grass	<i>Scirpus cyperinus</i>
Yellow birch	<i>Betula alleghaniensis</i>

Appendix 2. Detailed descriptions of specific habitats within the Fifield study area's five general community types. See Figure 1 for location within the study area.

Upland Deciduous Community:

Aspen (19 acres) was a mature stand of quaking and big-tooth aspens with an understory of sugar maple, balsam fir, leatherwood, and black cherry. The dominant ground cover vegetation consisted of large-leaved aster, barren strawberry, round-lobed Hepatica, and sugar maple seedlings.

Aspen Road (19 acres) was also a mature stand of quaking and big-tooth aspen. However, it had a more open understory than Aspen, consisting of hazelnut, scattered balsam fir, and leatherwood. The ground cover was predominantly composed of sugar maple seedlings, starflower, barren strawberry, Pennsylvania sedge, bracken fern, and large-leaved aster.

Northern Hardwoods (5 acres) consisted of a mature stand of sugar and red maples and yellow birch, with a dense understory of balsam fir, white pine, maple, hazelnut, and choke cherry. The ground cover consisted mostly of Pennsylvania sedge, large-leaved aster, round-lobed Hepatica, Canada mayflower, bunchberry, and sugar and red maple seedlings.

Paper Birch (4.5 acres) was a mature stand of paper birch with a dense understory of hazelnut, balsam fir, sugar maple, and black cherry. The ground cover consisted primarily of large-leaved aster, round-lobed hepatica, partridgeberry, red and sugar maple seedlings, and bracken fern.

Lowland Conifer Community:

Black Spruce (9 acres) was a well-spaced stand of pole-sized black spruce with a few scattered tamarack on a site where the soil was saturated most of the year. There was essentially no understory. The ground cover consisted predominantly of Sphagnum moss, with creeping snowberry, three-leaved Solomon's seal, blueberry, small cranberry, pink lady's slipper, wintergreen, and scattered patches of Labrador-tea.

Hemlock (8.75 acres) was a dense, closed-canopy stand of hemlock with scattered big-tooth aspen occurring as super-canopy trees. The sparse ground cover consisted of princess pine clubmoss, lady fern, Canada mayflower, blue bead lily, and aspen seedlings. The soils were slightly drier than those of other lowland conifer stands, except after winter snow-melt and heavy rains.

Mixed Conifer (6.5 acres) was a stand of balsam fir, white cedar, hemlock, white spruce, and white pine, bordered on three sides by an alder shrub swamp. The dense understory was predominantly speckled alder, hazelnut, and willow. Sphagnum moss, princess pine clubmoss, running pine clubmoss, goldthread, and bunchberry were the most common ground cover vegetation.

Tamarack (1.5 acres) consisted of a stand of mature tamarack with scattered black spruce and no understory. The ground cover was predominantly Sphagnum moss, Labrador-tea, blueberry, and creeping snowberry.

Mixed Deciduous-Conifer Community:

Lowland Mixed Deciduous-Conifer (11 acres) was a mixed stand of balsam fir, quaking aspen, and scattered white pine, with an understory of balsam fir, sugar maple, hazelnut, and black cherry. Bunchberry, wood fern, blue bead lily, dewberry, and barren strawberry were the dominant ground cover species.

Upland Mixed Deciduous-Conifer (2.5 acres) was a mixed stand of big-tooth and quaking aspen, paper birch, and red maple with an understory of white pine, balsam fir, hazelnut, and choke cherry. The ground cover was primarily composed of red and sugar maple seedlings, Pennsylvania sedge, bracken fern, large-leaved aster, and barren strawberry. A seasonal creek flowed through the area.

Wetland Community:

Alder Shrub (5 acres) consisted mostly of dense speckled alder with scattered, slow-growing sapling and pole-sized paper birch, tamarack and black spruce. Sphagnum moss, leatherleaf, blue-joint grass, and the beaked sedge, were the primary ground cover species.

Willow Shrub (1 acre) was a dense shrubby habitat containing mostly Bebb's willow, with some alder and pockets of black spruce and tamarack trees. Ground cover consisted of primarily blue-joint grass, reed canary grass, wool grass, Sphagnum moss, bunchberry, and common blueberry.

Sedge Meadow (1 acre) was an open meadow of blue-joint grass, reed canary grass, soft rush, three-leaved Solomon's seal, and Sphagnum moss. Thickets of meadowsweet, alder, and Bebb's and meadow willows bordered the open canopy wet meadow.

(continued)

Appendix 2. (*continued*)**Upland Conifer Community:**

White Pine (3.5 acres) was a naturally-regenerated, approximately 26-year-old stand of white pine with a few balsam fir and paper birch. The sparse understory consisted of a few younger white pine and balsam fir. The ground cover was mostly needle litter with a few Canada mayflower, orange hawkweed, violets, wild sarsaparilla, and bracken fern where some light penetrated to the forest floor.

Red Pine (3 acres), which was hand planted in 1960, consisted of rows of red pines approximately 6 ft apart. There was no understory, and needle litter covered the ground.



Northern Saw-whet Owl by *Dennis Malueg*