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Avian Succession on Lake Michigan Sand Dunes

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by

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INTRODUCTION

Lake Michigan sand dunes have long been the subject of ecological study. Plant succession has been well documented for sand dunes on the southern end of Lake Michigan (Cowles, 1899; Olson, 1958). Both Cowles and Olson found plant succession would usually begin with pioneer vegetation such as beach grass (Ammophila breviligulata), sand reed (Calamovilfa longifolia), and little bluestem grass (Andropogon scoparius). Cottonwood (Populus deltoides) and various shrubs often helped in the stabilizing process. Typically jack pine (Pinus Banksiana) or white pine (Pinus Strobus) invaded the pioneer plants and were rather quickly replaced by black oak (Quercus velutina). Olson (1958) found that the black oak community appeared to be relatively stable and suggested the "climax" beech-maple communities may not develop except in special mesophytic sites.

Succession on west Michigan sand dunes follows this "normal" sequence through the pine stage. As one proceeds north, however, black oak becomes increasingly rare along the lake shore. Northern red oak (Quercus borealis), which Olson found only in mesophytic pockets at the southern end of Lake Michigan, seems to invade the pine communities instead of black oak. Northern red oak communities, being more mesic than black oak forests, may be more likely to develop into climax beech-maple communities. At least,

beech-maple is much less restricted to favorable microclimates here than it is further south. On west Michigan sand dunes beech-maple (with hemlock added as one proceeds north) is considered the climax community for most sites.

Thus, while plant succession on sand dunes is now reasonable well understood bird succession has been virtually ignored. It is the purpose of this paper to present bird communities associated with various west Michigan sand dune communities and interpret these data from a successional viewpoint.

METHODS

Four study areas representing stages of Lake Michigan sand dune succession were surveyed during the 1974-75 winter. The plots ranged in size from 9.6 hectares (23.7 acres) to 10.2 hectares (25.3 acres). Wood stakes were placed every 80 meters to mark a grid which was then reproduced on paper. Each plot was censused eight to ten times from late April through July with the majority of censuses in May and June. In addition two night censuses were taken in June in all the plots except the beach grass-cottonwood community. The total number of hours spent in censusing ranged from 25 (beach grass-cottonwood) to 40 (oak-beech-maple-hemlock).

A typical census began at sunrise with the observer traversing the grid carrying a map of the area. Symbols were placed on the map to represent locations of singing males, females, young, nests, and territorial conflicts. Information from each daily census was placed on a composite map for each species. The territories of individual males soon became apparent on composite maps. A tape recorder was carried on every census. Where territories were vague the song of the species in question was played. The territorial song would often not only rouse a silent male into revealing its presence but also stimulate other acti-

vity which aided determination of territory boundaries. On several occasions two males responded to the tape in an area which previously had been thought to be one territory. In calculating density, fractions were used for territories which extended outside the grid.

This is the familiar "spot-map method" of Williams (1936). Best (1975) has suggested that this method can produce highly variable estimates of absolute numbers due to observational and interpretational biases. Despite potential biases, the spot-map method is a useful tool for estimating breeding bird populations. Error can be reduced by increased observation of individual birds and regular use of a tape recorder to clarify territories.

A rough estimate of tree composition in each forested grid was obtained by recording all trees over 5 inches dbh along several lines of random compass directions. A percentage based on number of individuals is given. All plant names were taken from Gleason and Cronquist (1963).

Diversity was measured using the index H' which is calculated from the equation $H' = \sum_{i=1}^{S} p_i - \log_e p_i$, where p_i is the proportion of the $_i$th species in the total population, and s is the total number of species (Shannon and Weaver, 1963). This diversity index is influenced both by species richness and relative abundance (equitability or evenness). The relative abundance component is often expressed a J' and is calculated from the formula $J' = H'/H'_{max}$ where H'_{max}

is the natural logarithm of the total number of species in the population. In calculating H' and J' species in Table 1 whose densities were impossible to determine were not included

A unique feature of sand dune communities when compared to similar communities inland is their close proximity to a large body of water. Since beaches may serve as a potential source of food and water it was decided to determine to what degree beaches are utilized by the avian component of adjacent communities. Three of the study areas had similar vegetation extending for considerable distances along the Lake Michigan shoreline. A cruise method, in which the observer walked briskly for 100 meters and then swept the beach ahead with binoculars was used. Care was taken to avoid double-counting birds pushed ahead of the observer or those counted beyond each 100 meter interval. A stop watch was used to record time. This method worked reasonably well when birds were few but its accuracy decreased during heavy utilization. Fortunately heavy avian utilization was the exception rather than the rule. Each beach was censused 3-5 times in June and July.

DESCRIPTION OF THE STUDY AREAS

Beach Grass-Cottonwood Area

The beach grass-cottonwood community was located south of Saugatuck Channel in Saugatuck Township, Allegan County (W½, Sec. 4, R 16 W, T 3 N). Lake Michigan lay to the west with the Kalamazoo River to the north. On the east side a marshy area associated with the river was visible. To the south the community became more wooded until some large established dunes were reached.

The 9.6-hectare (23.7-acre) plot contained small dunes, several ponds, and a few blowouts. The dominant plant was beach grass. Scattered cottonwoods were also present. The ponds (approximately 9% of the total surface area) remained rather constant throughout the study period; however, they have shown fluctuation in extent and depth over the past decade (Scott van Leeuwen, personal communication to R. Brewer). Other plants in the study area were sand-cherry (Prunus pumila), little bluestem grass, wormwood (Artemisia caudata), hairy puccoon (Lithospermum arvense), dwarf juniper (Juniperus communis), riverbank grape (Vitis riparia), dune willow (Salix glaucophylloides), creeping juniper (Juniperus horizontalis), horse-mint (Monarda punctata), and goldenrod (Solidago spp.). Sedges (Carex spp.), rushes (Juncus spp.), and scouring rush (Equisetum hyemale) were associated with the ponds.

Jack Pine Area

The jack pine community was located in Muskegon State Park just north of the Muskegon Channel (NE ¼ of NW ¼, Sec. 28, R 17 W, T 10 N). To the west an open dune area lay between the study area and Lake Michigan. The jack pine gradually merged into deciduous woodland to the north. A campground was located outside the study area in jack pines to the east. The study area consisted of a dense forest of jack pine 10-15 meters high. The jack pine tended to grow in the lower, protected areas leaving the ridges and dunes bare. Because of this the forest covered only 50% of the study plot with the remainder more or less open and similar to the beach grass-cottonwood community. Scattered ponds were found throughout the wooded area. Groups of dead jack pine were often found in or around these ponds. Other plants found in the study area were northern red oak, white pine, black cherry (Prunus serotina), willow (Salix sp.), cottonwood, riverbank grape, goldenrod, milkweed (Asclepias syriaca), false solomon's seal (Smilacina stellata), wormwood, hairy puccoon, beach grass, sand-cherry, and little bluestem grass. The plot measured 320 meters square or 10.2 hectares (25.3 acres).

Small Oak Area

Because black oak becomes rare along the shoreline as one proceeds north, data from two inland oak forests

were used for comparative purposes. Both of these forests developed on old Lake Michigan sand areas.

The small oak area was censused in 1966 (Gottshall, 1969). It is located three miles northwest of Allegan on 118th Avenue (SE ¼ of SW ¼, Sec. 16, R 14 W, T 2 N). The plot is generally flat compared to the four along the lake. It did, however, have a 20-foot ridge running across the southwest third of the area. White oak (Quercus alba) and black oak make up 97% of the larger trees. The canopy was approximately 12-16 meters high. The forest contained sparse cover for low-nesting birds. Other plant species found were cherry (Prunus sp.),white pine, flowering dogwood (Cornus florida), and sassafras (Sassafras albidum). The plot was 6.7 hectares (16.5 acres). A more detailed description can be found in Brewer et al. (1973).

Large Oak Area

This plot totaled 7.5 hectares (18.4 acres) and was censused during three breeding seasons (1966-1968) by Wenger (1970). The last census was arbitrarily used for comparison. Topography was the flattest of all six areas. It is located west of the city of Allegan in Valley Township, Allegan Co. (W ½ of NW ¼, Sec. 30, R 14 W, T 2 N). Essentially a black oak forest it differed from the small oak area in having larger trees with greater spacing and a relatively diverse understory consisting of white pine, black oak, white oak, sassafras, black cherry, red maple (Acer rubrum), and flow-

ering dogwood. A more detailed description is given by Brewer et al. (1973).

Oak-Beech-Maple-Hemlock Area

The oak-beech-maple-hemlock study area consisted of 10.2 hectares (25.3 acres) of land owned by the Presbytery of Chicago. It is located just south of Mt. Baldhead in Saugatuck Township, Allegan County (NW ¼ of SW ¼, Sec. 9, R 16 W, T 3 N). Topography is extremely rugged consisting of several large dunes surrounded by ridges, smaller dunes, and valleys. Very few flat areas exist. Approximately 35% of trees over 5 inches dbh were northern red oak. Other dominant trees were beech (Fagus grandifolia) 25%, sugar maple (Acer saccharum) 20%, and hemlock (Tsuga canadensis) 20%. The canopy was approximately 20 meters high. A well-developed understory of sugar maple and hemlock was present in most areas. Ground cover was well developed on the slopes becoming thicket-like in places. It was much less developed in other areas. Typical ground cover plants found on slopes were common greenbrier (Smilax rotundifolia), arrow-wood (Viburnum acerifolium), and riverbank grape. Other species encountered were white oak, hickory (Carya sp.), witch hazel (Hamamelis virginiana), false solomon seal (Smilacina racemosa), hepatica (Hepatica americana), spring beauty (Claytonia virginica), wintergreen (Gaultheria procumbens), baneberry (actaea alba), dutchman's breeches (Dicentra Cucullaria), squirrel-corn (Dicentra canadensis),

and late-flowering thoroughwort (Eupatorium serotinum).

Beech-Maple-Hemlock Area

The beech-maple-hemlock study area totaled 10.2 hectares (25.3 acres). It was located on private land along Lake Michigan in Laketown Township, Allegan Co. (S ½ of SE ¼, Sec. 16, R 16 W, T 4 N). Topography is similar to the previous plot. Approximately 80% of the trees over 5 inches dbh are beech and sugar maple. The remaining 12% included northern red oak, black cherry, hickory, basswood (Tilia americana), sassafras, and hornbeam (Carpinus caroliniana). Ground cover is also similar to the previous study area being dense on slopes and crests and becoming sparse in low areas. Its understory differs in that it is mostly maple with less hemlock. Hemlock tended to occur in aggregations along the north-facing slopes much more frequently here than in the oak-beech-maple-hemlock community. Other species found were common greenbrier, riverbank grape, poison-ivy (Rhus radicans), gooseberry (Ribes sp.), false solomon seal (Smilacina racemosa), Solomon seal (Polygonatum biflorum), arrow-wood, hepatica, dutchman's breeches, and squirrel-corn.

RESULTS AND DISCUSSION

Breeding Bird Populations

Beach grass-cottonwood community

Sparrows were the dominant inhabitants of the beach grass-cottonwood community, comprising 45% of the total number of individuals (Table 1). The high density of Red-winged Blackbirds was due to the large amount of ponded water in the study area. Eastern Kingbirds and Starlings utilized the cottonwood trees for nesting while Brown Thrashers used small thickets often found associated with the cottonwood trees. One Mallard nest was found in dense beach grass.

An additional species, the Prairie Warbler, could also be considered an inhabitant of this successional stage. Two males were heard repeatedly throughout the breeding season in a slightly more overgrown area just south of the study plot. Walkinshaw (1959) gives the Prairie Warbler's nesting habitats as "brushy fields, areas grown to brush which have burned five to ten years earlier, or brush grown sand dunes." In southern Michigan, although not throughout its range (which is largely south of the state), the Prairie Warbler seems almost wholly restricted to sand dune vegetation (R. Brewer, personal communication).

The open nature of the beach grass-cottonwood community

Table 1. Territorial males per 100 acres in study plots.[1]

Species	BC	JP	SO	LO	OBMH	BMH
Field Sparrow	21.1	-	-	-	-	-
Starling	6.3	-	-	-	-	-
Killdeer	2.5	-	-	-	-	-
Red-winged Blackbird	21.1	14.2	-	-	-	-
Song Sparrow	12.7	6.3	-	-	-	-
Vesper Sparrow	11.4	8.7	-	-	-	-
Mallard	8.4*	7.9*	-	-	-	-
Brown Thrasher	6.8	13.8	-	-	-	-
Eastern Kingbird	4.6	6.7*	-	-	-	-
Brown-headed Cowbird	6.3*	7.9*	+	5.4	4.0*	7.9*
House Wren	-	6.7	-	-	-	-
Rufous-sided Towhee	-	2.0	-	-	-	12.3
Chipping Sparrow	-	3.6	-	-	-	-
Northern Oriole	-	7.9	12.7	5.4	-	-
Mourning Dove	-	7.5	-	-	9.1	-
Cardinal	-	13.4	+	-	13.4	15.8
American Robin	-	7.9	-	3.8	17.0	14.2
Blue Jay	-	7.9	12.1	5.4	13.0	9.9
Great Crested Flycatcher	-	5.1	7.3	6.0	12.3	4.0
Black-capped Chickadee	-	5.1	20.6	4.3	13.0	5.9
Cuckoo (Yellow and Black-billed)	-	-	12.7	7.6	-	-
Ruffed Grouse	-	-	+	-	-	+
Scarlet Tanager	-	-	15.8	20.7	12.6	19.4
Ovenbird	-	-	13.3	4.9	18.6	23.7
White-breasted Nuthatch	-	-	11.5	9.8	15.0	5.9
Tufted Titmouse	-	-	10.3	3.3	7.9	8.7
Eastern Wood Pewee	-	-	10.3	15.2	18.2	22.5
Red-eyed Vireo	-	-	9.1	19.0	23.2	22.5
Wood Thrush	-	-	9.1	+	25.7	24.1
Downy Woodpecker	-	-	1.8	5.4	8.7	9.1
Rose-breasted Grosbeak	-	-	+	23.9	6.7	20.0
Common Flicker	-	-	+	5.4	7.9	6.3
Blue-gray Gnatcatcher	-	-	-	3.8	-	-
Yellow-throated Vireo	-	-	-	.5	-	-
Red-bellied Woodpecker	-	-	-	+	-	-

[1]BC indicates beach grass-cottonwood plot; JP, jack pine plot; SO, small oak plot; LO, large oak plot; OBMH, oak-beech-maple-hemlock plot; BMH, beech-maple-hemlock plot. A plus indicates bird was present on grid but density was impossible to determine.
* indicates estimated density.

Table 1. (continued)

Species	BC	JP	SO	LO	OBMH	BMH
Hairy Woodpecker	-	-	-	3.8	2.0	5.1
Wood Duck	-	-	-	+	+	+
Blackburnian Warbler	-	-	-	-	7.9	-
Great Horned Owl	-	-	-	-	+	-
Acadian Flycatcher	-	-	-	-	8.3	19.7
American Redstart	-	-	-	-	.8	41.9
Ruby-throated Hummingbird	-	-	-	-	+	+
Black-throated Green Warbler	-	-	-	-	-	14.6
Veery	-	-	-	-	-	7.9
Hooded Warbler	-	-	-	-	-	4.0
Red-tailed Hawk	-	-	-	-	-	+
Worm-eating Warbler	-	-	-	-	-	+

made it easy to observe visitors which utilized the area for feeding. The swallow family was the best represented. Barn Swallows, Tree Swallows, Purple Martins, and Bank Swallows were seen regularly. Bank Swallows nested in a wave-cut cliff adjacent to the study area. Other visitors included Common Grackles, Northern Orioles, Common Flickers, Mourning Doves, Black-capped Chickadees, and American Robins.

Studies of open sand dune communities elsewhere indicate that these areas generally contain few species and never reach high breeding densities. Densities can be variable, however, depending on the amount of water present, type of vegetation, and nature of adjacent communities. A number of breeding bird censuses have been conducted on open sand dune communities of Long Point, Ontario, a spit of sand running easterly 20 miles into Lake Erie from the Canadian shore. Bernstein, Harris, McGowan, Miller, Moses and Schugar (1974) censused a beach and adjacent grass and sandy ridge of cottonwood trees on Long Point and found it practically devoid of nesting birds. Other Long Point censuses of areas containing only dune grasses and occasional cottonwood trees also reported low densities of 6 to 8 males per 100 acres.(Evans and Nakashima, 1973; Moses, Harris, Schugar, Bernstein, Miller, McGowan, 1974). The few species found utilizing this marginal habitat for nesting were Mallards, Spotted Sandpipers, Red-winged Blackbirds, and Eastern Kingbirds.

Long Point censuses of communities containing damp areas, ponds, and shrubs reported higher breeding populations. Moses, Harris, Schugar, Bernstein, Miller, and Mc Gowan (1974) reported a density of 154 males per 100 acres in a dry juniper-cottonwood savannah which had adjacent marsh and open water. Species often found in these shrubby stages were Brown Thrasher, Brown-headed Cowbird, Field Sparrow, Song Sparrow, Vesper Sparrow, Chipping Sparrow, and Killdeer. Common Grackles may also nest but do not appear to be consistent inhabitants. The study of Moses et al. (1974) reported 44 male Common Grackles per 100 acres in 1974; in 1973 none had nested there (Evans, 1973). Perhaps for some species these areas may serve as marginal nesting habitat for surplus birds from surrounding areas.

Species which may be classified as occasional open dune nesters are Mourning Dove, American Robin, Eastern Meadowlark, Blue-winged Teal, and Black Duck. Hole-nesters (Common Flicker, Tree Swallow, and Starling) will also nest if sufficient sites are available. Species which apparently are rare inhabitants are the Prairie Warbler, Mockingbird, and Common Yellowthroat.

An apparent characteristic of this stage is large fluctuations of breeding bird populations from year to year. This may be partly caused by the presence of surplus birds mentioned previously. Cobus, Davis, Fairfield, Holroyd, and Montgomery (1965) found a density of 29 males per 100

acres on a Long Point sand dune with scattered cottonwood trees. In 1969 the same area contained 64 males per 100 acres (Bradstreet, Page. 1969). The change was due largely to an increase in Eastern Kingbirds, Starlings, and Eastern Meadowlarks. The dry juniper-cottonwood savannah mentioned previously contained 154 males per 100 acres in 1974 (Moses et al. 1974). In 1973 the same plot contained only 59 males per 100 acres (Evans, 1973). The higher density in 1974 was due mainly to an increase in Common Grackles and Red-winged Blackbirds (neither nested in 1973), Field Sparrows and Mallards.

Jack pine community

Seventeen species nested in the jack pine community. Due to the presence of permanent water the Red-winged Blackbird was again the most abundant species although it did not reach the high density attained in the more open beach grass-cottonwood community. Brown Thrashers and Cardinals were the next most abundant species. Although Kendeigh (1948) notes that Brown Thrashers are usually not characteristic of pine communities the combination of dense jack pine interspersed with occasional open areas evidently meets their requirements. Nests of Brown Thrashers were found in jack pine as were also nests of Mourning Doves. Cardinals, American Robins, and Blue Jays. The presence of the Northern Oriole is interesting as it is usually considered a species of

deciduous communities. Bond (1957) notes its preference for pioneer deciduous communities. No nests were found but nesting in coniferous trees has been reported (Eaton, 1914). Another puzzling phenomenon associated with this species was occasional invasions of small flocks, mostly males, into the jack pine community. The largest group was observed on June 9 when at least ten males remained in the area throughout the morning. It is possible that these were unmated birds unable to establish territories in surrounding deciduous woodland. No similar groups were seen in the oak forests (R. Brewer, personal communication), where the species nested, nor the mesic forests where it did not.

Owing to the heterogeneity of this plot half the area was suitable to members of the beach grass-cottonwood community. Only three species (Field Sparrow, Starling, and Killdeer) dropped out, and these were all present outside the grid. This structural characteristic also accounts for the good representation of forest-edge species.

Many visiting species used the community for feeding during the breeding season. These included Common Grackles, Northern Orioles, Barn Swallows, Purple Martins, Tree Swallows, Belted Kingfishers, American Goldfinches, Green Herons, Spotted Sandpipers, and a Red-eyed Vireo on June 9.

Breeding bird populations in jack pine communities vary considerably depending on such factors as the age of the community, latitude, and type of vegetation which comes

into the jack pine. Munn (1974) found a density of 78 males per 100 acres in young jack pine barrens in Oscoda County, Michigan. Most common species were the Brown Thrasher, Vesper Sparrow, Chipping Sparrow, Field Sparrow, and Eastern Bluebird. A three-year census in the same county on an older plot reported an average of 140 males per 100 acres (Van Tyne et al., 1942, 43, 44). This pine barrens contained considerable deciduous growth and some open areas. Chipping Sparrows were the most common along with Brown Thrashers, Kirtland's Warblers, Clay-colored Sparrows, Prairie Warblers, and Vesper Sparrows.

A more northern mature jack pine forest in St. Louis County, Minnesota, yielded higher densities (169 males per 100 acres) and a much different avian composition (Niemi, 1974). Ovenbirds were the most common (40 males per 100 acres) followed by Blackburnian Warblers (34 males per 100 acres), Nashville Warbler, Golden-crowned Kinglet, Yellow-bellied Sapsucker, and Chipping Sparrow. Evidently, avian density increases as jack pine matures. Much of the difference in species composition is due to the difference in latitude (Blackburnian Warbler, Nashville Warbler, Golden-crowned Kinglet, and Yellow-bellied Sapsucker are considered northern species) and maturity of the forest.

Kammeraad (1963, 64) found much lower densities in a jack pine-deciduous forest on sand dunes located close to the author's jack pine community. This xerophytic forest

(67% jack pine and 23% northern red oak) contained 59 males per 100 acres in 1963 and 87 males per 100 acres in 1964. Over a 2-year average Chipping Sparrows were the most common followed by the Common Flicker, Black-capped Chickadee, and Eastern Wood Pewee. Disregarding the Red-winged Blackbird, Brown Thrashers and Cardinals declined the most as northern red oak invaded the jack pine community.

Small oak community

Both oak communities lacked close proximity to Lake Michigan and typical sand dune topography. Thus they may or may not be representative of true sand dune communities. The change from coniferous to deciduous woodland is reflected in the avian composition as twelve new species were added and eleven drop out. Only seven species (Northern Oriole, Brown-headed Cowbird, Cardinal, Blue Jay, Great Crested Flycatcher, and Black-capped Chickadee) were present in both the jack pine and small oak communities. The Black-capped Chickadee was the most abundant species and also reached a peak in this stage. The Scarlet Tanager and Ovenbird were the second and third most abundant species respectively. Other species which reached peaks in this stage were the Northern Oriole, Cuckoo, and Tufted Titmouse.

The four species reaching peaks in this stage support Bond's findings regarding them as favoring xeric stands (Bond, 1957). The preference of the Tufted Titmouse, how-

ever, is not as clear as the other three. In Bond's study of southern Wisconsin forests the Tufted Titmouse was uncommon. In this study densities almost as high as the small oak stage were reached in the last two mesic forests.

The absence of the American Robin is interesting as its presence in all other forested study areas suggest a requirement not met by this community. Its low density in the large oak plot is a further indication that xeric oak forests on sand are unsuitable for this species.

Large oak community

Avian composition of the large oak forest was similar to the small oak tract. Sixteen species were common to both areas. Two species (Cardinal and Ruffed Grouse) dropped out, and six species (Wood Duck, Hairy Woodpecker, Red-bellied Woodpecker, Yellow-throated Vireo, Blue-gray Gnatcatcher, and American Robin) were added.

Despite their similarity two conspicuous differences do exist between the two areas. Density of Black-capped Chickadees dropped from 20.6 pairs per 100 acres in the small oak to 4.3 pairs per 100 acres in the large oak. This drop, however, was an unexplained peculiarity of that year and was not typical of the large oak forest generally (Wenger, 1970). A consistent difference (Wenger, 1970; R. Brewer, personal communication) in density of Rose-breasted Grosbeaks between the two forests is not easily explained. Its density was too low to be determined in the small oak

while the large oak contained 23.9 pairs per 100 acres, the maximum density attained by this species in all plots.

Apparently, oak forests on sand are lower in both density and species richness when compared with other deciduous forests. A seven-year average of the Anoka Sand Plain, a jack-oak (Quercus ellipsoidalis) forest, yielded 206 males per 100 acres with 17 species (Mitchell, 1960). This area was comparable to both Michigan oak forests in having oak, sandy soil, and essentially flat terrain. Although this density is greater than the two Michigan forests it is still below those reported for many other temperate deciduous forests.

Black-capped Chickadees, Scarlet Tanager, Red-eyed Vireos, Ovenbirds, and Eastern Wood Pewees were important members of both Michigan oak forests and the Anoka Sand Plain. Differences include Northern Orioles (common in the Michigan forests but absent in the Anoka Sand Plain) and Least Flycatchers (second most common species in the Anoka Sand Plain but absent in both Michigan oak forests). The Rose-breasted Grosbeak was also absent in the Anoka Sand Plain.

More censuses of xeric oak forests on sand dunes are needed to determine if low density and richness are generally true of both inland and lakeshore oak xeric forests.

Oak-beech-maple-hemlock community

The change from uniform oak communities to the oak-

beech-maple-hemlock community is essentially a change from xeric to mesic conditions. The Wood Thrush was the most common inhabitant followed closely by the Red-eyed Vireo. The Acadian Flycatcher, a bird noted for its preference for mesic stands (Bond, 1957; Walkinshaw, 1966), made its first appearance. Two species (Mourning Dove and Cardinal) which were present in the jack pine but absent or unimportant in both oak communities reappeared in the succession.

Two species were found only in this stage. A young Great Horned Owl was found sitting on a fallen log in the southwest corner of the grid on May 27. An adult was sighted on three occasions in the same vicinity. Two Blackburnian Warbler territories were also established on the plot. Wood (1951) gives the present summer range as south to Muskegon and formerly to Kalamazoo County. Thus this represents the extreme southerly limit of this species breeding range. The territory of the first pair included several large hemlock trees. A second pair was discovered a week later and subsequent activity centered around a large white pine. No nests were found for either pair.

Wood Ducks were very conspicuous in early spring but as the season progressed became very difficult to locate, if, indeed, they remained. This was also true of the large oak and beech-maple-hemlock community.

The Common Flicker, American Robin, Blue Jay, Great Crested Flycatcher, White-breasted Nuthatch, Red-eyed Vireo, and Wood Thrush all reached peaks in this stage. Of these

species the Blue Jay and Great Crested Flycatcher attained moderate density in all forested plots. The Red-eyed Vireo along with the American Robin and Wood Thrush all showed a much greater density in the oak-beech-maple-hemlock and beech-maple-hemlock stages.

Censuses of mixed hardwood forests are many and their results vary. Combinations of oak, beech, maple, and various conifers are no exception. Very few sites contain exactly the same composition of plants or conditions. This multitude of variables contributes to a continuing lack of knowledge of habitat selection and community interaction.

A census of a northern red oak-sugar maple forest located on Long Point, Ontario, reported a density of 300 males per 100 acres (Johnston and Fearis, 1973). This community was an earlier successional stage, however, as the canopy was only 70% closed and ground cover consisted mostly of bluegrass (Poa spp.). The gently rolling dune topography also contained several marsh areas. Bird composition was very different from the present study as House Wrens (65 pairs per 100 acres), were the most common species followed by the Eastern Wood Pewee (35 pairs per 100 acres) and Red-winged Blackbird (24 males per 100 acres). Other species were those typical of pioneer forests.

A census of upland oak hardwood forest (40% northern red oak, 20% yellow birch, 20% sugar maple, 10% white pine, and 5% hemlock) on rocky hills in New Hampshire recorded

330 males per 100 acres (Herbert, 1958). This plot was bisected by a highway and therefore included a good number of forest-edge species. Red-eyed Vireos (34 males per 100 acres), American Redstart (23 males per 100 acres), Veery (21 males per 100 acres), and Ovenbirds (21 males per 100 acres) were the most common species. The same forest was censused in 1963 after a superhighway had been built through it (Herbert, 1963). In this census density had dropped to 145 males per 100 acres and the Veery, Red-eyed Vireo, Canada Warbler, and Ovenbird were the most common species.

A white oak-beech-sugar maple forest community on Karst topography in Indiana approximated the present oak-beech-maple-hemlock census in density and composition (Adams and Webster, 1971). Acadian Flycatchers, Red-eyed Vireos, Eastern Wood Pewees, and Wood Thrushes were the most common. A density of 247 pairs per 100 acres was reported.

Beech-maple-hemlock community

In the beech-maple-hemlock community the American Redstart was the most abundant species with the Ovenbird, Eastern Wood Pewee, Red-eyed Vireo, Wood Thrush, and Rose-breasted Grosbeak all reaching densities of 20 males or more per hundred acres. Seven species (Cardinal, Ovenbird, Eastern Wood Pewee, Downy Woodpecker, Hairy Woodpecker, Acadian Flycatcher, American Redstart) reached peaks in this stage. This community also contained the largest

number (5) of unique birds, that is, species found only in one community in the study.

Several puzzling differences arose between the beech-maple-hemlock plot and somewhat similar oak-beech-maple-hemlock area. The most obvious is 41.9 American Redstart territories per 100 acres in the beech-maple-hemlock plot compared to .8 territories in the oak-beech-maple-hemlock site. Bond (1957) found the American Redstart to be most common in intermediate stands rather than climax forests. He suggested that the American Redstart, being a sapling nester, has not only a greater variety of species but also sturdier branches to utilize in intermediate stands. This is true even though the climax forest may have a greater sapling density because most saplings produced in a mature forest would be tall spindly maples which provide less suitable nesting sites. Suitable nesting sites appeared to be ample in both plots in the present study, however, owing to the more open canopy which existed on the slopes and crests of most dunes. Of five American Redstart nests found, all were in maple.

High density figures for the American Redstart have been reported elsewhere. Thirty-seven pairs per 100 acres were found in an almost virgin beech-sugar maple-white pine community in northern lower Michigan (Kendeigh, 1948). Profitt found a density of 60 pairs per 100 acres in a sugar maple-beech-red maple stand in the same area (Kendeigh, 1948).

A summary of bird censuses for forest stands in the central part of eastern North America produced an average of 52 pairs per 100 acres in eastern lowland forests (Webster and Adams, 1972). These high density figures are usually explained in terms of available nesting sites but a low density figure in spite of suitable nesting sites is less easily explained. A few observers have noticed a tendency for American Redstarts to occur in aggregations or to be spotty in distribution in some areas (Kendeigh, 1946).

A similar but less dramatic difference is the presence of Black-throated Green Warblers in the beech-maple-hemlock tract but not in the oak-beech-maple-hemlock area. This species is usually associated with conifers but has shown some adaptiveness by nesting in deciduous trees (Brooks, 1940). In this study a decided preference was shown for hemlock. In early spring 5 males held territories in an almost pure stand of hemlock on the north side of a large dune. By the first week of June three of the males had enlarged their territories displacing two males to areas with less hemlock. The lack of Black-throated Green Warblers in the oak-beech-maple-hemlock grid could be the result of a lack of concentrated hemlock stands or the rarity of the species this far south.

An interesting intermingling of warblers occurred in this community. A pair of Hooded Warblers established a territory on the slope of a large dune. A Worm-eating

Warbler was localized for three weeks on the exteme northwest corner of the grid. These two species represent southern species. The Black-throated Green Warblers along with the Blackburnian Warblers of the oak-beech-maple-hemlock tract represent the northern complement in this intermingling of deciduous and coniferous species.

Both mesic forests contained species which are often considered as forest-edge birds. They also contained a good representation of species which Bond (1957) found to be more typical of earlier successional stages (Downy Woodpecker, Rose-breasted Grosbeak, Cardinal, Blue Jay, and Rufous-sided Towhee).

Forest-edge birds are possibly responding to the scattered hemlock understory which structurally may fulfill all the requirements of true forest edge. Odum (1950) found that the high bird populations of shrubland stages were maintained in hemlock seres but not in the oak-chestnut seres of North Carolina. Since a more open canopy and thick tangles were characteristic of many of the slopes and crests a habitat also suitable to birds of less mature forests is probably achieved in mesic forests of sand dunes.

A comparison with inland beech-maple-hemlock communities reveals a good similarity in species composition. Williams (1947) found the Red-eyed Vireo, Ovenbird, Wood Thrush, Hooded Warbler, American Redstart, and Eastern Wood Pewee to be the six most common species in a beech-maple-hemlock woods in Ohio over a fifteen-year period. The

present study also found this to be true with the exception of the Hooded Warbler which is a more southerly species. Indeed, of the sixteen summer resident species listed by Williams only four (Louisiana Waterthrush, Yellow-throated Vireo, Cerulean Warbler, Eastern Phoebe) were not found in the present study. Williams also found that 11.5% of the breeding bird population was made up of permanent resident species. Of the eleven permanent resident species listed by Williams only three (Barred Owl, Red-bellied Woodpecker, Pileated Woodpecker) were absent in the beech-maple-hemlock community situated on sand dunes.

It would appear that generally beech-maple-hemlock forests on sand dunes will not differ greatly in avian composition from more level inland beech-maple-hemlock forests except for possibly a greater density of forest-edge species or pioneer woodland species on the slopes and crests of the dunes.

Avian Utilization of Beaches

Beach utilization for the three communities which had sufficient similar vegetation along Lake Michigan is summarized in Table 2. The Common Grackle was the most common beach exploiter, especially on the beach adjacent to the beach grass-cottonwood community. Grackles were observed flying over this area from the marshes on the east side of the study area. Usage was especially heavy on two mornings in which many dead alewives (Alosa pseudoharengus) littered the beach. Grackles were observed to grasp an alewife with their claws and rip strips of flesh from the carcass starting just behind the gills. American Robins behaved in sandpiper fashion and were never observed feeding on alewives. Empidonax flycatchers were observed on posts and flycatching over the beach. One landed on the beach after one foray. Female Red-winged Blackbirds occasionally obtained food on the beach throughout the breeding season but no males were seen until late July, when territories were beginning to break up. The few Cardinals and Gray Catbirds counted were in areas where the forest was extending over the water and beach area was almost non-existent.

Overall, beach utilization was slight. The confining aspects of territory, lack of plasticity to exploit new food resources, and/or danger such as predation in an open environment evidently prevent most species from using neighboring beaches as a food resource.

Table 2. Birds encountered utilizing beaches.[1]

Species	Number of Individuals		
	BC	OBMH	BMH
Great Blue Heron	-	-	1
Snowy Egret	1	-	-
Mallard	2	2	3
Spotted Sandpiper	4	6	4
Empidonax Flycatcher	-	-	3
American Crow	-	-	5
Gray Catbird	-	1	2
American Robin	-	8	-
Starling	9	14	6
Red-winged Blackbird	12	-	-
Common Grackle	111	16	5
Cardinal	-	-	3
Song Sparrow	-	17	1
Totals	139	64	33

[1]Total elapsed time for the three censuses were: beach grass-cottonwood=231 minutes; oak-beech-maple-hemlock=211 minutes; beech-maple-hemlock=245 minutes.

Density and Diversity

Studies in avian succession have shown a general increase in number of species (richness) and density (number of birds per unit area) with increasing age of the community (Saunders, 1936; Kendeigh, 1948; Odum, 1950; Karr, 1968; Shugart and James, 1973). These studies have differed, however, as to whether the peak occurs at the end or some intermediate seral stage. In this study both richness and density increased throughout the succession peaking at the final stage (Table 3). Diversity also showed a general increase with age. Care must be exercised in interpreting relativized diversity indices, however, as Peet (1975) has shown that such indices exhibit several undesirable qualities when used for ecological applications.

Tramer (1969) found that in breeding bird populations the diversity index is influenced most by richness. In this study the same was true. Equitability remained stable while both richness and diversity showed a general increase and peaked in the beech-maple-hemlock forest. The jack-pine plot produced a higher-than-expected diversity; this is here attributed to heterogeneity of habitat, including topography, and water. All these traits were lacking in the oak forests.

Since the equitability component influences the diversity index mostly in early seral stages or non-breeding avian populations (Kricher, 1973), richness appears to be

Table 3. Successional trends in study areas.

	BC	JP	SO	LO	OBMH	BMH
Number of species	10	17	18	22	24	28
Density (number of males per 100 acres	101.2	132.6	146.6	153.6	245.3	325.4
Diversity (H')	2.13	2.75	2.48	2.67	2.89	2.95
Equitability (J')	.93	.97	.97	.91	.95	.94
Standing crop biomas (grams per 100 acres)	27,490	31,908	9,608	10,767	19,701	20,196
Standing crop biomass. (passerines only)	6,732	10,302	8,043	7,542	14,226	17,202
Metabolic energy expenditure. (kcal/day)	9,234	11,970	6,766	7,533	12,113	15,273
Metabolic energy expenditure. (passerines only)	5,210	7,657	6,113	6,255	11,387	14,115

a reliable indicator of diversity for territory-maintaining breeding birds. Thus whether or not density, richness, and diversity will increase as a forest matures depends on whether the forest can maintain species from former seral stages while continuing to add more niches so that new species will be added to the population.

Apparently the presence of enough hemlock in both the oak-beech-maple-hemlock and beech-maple-hemlock forest is responsible for maintenance of these parameters. By creating a pseudo-forest-edge environment, increasing foliage height diversity, and allowing both coniferous and deciduous populations to coexist a high density, diversity, and richness is maintained or increased. Maintenance of these parameters is probably also aided by the more pioneer conditions found on slopes and crests. On sites with different topography and/or soil a trend toward structural uniformity and dominance by beech and maple might lead to an eventual decrease in diversity in some seres of this area.

Biomass and Energetics

Biomass for the six communities was calculated from bird weights taken from the literature. Care was taken to use data from approximately the same latitude and during the breeding season whenever possible. Each territorial male was considered a pair and different weights were used for male and female if available. The number of females of polygynous species was estimated from field observations.

Previous studies have shown avian biomass to increase as the community ages (Johnston and Odum, 1956; Karr, 1968). In this study biomass was the greatest in the beach grass-cottonwood and jack pine communities (Table 3). The biomass of these two communities was due primarily to nesting waterfowl and a high density of Red-winged Blackbirds. When biomass was calculated for the passerine component of each community, a general increase in biomass with age of the community was obtained.

Avian population studies have recently been combined with laboratory work on avian energetics to yield a crude estimate of the avian metabolism component in various communities. Karr (1968; 1971) employed this technique for communities in Illinois and Panama. Criticism centers on the transfer of data from captive restrained laboratory birds to wild bird populations. Holmes and Sturgis (1973), however, have shown that the method can produce results very close to those predicted from energy transfer efficien-

cies.

To compare metabolism through successive stages two equations from Lasiewski and Dawson (1967) were used. The formula $M=129\ W^{\cdot 724}$ was used for passerines and $M=78.3\ W^{\cdot 723}$ for non-passerines. In these equations M=standard metabolic rate in kcal./day while W= the weight of each species in kilograms. These formulas represent metabolism under laboratory conditions. Calculated standard metabolism was multiplied by a factor of 2.5 (Holmes and Sturgis, 1973) to approximate energy expenditure under more natural conditions.

In this study daily energy expenditure showed a general increase as the communities aged. A significant drop occurred in the two oak stages, however. When only the passerine segment of the populations are considered the trend is more evident with the only exception being a higher metabolism recorded for the jack pine community over the two oak stages.

Intermingling of Northern and Southern Species

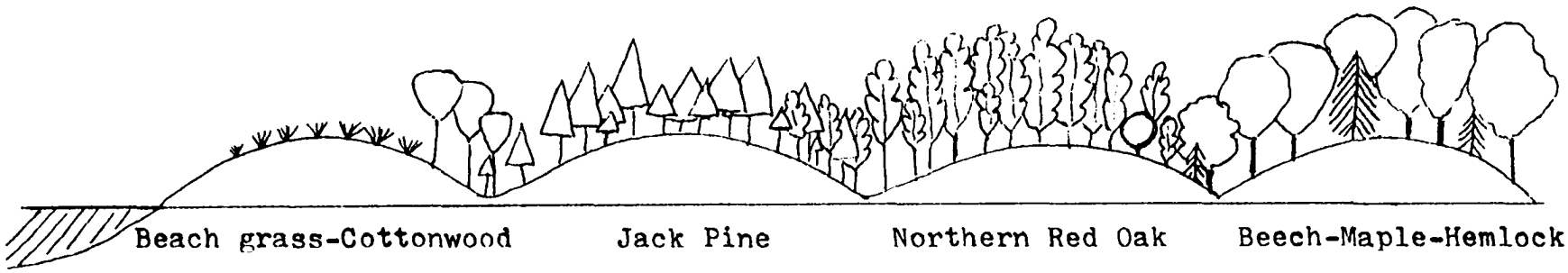
Bird populations established along the west Michigan shoreline are inhabitants of the ecotone between the coniferous biome of the north and the deciduous forest biome of the south. Thus the breeding bird populations are not characteristic of a single biome but are the result of an intermingling of birds from two differing regions of the earth. This intermingling was most evident in the warbler popula-

tions of the two mesic forests studies, and a general impression indicates that it is possibly intensified along the lakeshore. If this general impression is correct, and not simply the result of increased observation along the lakeshore then a northward penetration of breeding range by a southern species would be strongest along the lakeshore. The same would be true for northern species in a southerly direction.

The possible reasons for increased intermingling of southern and northern species are: 1) migration may be strongest along the lakeshore for such species, 2) disoriented individuals may wander until being stopped by Lake Michigan, 3) various climatic factors related to the presence of Lake Michigan, 4) increased presence of suitable vegetation for both northern and southern species.

Fig. 1. Diagram of "normal" succession on west Michigan sand dunes.

Vesper Sparrow	Brown Thrasher	Eastern Wood Pewee	Eastern Wood Pewee
Field Sparrow	Cardinal	Wood Thrush	Wood Thrush
Song Sparrow	Red-winged Blackbird*	Red-eyed Vireo	Red-eyed Vireo
Red-winged Blackbird*		Ovenbird	Ovenbird
		Scarlet Tanager	American Redstart



*Abundant only if water is present.

GENERAL DISCUSSION

Traditionally a sere refers to a series of communities which develop in a predictable sequence in a locality over a period of time. Each distinct community is called a seral stage. The final relatively stable seral stage is usually called the climax. Olson (1958) has shown that on sand dunes a rigidly fixed sequence, despite its frequent use as a pedagogical tool, may often not occur in nature. A variety of pathways may occur in any one site often with setbacks such as fire or blowouts reversing the process.

While the majority of terrestrial successional studies have been vegetational, all groups of organisms will show population changes as the entire community changes. Thus a bird sere, mammal sere, insect sere, etc. should be recognizable. In other words, each distinct community will have a distinct group of species common to that particular community. Table 1 reflects these changes in the bird sere of west Michigan sand dunes (see also Fig. 1). Although considerable overlapping occurs certain species are apt to be found in greater numbers in one particular seral stage than in another. Kendeigh (1948) has suggested that communities may even be classified according to dominant bird species as is commonly done with the dominant vegetation.

The existence of such avian groupings naturally leads one to speculate why certain species are common to a specific

seral stage and to what degree birds may have a part in the successional process. Obviously vegetation is important to most avian activity. Vegetational structure rather than species seems to be more important in habitat selection (Pitelka, 1941; Terborgh and Weske, 1969,). In many instances a bird sere is probably the result of whatever plant structure replaces another and what birds are available and able to utilize that structure. The view of the community as an integrated whole, however, with a maze of subtle relationships would suggest that a bird sere may not be entirely a result of vegetational structure but may be affected by many additional factors such as competition and predation. Sand dune bird seres do not appear to be highly integrated, however, and in most instances are probably the result of vegetational structure.

The role birds may play in succession at present must be largely speculation. Additional studies like those of Smith (1975) might help to clarify matters. Most studies into the why of succession talk only in terms of the mechanics of plant replacement, usually excluding the role of the animal component of the community. If the entire animal segment of a community could be experimentally removed many now unknown subtle relationships might emerge which affect succession. It is possible that at times birds may contribute to successional change even if only to speed up or slow down the process. Control of various insects, destruction of young plants or seed, or seed dispersal would all

affect succession to some extent. Although birds may well serve to introduce seeds of some plants such as cherries, junipers, dogwoods, and sassafras, the overall role of birds in the major features of succession on sand dunes seems minor.

SUMMARY

Bird populations of four west Michigan dune communities representing stages of sand dune succession were censused. Data from two inland oak forests on sand were also included and results were compared with censuses from similar communities elsewhere. Bird populations on open dune areas were generally low but results were highly variable depending on type and amount of vegetation, presence of water, and nature of adjacent communities.

Richness and density were found to increase as the community aged. Diversity also increased without a decline in the final stage. Since the diversity index was most influenced by the number of species the presence of hemlock in the mesic forest communities was thought to be responsible for increasing diversity by creating a pseudo-forest-edge structure which was attractive to species of earlier stages. The more pioneer conditions of slopes and crests of dunes were also thought to contribute to increasing diversity. The jack pine community, however, reached a higher diversity than either the small oak or large oak plot. This was attributed to a much more heterogeneous habitat. Equitability changed little between communities.

Standing-crop biomass was very high in the beach grass-cottonwood and jack pine community because of nesting waterfowl and large numbers of Red-winged Blackbirds. Standing

crop biomass for passerines increased as the community aged with the exception of a drop in both oak communities. Metabolic energy expenditure was also found to increase with age except for a drop in the oak communities.

Beach utilization by adjacent dune populations was slight for most species. Common Grackles were found to be the most frequent exploiter.

The possibility of increased intermingling of southern and northern species on dune communities is suggested and possible reasons given.

The concept of a bird sere is discussed and found to be poorly integrated on sand dunes. The role of birds in sand dune succession is considered to be insignificant.

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Appendix I

SCIENTIFIC NAMES OF BIRDS REFERRED TO IN THE TEXT

Great Blue Heron	*Ardea herodias*
Green Heron	*Butorides virescens*
Snowy Egret	*Egretta thula*
Mallard	*Anas platyrhynchos*
American Black Duck	*Anas rubripes*
Blue-winged Teal	*Anas discors*
Wood Duck	*Aix sponsa*
Red-tailed Hawk	*Buteo jamaicensis*
Ruffed Grouse	*Bonasa umbellus*
Killdeer	*Charadrius vociferus*
Spotted Sandpiper	*Actitis macularia*
Mourning Dove	*Zenaida macroura*
Cuckoo (Yellow-billed, Black-billed)	*Coccyzus americanus* *Coccyzus erythropthalmus*
Great Horned Owl	*Bubo virginianus*
Barred Owl	*Strix varia*
Ruby-throated Hummingbird	*Archilochus colubris*
Belted Kingfisher	*Megaceryle alcyon*
Common Flicker	*Colaptes auratus*
Pileated Woodpecker	*Dryocopus pileatus*
Red-bellied Woodpecker	*Centurus carolinus*
Yellow-bellied Sapsucker	*Sphyrapicus varius*
Hairy Woodpecker	*Dendrocopos villosus*

Downy Woodpecker	Dendrocopos pubescens
Eastern Kingbird	Tyrannus tyrannus
Great Crested Flycatcher	Myiarchus crinitus
Eastern Phoebe	Sayornis phoebe
Acadian Flycatcher	Empidonax virescens
Least Flycatcher	Empidonax minimus
Eastern Wood Pewee	Contopus virens
Tree Swallow	Iridoprocne bicolor
Bank Swallow	Riparia riparia
Barn Swallow	Hirundo rustica
Purple Martin	Progne subis
Blue Jay	Cyanocitta cristata
American Crow	Corvus brachyrhynchos
Black-capped Chickadee	Parus atricapillus
Tufted Titmouse	Parus bicolor
White-breasted Nuthatch	Sitta carolinensis
House Wren	Troglodytes aedon
Mockingbird	Mimus polyglottos
Gray Catbird	Dumetella carolinensis
Brown Thrasher	Toxostoma rufum
American Robin	Turdus migratorius
Wood Thrush	Hylocichla mustelina
Veery	Catharus fuscescens
Eastern Bluebird	Sialia sialis
Blue-gray Gnatcatcher	Polioptila caerulea
Golden-crowned Kinglet	Regulus satrapa
Starling	Sturnus vulgaris

Yellow-throated Vireo	Vireo flavifrons
Red-eyed Vireo	Vireo olivaceus
Worm-eating Warbler	Helmitheros vermivorus
Nashville Warbler	Vermivora ruficapilla
Black-throated Green Warbler	Dendroica virens
Cerulean Warbler	Dendroica cerulea
Blackburnian Warbler	Dendroica fusca
Kirtland's Warbler	Dendroica kirtlandii
Prairie Warbler	Dendroica discolor
Ovenbird	Seirus aurocapillus
Louisisana Water-thrush	Seiurus motacilla
Common Yellow-throat	Geothlypis trichas
Hooded Warbler	Wilsonia citrina
Canada Warbler	Wilsonia canadensis
American Redstart	Setophaga ruticilla
Eastern Meadowlark	Sturnella magna
Red-winged Blackbird	Agelaius phoeniceus
Northern Oriole	Icterus galbula
Common Grackle	Quiscalus quiscula
Brown-headed Cowbird	Molothrus ater
Scarlet Tanager	Piranga olivacea
Cardinal	Cardinalis cardinalis
Rose-breasted Grosbeak	Pheucticus ludovicianus
American Goldfinch	Spinus tristis
Rufous-sided Towhee	Pipilo erythrophthalmus
Vesper Sparrow	Pooecetes gramineus

Chipping Sparrow	Spizella passerina
Clay-colored Sparrow	Spizella pallida
Field Sparrow	Spizella pusilla
Song Sparrow	Melospiza melodia