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BIRD POPULATIONS IN SUCCESSIONAL COMMUNITIES FOLLOWING WILDFIRE AND LOGGING, AND IN PINE PLANTATIONS, IN THE QUETICO-SUPERIOR, IN NORTHEASTERN MINNESOTA AND ADJACENT CANADA

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INTRODUCTION

This study provides an analysis of avian data from 13 post-wildfire communities, 7 logged communities, and 4 pine plantations in Superior National Forest, Minnesota, and adjacent Quetico Provincial Park, Ontario (Lat. 50⁰N., Long. 91030'W.). All communities were located on upland sites which naturally support Jack Pine and Black Spruce during mature stages of successional development following wildfire. Post-wildfire community ages ranged from 1 to 370 years, representing a successional series (sere) following disruption of upland forests by fire. Logged communities ranged from 1 to 50 years since disturbance; none had been disturbed by fire or management practices following logging. The 50-year community is the oldest community we have been able to locate which has developed following clear-cutting; most logging prior to 1950 was selective cutting which left various amounts of standing trees, thus altering the successional pattern and community structure during subsequent development. Plantations that we have studied ranged from 3 to 67 years of age, the latter being the oldest pine plantation in Minnesota.

Successional studies usually compare different communities in similar environments, although some shortterm successional studies have documented changes in the same community. In eastern United States, especially, most avian studies have examined secondary succession in fallowed fields or anthropogenically disturbed forest communities. Wilderness areas, such as parts of the Boundary Waters Canoe

Area Wilderness, and Quetico Provincial Park, offer opportunities to examine succession influenced, primarily, by natural forces. The forest lands around the wilderness, subjected to silvicultural practices including logging, site preparation and establishment of pine plantations, provide an opportunity to contrast natural community structure to the forest communities that develop with forest management. A comparison of bird populations in the natural communities with those that develop with anthropogenic management in the Quetico-Superior Region is the purpose of this study.

Fire has been a natural perturbation in the northern Great Lakes area for many centuries, and probably much longer (Maissurow 1941, Heinselman 1973, Swain 1973). Logging was introduced into the study area within the past 100 years, and intensive forest management, including site preparation and establishment of conifer plantations, has been applied only within the past 50 years. Opportunities to do controlled studies of logging impacts from timber cutting more than 50 years ago is limited by inaccurate or unavailable records of how and when timber harvesting was done. Good records of logging are largely limited to 25 years; beyond that, most logging was more selective, often high-grading, with removal of only the larger, or more valuable trees, with sparse information on the residual community.

Fallowed agricultural fields, in contrast to wilderness, frequently are islands in a mosaic of communities where species invasion is proportional to the degree of temporal and spatial isolation. Moreover, vegetation of early successional communities includes many non-native species in less natural associations. The diversity and structural patterns, therefore, may differ from those patterns found in wilderness. Moreover, effects of fire on forest patterns are probably different from effects of agriculture or silviculture on subsequent succession of bird communities.

The basic principles of avian succession have been well established (Adams 1908, MacArthur and MacArthur 1961, Willson 1974, Karr 1980). Many have examined changes in bird populations during succession after fire (Bock et al. 1978, Taylor and Barmore 1980. Taylor 1973) and effects of fire on various aspects of bird populations (see MacMahon 1980 and Anderson 1979 for recent reviews). We (Apfelbaum and Haney 1981) and Niemi (1978) have studied short-term responses of birds following fire in Superior National Forest. Effects of logging and reforestation practices on bird populations have been studied (Ambrose 1975, Conner and Adkisson 1975, Conner et al. 1979, Debyle 1975, Conner et al. 1979, Debyle 1981, Franzreb 1977, Pfannmuller 1979, Titterington et al. 1979), although few authors have attempted to compare and contrast populations in natural and anthropogenically altered communities. Several studies have examined trends in bird populations during succession within a sere (Smith and MacMahon 1981, Austin and Perry 1979, Meslow and Wight 1975, Kricher 1973, Haapanen 1965, Johnson and Odum 1956, Odum 1950).

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DESCRIPTION

Kuchler (1964) described the regional vegetation of the study area as the "Great Lakes pine transition forest" in reference to the presence of Eastern White Pine (Pinus strobus L.) and Red Pine (P. resinosa L.). These species were prevalent in advanced successional communities prior to heavy timbering and subsequent increase in fire frequency and intensity before the beginning of this century. A few communities, protected to some degree on islands or peninsulas, were not timbered and represent remnants of oldgrowth forests (Heinselman 1973). Overstory White and Red Pine are usually common in these oldgrowth communities. A more common pine now, throughout the region, is Jack Pine (P. banksiana L.). This smaller species produces serotinous cones that release seeds following heavy fire. With increasing frequency of fire, Jack Pine has become an increasingly important tree since 1900, often dominating upland communities for 100 to 125 years after fire, giving way successionally to spruces (Picea mariana [Mill.] BSP and P. glauca [Moench] Voss.) and Balsam Fir (Abies balsamea L. Paper Birch (Betula papyrifera Marsh.) may [Mill.]). persist in all upland communities but is more frequent in areas after recurring fire (Heinselman, personal communication).

Ohmann and Ream (1972) described 12 upland plant community types for this area, four of which contained important Jack Pine components. All of our study sites were in agreement with Ohmann and Ream's "Jack Pine-Black Spruce" and "Jack Pine-fir" community types. These correspond to the Society of American Foresters (1954) Forest Cover Type 6, occupying slopes and ridges, especially over glacial till and rock outcrops, particularly with north to northeast exposures. In all study areas, Jack Pine community types represented patches in a mosaic that also included aspen (Populus tremuloides L. primarily, with some P. grandi-

dentata L.) dominated draws and small Black Spruce bog communities.

Communities in this area are developed through synergistic effects of fire and physiographic variables (Heinselman 1973). Fire frequency and intensity varies in each forest type, being most severe in Jack Pine forests and usually not greatly disrupting the larger bogs. Crown fires are frequent and often burn large areas. Within burned areas, aspen draws are often swept only by ground fires, or occasionally missed altogether; bogs seldom are burned except during exceptionally dry conditions, and then, usually, vegetation is only partially consumed by fire. Older communities have greater amounts of fuel and increased dominance of spruce and fir which are more vulnerable to fire; thus, they tend to be altered more radically by fire. Aspen reseeds and resprouts rapidly after fire. Jack Pine reseeds successfully on most slope and ridge sites where it was present before fire. Jack Pine establishes more successfully on drier, upland sites, whereas aspen are more successful on moist sites in finer soils. Black Spruce and, to a much lesser extent, Balsam Fir, reseed after fire, but less successfully than Jack Pine or aspen (Ohmann and Ream The latter probably become reestablished more from 1972). root sprouts than from seed.

Early communities. Within two years after fire, upland communities have abundant dead, standing trees with heavy infestation of wood-boring and bark-dwelling beetles; percent of fire-killed trees varies depending on site, fire conditions and age of the community before fire (Apfelbaum and Haney 1981). The more severe the fire, often, the heavier the regrowth of ground cover. In addition to Jack Pine and scattered Black Spruce seedlings, and aspen seedlings and sprouts, many herbs and shrubs become established or resprout, including Fireweed (Epilobium <u>augustifolium L.), Thimbleberry (Rubus parviflorus Nutt.),</u> Big-leaved Aster (Aster macrophyllus L.), Geranium (Geranium

<u>Bicknellii</u> Britt.), Fringed Bindweed (<u>Polygonum cilinode</u> Michx.), roses (<u>Rosa spp.</u>), gooseberries (<u>Ribes</u> sp.), Beaked Hazel (<u>Corylus cornuta</u> Marsh.) and grasses and sedges. Mature White and Red Pine usually survive fires and may reseed in mineral soil. The appearance of early post-fire communities is one of heavy ground cover, standing dead trees, pockets of surviving trees, especially aspen in draws and Black Spruce in bogs, and scattered older White and Red Pine, if any existed in the community prior to fire.

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Within 10 to 15 years, most fire-killed trees have fallen and the Jack Pine and aspen regrowth has closed the canopy at a height of 3 to 5 m. Under the dense canopy, many of the herbs and smaller shrubs disappear, and mosses and lichens begin to carpet the ground. Grass and sedge dominated openings persist, especially on wetter sites, with willow (<u>Salix</u> spp.) and Speckled Alder (<u>Alnus rugosa</u> [Dukoi] Spreng) thickets around the edges.

Intermediate communities. By 60 to 70 years after fire, the dense Jack Pine and aspen forest have matured and thinned to a more open, evenly spaced, homogeneous forest with dense carpets of lichens and bryophytes. Openings, except for lichen-dominated rock exposures, are filled with Black Spruce on wet sites and ericaceous shrubs (Vaccinium spp. and <u>Gaylussaccia</u> spp.) on excessively drained sites. Spruce and fir are scattered in the canopy and are common seedlings and transgressives in the understory. Aspen communities retain more shrub and herbaceous understory, especially willow, and establishment of spruce and fir may be farther advanced.

The canopy of the 112-year-old stand is comprised of oldgrowth Jack Pine and aspen, often as overstory, among increasing numbers of spruce and fir of differing age classes. The community has more structural diversity than preceding communities. Shrub species are common, especially Beaked Hazel, dogwood (<u>Cornus rugosa</u> Lam.), and Mountain Maple (<u>Acer spicatum Lam.</u>). Ground cover of bryophytes,

Clinton's Lily (<u>Clintonia borealis</u> L.), Bunchberry (<u>Cornus Canadensis</u> L.), Big-leaved Aster and other herbs, as well as seedlings of spruce and fir, is well developed.

<u>Mature communities</u>. Mature communities develop within 175 years and resemble the 112-year-old community except that most of the Jack Pine and aspen have died and fallen. Dominant tree cover is a multi-layered spruce and fir canopy with a dense understory of younger trees and all the shrubs and herbs mentioned above. Oldgrowth Red and White Pine may still occur as an overstory. More than any other community, these mature forests are characterized by dense vegetation at all levels, from the ground to the canopy.

Oldgrowth communities. The oldest communities in our study were characterized by scattered old Red Pine and White Pine that formed an overstory in a somewhat open forest of spruce and fir with most of the species that were present in the mature communities described above. Pockets of disturbance, especially blowdown of larger trees, result in openings in which White and Red Pine regenerate, along with spruce and fir, and many of the shrubs and herbs also found in younger communities. Edge and horizontal diversity are increased by these small openings. The oldest stand we studied, a 370-year-old community, also had an important component of Northern White Cedar (Thuja occidentialis L.), supporting the observation of Grigal and Ohmann (1975) that, in the absence of disturbance, upland forests may eventually succeed to Northern White Cedar.

Unlike post-fire communities, plant succession after logging is often initiated from a sparse and patchy ground cover, absence of a vertical structural habitat component, and scattered patches of woody debris. Seedling establishment by conifers, especially Jack Pine, is less and more patchy than after wildfire on similar sites. Within ten years after logging, aspen root suckers 2 to 3 m. tall often dominate, if aspen was present in the cutover forest, with scattered Jack Pine and spruce seedlings of somewhat

lower stature. The growth of graminoids and disturbed site herbs, such as fringed bindweed, usually begins to decline within ten years on both post-fire and post-logging seres, except in lower, wet areas where grasses and sedges may persist after disturbance for 30 years and longer. Fifteen years after logging, aspen and Jack Pine begin to close the canopy at 3 to 5 m. in all but wet or rock outcrop areas. Ground cover decreases as the canopy closes, but the more sparse regrowth of trees after logging often allows greater persistence of grasses, sedges and herbs than found in postfire communities.

Fifty years after logging, jack pine and aspen approach maturity with the development of a spruce-fir understory. Ground cover of herbs and graminoids is usually much greater in this community than in the corresponding post-fire community which generally has an open, bryophyte dominated ground cover. Shrub growth in logged communities is locally thick, especially alder in and around lower areas, and beaked hazel in better drained areas. Density of aspen and Jack Pine is substantially lower compared to post-fire communities. The pines, therefore, have a fuller canopy with numerous live lower branches. In contrast, the canopy of post-fire communities is dense and limited to 3 to 4 m. depth.

Development and subsequent growth and succession of pine plantations can be quite variable depending on site preparation and use of herbicides to release planted conifers (Haney and Apfelbaum 1984). Conifers are planted after most standing trees and shrubs are removed, sprayed, or piled, and sometimes burned. Planting may proceed immediately, or may be delayed for one or more years after logging and site preparation. Plantations usually start as open fields, with transplants in rows on set spacing. After 1 to 5 years, conifers are typically released from woody competition by use of an herbicide. Graminoids, shrubs, and aspen sprouts often proliferate in unsprayed plantations.

Spraying reduces forbs and shrub cover on most sites, but may lead to increased graminoid cover (Haney and Apfelbaum 1984). Three years after planting, conifers usually start to emerge from the graminoid and forb cover of 1 to 2 m. height. After 15 years, conifers are 2 to 4 m. tall and dominate the community, except where aspen or shrubs were not controlled, or on included wet sites that were not planted or where herbicides failed to eliminate competition with shrubs.

Within 50 years, red pines that we examined were at a height of 15 m. and formed a relatively dense canopy with an open, park-like understory, more similar to the forests of this age class that originate following fire. In the 67year-old plantation we studied, red pines were 20 to 25 m. tall with well developed bryophyte ground cover. Beaked hazel persisted in dense patches in some areas that were not sprayed with herbicides. Forb and graminoid cover was sparse in these older plantations.

We have found that horizontal diversity (patchiness) is high after fire, primarily because of surviving pockets of vegetation and uneven burning. Logging and plantations tend to create homogeneous forests. For the first 75 years after fire, horizontal diversity decreases as even-aged, homogenous stands of Jack Pine and aspen mature. As these pioneer species die, the understory of spruce and fir increases and shrubs and herbs become reestablished. This increase in vertical diversity continues slowly, probably stablizing at 200 to 250 years when the oldest spruce and fir begin to suffer blow-down or insect attack on an irregular basis, creating more horizontal diversity. It is not clear if the vertical diversity of these oldgrowth stands is lower, but patchiness, or horizontal diversity, is definitely greater than in the intermediate and mature forest communities. Vertical and horizontal diversity, total diversity, of the vegetation, in our opinion, is least

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in the intermediate-aged communities, and greatest in the mature communities primarily because of patchiness and continued, although somewhat reduced, vertical diversity, compared to mature communities. Recently burned communities have less vertical diversity, but much greater horizontal diversity. Recently logged and planted areas have low vertical and horizontal habitat diversity. Although vertical diversity in these communities increases with time, horizontal diversity remains low.

METHODS

Study sites were selected in communities that burned 1, 3, 3, 7, 15, 67, 73, 112, 175, 176, 366, 367, and 370 years before our fieldwork was initiated. Logged communities were studied 1, 2, 7, 14, 15, 23, and 50 years after disturbance. Plantation ages were 3, 15, 49, and 67 years old. Ages of communities were determined from stand origin maps, discussions with Forest Service and Park personnel, and Forest Service records. Ages were verified in the field by coring trees. All study sites were selected in upland sites, generally more than 100 m. from water or large bogs.

In each area, a 250 x 250 m. grid, internally flagged at 50 m. intervals, was established with compass and tape in a representative area determined by reconnaissance. These 6.25 ha. (15.4 a.) areas invariably included exposed rock communities, small bogs, and frequent draws with colluvial or till mineral substrates. Draws with small bogs included, averaged 5 to 20 percent of the study sites, the balance being accounted for by ridge and slope. Methods of sampling birds and vegetation, and analysis of data have been detailed elsewhere (Apfelbaum and Haney 1981) and are summarized here.

Birds were censused daily from dawn to mid-morning, for 3 to 5 hours per census, over several consecutive days.

Each census involved both investigators working together, slowly walking grid lines, plotting locations of each bird heard or seen. Censuses were continued until no additional territories were added. Time required to achieve a complete survey varied from about 20 person hours, in the least complex community, to over 50 hours in more diverse communities with an average of just over 35 person-hours per grid or 5.5 person-hours per hectare. Another 50 to 100 person-hours per site were spent studying vegetation.

In mapping territories of birds, we employed both the spot-map (Williams 1936) and the flush-plot (Kendeigh 1944) techniques to better delimit territories. All birds were plotted. Birds that were transient or visitors were revealed by sporadic and inconsistent points or lines across our data sheets. Communities censused in late May or early June were recensused in mid or late June to ensure that territories had not been influenced by late migrants. Territories were defined by repeated points and flush-plot lines that were clustered.

Data were examined in several ways. Species richness and number of individuals as well as relative density of each species were determined for each community. Frequency, the percent of 50 x 50 m. grid sections in which a species was found, was determined, and relative frequency for each species was calculated. Relative territory cover, measured by the total area within each 6.25 ha. study area occupied by the combined territories of each species, was calculated. Numbers of individuals of each species (density) and area of the community they occupied (cover) and distribution within a community (frequency) still does not address the total resource utilization of a species. To better determine the total use of each species, we also calculated existence energy (Kendeigh 1970) as discussed previously (Apfelbaum and Haney 1981). A composite comparison index for species was derived by the sum of relative cover, frequency, and existence energy, density being a part of these parameters.

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This importance value is useful not only to compare species within each community (Curtis 1959), but also to compare guilds (Apfelbaum and Haney 1981). Guild designations of Bock and Lynch (1970) were used.

We report diversity (H', base 10) for information on richness and evenness combined (Hurlbert 1971, Rabenold 1978) but recognize the biases and limitations of this index. Bird weights and derived population biomasses are based on published data (Stewart 1937, Poole 1938, Stegeman 1955, Tordoff and Mengel 1956, Johnston and Haines 1957, Graber and Graber 1962, and Murray and Jehl 1964) and our survey data.

RESULTS

<u>Wildfire</u>. Relative importance values of the 51 bird species that had identifiable territories on the 3 burned study sites are summarized by guild (Table 3). Twenty additional species, either peripheral to the study sites or transient through the grids, some as late migrants, also were recognized. The Common Merganser, Ruby-throated Hummingbird, and 3 raptor species were not assigned to specific guilds. None of the 69 species recorded were ubiquitous to all communities, but 11 of the most important species nesting on study sites were present in at least 10 of the 13 communities.

Successional trends were evident. Based on importance values, recently disturbed communities were dominated by White-throated Sparrows, Chestnut-sided Warblers, Mourning Warblers, Robins, and Northern Three-toed Woodpeckers. The Olive-sided Flycatcher and other flycatchers were most common the first three years after fire. In the 15-year community, the White-throated Sparrow was the most important bird species followed closely by the Magnolia Warbler. The Ovenbird, Canada Warbler and Red-eyed Vireo were also

important in this nearly impenetrable cover of 3-meter Jack Pine and aspen.

The Blackburnian Warbler attained the greatest relative importance of any species in the 67- and 73-year communities. The Ovenbird reached its greatest importance here also, and was only 1 of 4 Ground-brush Foragers found nesting in the sparse, park-like understory of this forest. The Bay-breasted Warbler and Red-eyed Vireo were also important Tree-foliage Searchers.

In the 112-year-old forest, bird species were much the same as in the 67- and 73-year forest, although importance was shifted. In the heavier spruce and fir cover, the Baybreasted Warbler was relatively more important than the Blackburnian Warbler. The Red-eyed Vireo, a nearly ubiquitous Tree-foliage Searcher, shared importance with the Black-throated Green and Black-throated Blue Warblers. Golden-crowned Kinglets were more important in this community than in others we studied. The Brown-creeper, nesting in 12 of the 13 communities, was dominant among the Timber Gleaners in this, and most other, communities. Nearer the ground, only the Ovenbird was relatively important.

In the 175- and 176-year mature forest communities, more species of Tree-foliage Searchers were found, with the most important being the Blackburnian and Bay-breasted Warblers. Ground-brush Foragers increased in importance, compared to the 73-year forest, but none dominated the avifauna.

In oldgrowth forests, compared to communities of intermediate ages, Ground-brush Foragers increased, but none dominated the guild. Tree-foliage Searchers, also, were important, but no species was consistently dominant. If any species tended to be associated with oldgrowth communities, it was the Magnolia and Parula Warblers.

In 3 communities and peripheral to a fourth, all in northern Cook County, Minnesota, we observed established

territories of the Gray-cheeked Thrush. Although we failed to locate nests, we did observe on two occasions birds carrying nesting materials. The Gray-cheeked Thrush has not been reported previously as a nesting species in Minnesota (Green and Janssen 1975).

Species richness, based on territorial species in our study grids, varied from 12 to 24 species in the sere (Table 2). After the first year, species richness appeared to be rather constant for several years, and nearly equal to that in mature forests. When visitors were included, as many species used the recently burned communities, the largest number being 32 species in one 3-year-old community. In 67and 73-year communities, in contrast, had the lowest richness and diversity of avian species (Table 2). Bird species richness peaked, again, in the 176-year-old community, then declined in the oldgrowth communities.

Guilds also were related to succession (Table 1). Flycatchers were most common during the first few years after fire. The Least Flycatcher, however, was generally distributed in the sere. Tree-foliage Searchers were, by far, more important in the intermediate-aged communities, particularly as the spruce-fir forest matured from 112 to 176 year after fire. Timber Gleaners, primarily the Brown Creeper and Red-breasted Nuthatch, were generally distributed in all communities. Timber Drillers were much more important the first three years after fire. This resulted, however, solely from the heavy use of recent burns by the Black-backed Three-toed Woodpecker. Likewise, Ground-brush Foragers were more common in recently burned communities.

Seventeen species were recorded only as visitors; nearly half were Ground-brush Foragers (Table 1). Some, such as the Blue Jay and Pileated Woodpecker, were found in almost all communities. Most visitation, however, occurred in the first 3 years after fire. Visiting species were

about twice as common in recently burned communities as in the communities 15 years and more after fire.

Average weight was greatest among those species using recently burned communities, averaging over 20 grams per bird during the first three years after fire (Table 2). In the communities 67 years and more after fire, average weight per bird was about the same. Greater average mass of birds in younger communities resulted from increased importance of Ground-brush Foragers, Flycatchers, and Timber Drillers. Population biomass tended to increase with community age (Table 2).

Numbers of individuals and existence energy varied similarly as population biomass (Table 2). Density was especially variable, ranging from 39 to 196 individuals per 6.25 ha., a five-fold difference.

Community groups are suggested by relations between bird species richness and density. Our data show a general positive correlation between these parameters as reported by others (Theberge 1976). More important, however, is the suggested generalizations about successional trends. Early communities had a lower density, but comparable richness to older communities. Intermediate communities had the highest richness and density. Oldgrowth communities had lower richness and intermediate density. The 67- and 73-year communities represent the condition that occurs when the pioneer trees reach maturity.

Logging Sere. Bird species richness following logging was least in most recently logged communities with increasing richness through 15 to 23 years, and a decline at 50 years. Although richness became comparable to that found after fire within 15 years, bird density was consistently depressed after logging, until about 50 years (Table 3). This was also reflected by population biomass and H' diversity.

Birds present in the first years after logging were limited to only Ground-brush Foraging species (Table 4).

The importance of other guilds increased with time, but Ground-brush Foragers maintained dominance for the first 15 years. In the 23-year-old community, Tree-foliage Searchers dominated but were less important, again, than Ground-brush Foragers in the 50-year-old community. This is in contrast to the observed pattern after fire where Tree-foliage Searchers dominated from 67 years through oldgrowth communities. Timber Drillers were absent and Timber Gleaners relatively less important in the post-logging sere. Both were relatively abundant immediately after fire and through much of the post-fire sere.

The Ground-brush Foraging bird species that dominated one year after logging included the Common Flicker, Chipping Sparrow, White-throated Sparrow, and Song Sparrow. Chestnut-sided Warblers nested in aspen and Jack Pine regrowth, while Song Sparrows, White-throated Sparrows, and Chipping Sparrows had territories that included slash piles and associated regrowth. Flickers nested in aspen and birch snags, and fed on rotting stumps and slash in more open Within two years, reductions in the importance areas. values of some of these species already was apparent. Ιn contrast, species such as the Chestnut-sided Warbler responded to increased growth of woody cover. The Yellowthroat, similarly, responded to similar regrowth, appearing within two years after logging.

Although flycatchers visited the logged communities, they did not breed on these sites for the first 6 years. Seven years after logging, the Least Flycatcher and Alder Flycatcher utilized shrub edges associated with lowland pockets. Olive-sided Flycatchers visited or were peripheral to these sites throughout much of the sere and nested in the 15-year-old community.

An increase in Tree-foliage Searchers occurred mostly from the 14-year-old through 50-year-old communities. Several of the species that increased in 14- to 23-year-old communities were less abundant in the 50-year-old community.

These included the Rose-breasted Grosbeak, Tennessee Warbler, Yellow-rumped Warbler, Veery, Red-eyed Vireo, Magnolia Warbler, and Canada Warbler. The Bay-breasted and Blackburnian Warblers appeared with development of the canopy at 23 years after logging, and persisted or increased in importance in the 50-year community. The Kinglets and Black-capped Chickadee showed similar trends.

Timber Gleaners represented by the Black-and-white Warbler and Red-breasted Nuthatch nested or visited the sere after 14 and 15 years, respectively. Woodpeckers only infrequently used the sere.

Birds of the early successional communities, such as the Chestnut-sided Warbler and White-throated Sparrow, declined with increasing community age beyond 23 years, as with the post-fire sere. Species that increased with development of vegetation included Overbird and Nashville Warblers.

<u>Plantations</u>. Relative to burned and logged communities, plantations showed a similar trend toward increasing richness with community age. Unlike these other seres, however, richness was substantially depressed (Table 2). The presence of 9 breeding species 3 years after planting was similar to the richness of logged communities of this age, but only half the richness of burned communities the same age. Richness in the 15-year-old plantation also was half that in the burned and logged seres. The population density in this community was similar to the logging sere but less than half that in the post-fire community of this age.

From 49 to 67 year, avian richness declined in the plantations, similar to the trend seen in the other two seres. Population density remained about half that found in the 50- and 67-year logging post-fire communities. These trends also were reflected by biomass and existence energy statistics. Average weight of individuals, however, showed increasing mass with increasing community age, opposite the

trend found in post-fire and post-logging seres. This resulted because of maintenance of the Ground-brush Foraging Guild in the plantations through the sere whereas, in postfire and post-logging seres, this guild dominated in younger communities but increasingly gave way to the smaller birds in the Tree-foliage Searchers Guild, as community age increased.

In the plantations, the Ground-brush Foragers had the highest importance value in the 3-year-old community but remained the dominant guild throughout, accounting for 78 percent of the importance value, on the average (Table 3). Timber Drillers did not breed in the plantations and Timber Gleaners, represented by Red-breasted Nuthatches, only nested in the 49-year-old plantation, but visited the 67year-old community (Table 5).

In contrast to the other seres, Flycatchers were present through the sere and increased with increasing community age. The trend developed because of the Eastern Wood Pewee, well established in the 49-year plantation, was the second dominant species in the 67-year plantation, exceeded only by the Ovenbird. Apparently, the Eastern Wood Pewee, not common in the other seres, found the open Red Pine canopy structure of these plantations to its liking. This species was represented otherwise only in the post-fire sere 3- and 7-year communities.

Tree-foliage Searchers increased to domination in the 49-year plantation, then declined in the 67-year plantation (Table 3). Blackburnian Warblers, in contrast, occurred in the 49- and 67-year plantations about equally, whereas the Red-eyed Vireo decreased to peripheral status. Most Treefoliage Searchers were recorded as visitors or peripheral.

Ground-brush Foragers showed similar changes in species composition as in burned and logged communities. Similarities included the high importance of Chestnut-sided and Mourning Warblers, and White-throated and Song Sparrows in younger communities with decreasing importance or absence

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with increased age (Table 5). Unlike logged or burned communities, the American Goldfinch was found to be a dominant species in the youngest plantations which resembled an oldfield. Overbirds and Robins were completely absent in the youngest plantations and increased substantially as the canopy maured and the ground cover decreased to produce open, parkland communities at 49 and 67 years of age.

DISCUSSION

Most avian successional trends, largely based on oldfield succession after agriculture, indicate increasing richness as communities develop vegetation structural diversity. Declines in richness at specific points during structural development were noted by a few authors (Odum 1950, Kricher 1973), while many authors reported declining richness after full maturity of forested communities (Karr and Roth 1971). This study suggests that post-fire species richness follows a bimodal model, with highest richness within 15 years after fire and again after 175 years of community development. The depression in richness in the 67- and 73-year forests appears to be consistent and real. In the Great Lakes Pine Forests, avian richness appears to decline with maturation of a pine canopy at 50 to 80 years of community development. During this time, Jack Pine forms an often homogeneous, thick canopy when succession is initiated after fire (Apfelbaum and Haney 1981), and although similar trends are found after logging and in plantations, the density of the canopy is less and crown development of dominant trees is fuller. Thus, the reduction in species in these maturing communities is proportionately less than the reduction in the fire sere. In all seres, nevertheless, reduction in bird richness occurred with initial canopy maturity, indicating some consistent changes in habitat structure, and resource quality and diversity.

Aside from similar trends in these seres, the lower richness and density of birds throughout all ages of plantations relative to corresponding communities after logging and fire is particularly noteworthy. Richness of avian species in the logging sere was more similar to the post-fire sere, although substantially more impoverished in the first years. Bird density in the logging sere, likewise, was consistently lower than that in the post-fire sere, although far more similar than the bird densities found in plantations of corresponding ages. Biomass and existence energy was similar to the density patterns.

The natural fire rotation in the Quetico-Superior region is generally considered to be between 70 and 100 years (Heinselman 1973). Birds, like plants, have adapted to fit into this rotation, with species and populations adjusted to available habitat and resources. Logging rotations are projected to be 50 to 70 years, whether cuts follow fire, natural regeneration after logging, or plantations established after logging. Forest management, therefore, which focuses on timber production, will result in reduced species richness and bird density as compared to naturally rotating forests. Important here, also, is the realization that fire rarely burned over extensive acreages or all sites within burned areas completely even in years when fires were unusually heavy. Thus, fire creates a mosaic of different aged communities, from bogs which rarely burn, to scattered oldgrowth communities that escaped fire for 300 and more years. Forest management for timber, in contrast, tends to reduce the natural mosaic, and render the entire forest region more homogeneous in composition and structure. Plantations go farther toward this reduction of potential avian habitat than logging followed by natural regeneration alone. The more intensively a forest is managed for timber, the greater the reduction in overall avian habitat.

Ream (1981) pointed out that the major effect of disturbances such as fire or logging on small mammals is through modification of vegetation. The same is true of birds. Titterington <u>et al</u>. (1979) reported differences between bird populations after clear-cutting and fire in spruce-fir forests with changes correlated to habitat structure.

Aside from the generally accepted relationships of animal populations to vegetation patchiness and structure, there exists confusion and disagreement in the literature. Austin and Perry (1979) found that no bird species was eliminated by logging in Lodgepole Pine, but many changes in species populations were reported. Similar conclusions also were reported by Franzreb (1977) and Jarvinen and Vaisanen (1978). In contrast, we found that some bird species were absent in successional communities for over 100 years following disruption by wildfire. Based on data from communities 1 to 23 years after logging, even more bird species were absent, compared to recently burned or uncut forests of the same type. In these recently cutover forests, however, we found other species nesting, such as the Killdeer, Common Nighthawks, and Common Snipe, as well as much greater foraging activity by Sparrow, Broadwing, Red-tailed, and Sharp-shinned Hawks. Haapanen (1965) reported that breeding bird density and species richness was greatest in undisturbed forests in Finland, but Conner and Adkison (1975) found the greatest bird diversity 3 to 12 years after clearcuts in oak-hickory forests. This tends to support observations of Ambrose (1975) who found highest diversity 3 years after small clearcuts, and Hooper (1967) who reported greatest diversity 6 years after clearcutting. In contrast, Meslow and Wight (1975) reported that more bird species utilized the mid-successional Douglas-fir forests of the Northwest. Some of these differences undoubtedly relate to the forest types and methods of harvest. Our previous studies have identified the importance of wildfire to

several special status species including the Black-backed Three-toed Woodpecker, and Brown Creeper (Apfelbaum and Haney 1977), Solitary Vireo, Winter Wren, Short-billed Marsh Wren, Black-throated Blue Warbler, Bay-breasted Warbler, Goshawk, Connecticut Warbler and White-throated Sparrow. Additional specific studies in the Great Lakes Pine Forests are also required to more fully document the effect of logging there on non-game species.

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1	Common Grackle (<u>Quiscalus quiscula</u>) V	(Corvus brachyrhynchos) Common Flicker (Colaptes auratus)	(Spizella passerina) Common Crow	(Dendroica pensylvanica) P Chipping Sparrow	(<u>Toxostoma rufum</u>) Chestnut-sided Warbler	(<u>Cyanocitta cristata</u>) V Brown Thrasher	<u>GROUND-BRUSH FORAGERSTOTAL 145</u> 1 Blue Jay	(Sphyrapicus varius)	TIMBER DRILLERS(Cont'd) Yellow-bellied Sapsucker	
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Community age in years since fire

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	(Turdus migratorius)	Robin	(Carpodacus purpureus)	Purple Finch	(Seiurus aurocapillus)	Ovenbird	(Selurus noveboracensis)	Northern Waterthrush	(Vermivora ruficapilla)	Nashville Warbler	(Oporornis philadelphia)	Mourning Warbler	(Hylocichla guttata)	Hermit Thrush	(Perisoreus canadensis)	Gray Jay	(Hylocichla minima)	Gray-cheeked Thrush	(Junco hyemalis)	Dark-eyed Junco	(Capella gallinago)	Common Snipe	GROUND-BRUSH FORAGERS(cont'd)		
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60 8 *** ********		n an for allera	et nagotus - ress sji		- 1940 (* 1940) - -			romo o Ésam			n negatar		Spruce Grouse
Ы	⊢1 ,₽			n on websoors,	atan ing ing	9-16, 1986-74 ₆ 4+	in gan	in-release	h11	μ ² .	ta ta T		(<u>Melospiza melodia</u>)
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					politik danny	- 500 - 1 0	nanin († 720€98)		an paga ang that bag	19. or og af som	e more editorio.	d)	GROUND-BRUSH FORAGERS (cont'd)
370	367	366	176	175	112	73	67			ω	ω	Ē	
		fire	nce	113 121 121	year	- T	/ age	unity	Communi	10			

TOTAL	(<u>Buteo platypterus</u>) (<u>Buteo platypterus</u>) Common Merganser (<u>Mergus merganser</u>) Ruby-throated Hummingbird (<u>Archilochus colubris</u>) Sharp-shinned Hawk (<u>Accipiter striatus</u>) Sparrow Hawk (<u>Falco sparverius</u>)	110
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300 299 304 301 303 300		367
300	4	370

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Table 2. Summary of bird parameters by community age in fire, logging and plantation seres.

PARAMETERS

COMMUNITY AGE

<pre>Existence energy/gm. biomass (Kcal./day/gm.)</pre>	Total existence energy (Kcal./day)	Population biomass (gm.)	No. individuals/6.25 ha.	Mean wt./Individual (gm.)	H'(base 10)	No. visiting/transient species	No. breeding species	Fire Sere
• 75	58 4	783	39	20.1	1.03	7	14	F3
1.56	066	636	72	18.3	1.16	7	20	w
യ ഠ	1259	1582	96	20.1 18.3 20.8	1,13	⊷+ ⊢→	20	ω
89	812	910	61	14.9	j 1	10	1- 5	7
• 44	1583	1895	109	17.3	.02 1.23	4	21	15
• 9 7	581	563	5 5	10.2	.76	ထ	10	67
.97	9 8 4	1014	82	12.7	95	U	Ч Т	73
• 79	2032	2569	166	5	1.08	42	20	112
.87	2315	2658	196	13.6		ហ	23	175
• •	2316	2359	177	13.3 3	1.10	7	24	176
• 7 7	2537	3 3 1	173	19.1	1- 1- 0	0	17	366
9 ω	1320	1426	108	ω.	1.05	ω	بے ری	367
1 • 0 2	1455	1429	120	12.0	1,05	\$	17	370

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Table 2. (Cont'd)

PARAMETERS

COMMUNITY AGE

10 10		49 11 6	N and a second	10 8 0		ωοω	Plantations No. breeding species No. visiting/transient species
•	1.04	ູ ວັງ	80 61	° 83 44	• 78	• 72	<pre>Existence energy/gm. biomass (Kcal./day/gm.)</pre>
689 9	519	917	769	5 6 0	N 5 N	324	Total existence energy (Kcal./day)
964	500	1068	892	669	323	449	Population biomass (gm.)
59	48 8	67	57	4 1-1	17	22	No. Individuals/6.25 ha.
16.3	10,4	15,9	15.7	16.5	19.0	20.4	Mean wt./individual (gm.)
1.07	1.19	1.02	•95	84	80	.74	H' (base 10)
	42	5	18	ர	9	13	No. visiting/transient species
 	19	21	14		7	6	No. breeding species
50	23	15	14	7	2		Logging Sere

<pre>Existence energy/gm. biomass (Kcal./day/gm.)</pre>	(Kcal./day)	Population biomass (gm.)	Total no. individuals/6.25 ha.	Mean wt./individual (gr.)	H'(base 10)	No. visiting/transient species	No. breeding species	Plantations
.80	530	659	47	11.9	86°	ω	9	ω
• 8 8 8	678	767	51	16.3	. 82	8	10	15
. 72	5 5 2	782	4	20.2	യ	б	السلم السلم	49
.76	452	592	29	20.4	• 70	10	ດ	67

communities following wildfire and logging, and Table 3. Comparison of importance values Уq in pine plantations. gui lả in successional

GUILD

COMMUNITY AGE

Table 3. (Cont'd)

COMMUNITY AGE

TOTAL, All Guilds		Ground-Brush Foragers	Timber Drillers	Timber Gleaners	Tree-Foliage Searchers	Flycatchers	Logging Sere	
301		301	0	0	0	0		
301		291	0	0	10	0	2	
301 301 300 301 298 302 302	α-1 κ. «δίξιξα - α _{παδ} ικατά ματη	265 2	0	0	2 1	14	7	
301		209	0	25	67	0	14	
298		164	0	N	66	ωω	15	
302		164 129	0	26	147	0	23	
302		р л л	0	1- 4-	118	н л	50	

COMMUNITY AGE

TOTAL, All Guilds	Ground-Brush Foraagers	Timber Drillers	Timber Gleaners	Tree-Foliage Searchers	Flycatchers	Pine Plantations
301 300 300 297	279	0	0	0	22	ω
300	272	, O	0	28	0	15
300	279 272 196 197	0	39	50	15	49
297	197	0	0	ω	6 4	67

<u>Table 4</u>. Importance values of breeding birds censused in logged communities. Importance values are based on relative frequency, relative territory size, and relative existence energy. Non-territorial species, called visitors (V), and species heard or seen outside the grid within the same vegetation type, called peripheral (P), are indicated. Binomials are from AOU Checklist, 5th Edition.

and the second							
GUILD and fam the			COMMU	NITY	AGE		
Species	1	2	7	14	15	23	50
FLYCATCHERSTOTAL	0	0	14	0	33	0	15
Alder Flycatcher							
(Empidonax traillii)	V	Р	2	V	- 7	\mathbf{P}	
Common Nighhawk							
(Choredeiles minor)		V	Р				
Least Flycatcher							
(Empidonax minimus)		12	V	7			15
Olive-sided Flycatcher							
(<u>Nuttallornis borealis</u>)		V	р	V	19	V	Р
Tree Swallow							
(Iridoprocne bicolor)		V		v			
TREE-FOLIAGE SEARCHERS TOTAL	0	10	21	67	99	147	118
American Redstart							· Autological constance
(Setophaga ruticilla)				V			
Bay-breasted Warbler							
(Dendroica castanea)						17	13
Blackburnian Warbler							
(Dendroica fusca)						17	50
Black-capped Chickadee							
(Parus atricapillus)				V	3	9	1.5
Canada Warbler							
(Wilsonia canadensis)				1	2	22	V
Evening Grosbeak							
(Hesperiphona vespertina)							Р

		СОММ	UNITY	AGE		
.1	2	7	14	15	23	50
TREE-FOLIAGE SEARCHERS(Cont'd	1)					
Golden-crowned Kinglet						
(<u>Regulus satrapa</u>)					8	5
Magnolia Warbler						
(Dendroica magnolia)			23	6	34	10
Red-eyed Vireo						
(Vireo olivaceus)			14	36	14	
Rose-breasted Grosbeak						
(Pheucticus ludovicianua)			18	22		3
Ruby-crowned Kinglet						
(Regulus calendula)						15
Solitary Vireo						
(<u>Vireo</u> solitarius)		Р		7		
Tennesee Warbler						
(<u>Vermivora peregrina</u>) V	Р	13	11	3		
Yellow-rumped Warbler						
(<u>Dendroica coronata</u>)		8	V	4	23	
Yellowthroat						
(<u>Geothlypis trichas</u>)	10			16		7
TIMBER GLEANERSTOTAL 0	0	0	25		26	14
Black-and-white Warbler						
(Dendroica striata)			25	2	7	
Red-breasted Nuthatch						
(<u>Sitta canadensis</u>)			· .	V	19	14
TIMBER DRILLERSTOTAL 0	0	0	0	0	0	0
Downy Woodpecker						
(Dendrocopos pubescens) V			V			
Black-backed 3-toed Woodpecker						
(Picoides arcticus)						Р
Pileated Woodpecker						
(Dryocopus pileatus)			V	V	Р	

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	1	2	<u>СОММ</u> 7	UNITY 14	<u>AGE</u> 15	23	
TIMBER DWELLERS(Cont'd)					• • • •		
Yellow-bellied Sapsucker							
(Sphyrapicus varius)		ť .					
GROUND-BRUSH FORAGERS.TOTAL	301	291	265	209	164	129	1
American Woodcock							
(Philohela minor)				V			
Blue Jay							
(Cyanocitta cristata)		V	V	V	V	V	
Brown Thrasher							
Toxostoma rufum			V				
Chestnut-sided Warbler							
(Dendroica pensylvanica)	29	51	97	50	51	21	
Chipping Sparrow						a.	
(Spizella passerina)	68	64		8	8	4	
Common Crow							
(Corvus brachyrhynchos)	V	V					
Common Flicker							
(Colaptes auratus)	73	V	V	V	V		
Common Raven							
(Corvus corax)				V			
Common Snipe							
(Capella gallinago)	V	57		V			
Connecticut Warbler							
(Oporornis agilis)	V						
Cowbird							
(Molothrus ater)					V		
Dark-eyed Junco							
(Junco hyemalis)	V						
Grasshopper Sparrow							
(<u>Ammodramus</u> savannarum)	Ρ						
Gray-cheeked Thrush							
(Hylocichla minima)						5	

			COMM	JNITY	AGE	
	1	2	7	14	15	23
GROUND-BRUSH FORAGERS (Con-	t'd)					
Gray Jay						
(Perisoreus canadensis)	V	V				V
Hermit Thrush						
(Hylocichla guttata)		Р		6	10	
Killdeer						
(Charadrius vociferus)	V	24				
Mourning Warbler						
(Oporornis philadelphia)	V	Р	11	21	8	7
Nashville Warbler						
(Vermivora ruficapilla)	V	Р	9	28	36	33
Northern Waterthrush						
(Sciurus noveboracensis)						
Ovenbird						
(Sciurus aurocapillus)				23	3	45
Purple Finch						
(Carpodacus purpureus)	V		Р		V	V
Robin						
(Turdus migratorius)	V	V	39	V	V	р
Ruffed Grouse						
(Bonasa umbellus)				Р		
Short-billed Marsh Wren						
(Cistothorus platensis)	Р					
Song Sparrow						
(<u>Melospiza melodia</u>)	45	41	17			
Spruce Grouse						
(Canachites canadensis)	'					Р
Swainson's Thrush						-
Hylocichla ustulate)						5
Swamp Sparrow						9
(Melospiza georgiana)	21					
Veery						
(Hylocichla fuscencens)			18	12	6	3
				*~)
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			COMMU	NITY	AGE		
	1	2	7	14	1.5	23	50
GROUND-BRUSH FORAGERS(Cont'	d)						
White-throated Sparrow							
(Zonotrichla albicollis) 6	5	54	74	61	42	6	30
Winter Wren							
(Troglodytes troglodytes)		Р			Р		Р

OTHER SPECIES Broad-winged Hawk (Buteo platypterus) V V V V Red-tailed Hawk (Buteo jamaicensis) V Ruby-throated Hummingbird (Archilochus colubris) V V Sharp-shinned Hawk (Accipiter striatus V Sparrow Hawk (Falco sparverius) V

Table 5. Importance values of breeding birds censused in pine plantations. Importance values are based on relative frequency, relative territory size, and relative existence energy. Non-territorial species, called visitors (V), and species heard or seen outside the grid but within the same community or vegetation type, called peripheral (P), are indicated. Binomials are from AOU Checklist, 5th Edition.

GUILD		PLANTAT	ION AGE	
Species			49	67
FLYCATCHERSTOTAL	22	0		64
Alder Flycatcher	4 ******	an a	n na manana ang kanana kanana kanana kanang kanana ka	
(<u>Empidonax traillii</u>)	13			
Least Flycatcher				
(Epidonax minimus)	9	Р	V	p
Eastern Wood Pewee				-
(Contopus sordidulus)			15	64
Great Crested Flycatcher				
(Myiarchus crinitus)			v	
TREE-FOLIAGE SEARCHERSTOTAL	0	28	50	36
Bay-breasted Warbler				- Mon Hand War - Fryn Naf - Fr - Ara
(Dendroica castanea)			7	
Blackburnian Warbler				
(Dendroica fusca)			23	36
Black-capped Chickadee				
(Parus atricapillus)		9	V	v
Black-throated Blue Warbler				
(Dendroica caerulescens)		Р	P	
Black-throated Green Warbler				
(<u>Dendroica virens</u>)				v
Evening Grosbeak				
(Hesperiphona vespertina)		V	Р	V
Red-eyed Vireo				
(Vireo olivaceus)		14	20	Р

		PLANTA	TION AGE	
	3	15	49	67
TREE-FOLIAGE SEARCHERS(Cont	'd)			
Rose-breasted Grosbeak				
(Pheucticus ludovicianua)		V	V	
Solitary Vireo				
(<u>Vireo</u> solitarius)		Р		
TIMBER GLEANERSTOTAL		<u>,</u>	2.0	
Black-and-white Warbler	0	0	39	0
(<u>Dendroica striata</u>) Red-breasted Nuthatch		Р		
			20	
(<u>Sitta canadensis</u>)			39	V
TIMBER DRILLERSTOTAL	0	0	0	о 1 О
Yellow-bellied Sapsucker				
(Sphyrapicus varius)		V		
CROWND DRUGU BODDORDO				
GROUND-BRUSH FORAGERSTOTAL	279	272	196	197
Blue Jay				
(Cyanocitta cristata)		V	V	V
Chestnut-sided Warbler	. .			
(<u>Dendroica</u> pensylvanica)	62	84	15	15
Chipping Sparrow				
(Spizella passerina)	V		V	
Common Crow				
(Corvus brachyrhynchos)	v		, j	
Common Flicker		~~		
(<u>Colaptes</u> <u>auratus</u>) Goldfinch	V	V	Р	V
	0.7			
(<u>Spinus tristis</u>)	27			
Gray Jay				
(<u>Perisoreus canadensis</u>)				V
Hermit Thrush				
(Hylocichla guttata)			26	22

		PLANTATION AGE			
	3	15	49	67	
GROUND-BRUSH FORAGERS (Cont'	d)				
Mourning Warbler					
(<u>Oporonis philadelphia</u>)	46	11	5	Р	
Nashville Warbler					
(Vermivora ruficapilla)	24	57	37	V	
Ovenbird					
(Seiurus aurocapillus)	Р	5	76	124	
Purple Finch					
(Carpodacus purpureus)		V			
Robin					
(Turdus migratorius)	V		51	36	
Ruffed Grouse					
(Bonasa umbellus)		V			
Song Sparrow					
(Melospiza melodia)	77	18			
Veery					
(Hylocichla fuscescens)				V	
White-throated Sparrow					
(Zonotrichia albicollis)	70	71	12	V	
TOTAL	304	300	300	297	

 $(h_{\mu}) = \frac{1}{2}$