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THE CHANGING BIRD ASSEMBLAGE ALONG A GRADIENT OF
AGRICULTURAL INTENSITY

by

ANDREW J. MCALLISTER, B.Sc.

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment
of the requirements for the degree of

Master of Science

Department of Biology
Carleton University
Ottawa, Ontario
January 18, 1996

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"The Changing Bird Assemblage Along a Gradient of Agricultural Intensity"

submitted by

ANDREW JOHN MCALLISTER, B.Sc.

in partial fulfilment of the requirements
for the degree of Master of Science

Chair, Department of Biology

Thesis Supervisor

Thesis Supervisor

Carleton University

ABSTRACT

Changes in the bird species assemblage were examined along a land-use gradient of agricultural intensity. Twenty-nine sites ranging from largely wooded landscapes to largely monoculture landscapes were each censused 5 times during the breeding season. Quantitatively, bird species richness, diversity and evenness all significantly decreased as agricultural intensity increased. Qualitatively, the assemblage was dominated by forest habitat specialists at low agricultural intensities. As intensity increased, forest species rapidly disappeared and were replaced by habitat generalists that persisted along the gradient. In areas of high agricultural intensity, habitat generalists dominated the assemblage. I suggest that the loss of native forest habitat and the gain of novel habitats, crops, are driving the observed changes in the assemblage. Many of these abundant generalists may have negative impacts on the structure of the assemblage. This study demonstrates that the hypothesis that conserving habitat diversity leads to the conservation of biodiversity may not be applicable to birds in agroecosystems.

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Introduction

In the agricultural landscape, extensive native forests have been reduced to remnant fragments. The forest has been replaced by non-native, novel resources in the intervening croplands (Burgess and Sharpe 1985). This system has become heterogeneous in a different manner than most natural systems because the heterogeneity was imposed on the landscape by humans at a variety of scales (Merriam 1988). This has had both direct and indirect effects on the survival of organisms in these areas (Freemark 1995). The direct effect of increased habitat fragmentation has both positively (e.g. Brittingham and Temple 1983) and negatively affected (e.g. Villard *et al.* 1995) some species. Increased nest predation and brood parasitism are indirect negative consequences of agricultural activity (Gates and Gysel 1978, Robinson *et al.* 1995).

The effects of agriculture occur at different levels of biological organization and over a range of spatial and temporal scales (Gilpin *et al.* 1992). In order to examine these effects, the choice of spatial scale(s) should reflect the organism's scaling of the environment (review by Wiens 1989). Spatially, most studies have been limited to the individual habitat element in the farm-landscape system. Bird populations in shelterbelts (Yahner 1983), fencerows (Best 1983), woodlots (Opdam *et al.* 1985) and fields (Fuller *et al.* 1991) have been examined as isolated units. In reality these different elements are all integrated in the matrix of the farm-landscape system and thus are not ecologically independent (Merriam 1990). Focusing at the scale of the habitat element and not taking into consideration the surrounding

landscape can often lead to erroneous interpretation of results (Andrén 1994). Effects of the surrounding landscape on bird populations have been demonstrated in a number of habitat-based studies (e.g. Freemark and Merriam 1986, Freemark and Collins 1992, Freemark and Csizy 1993, Pearson 1993, Hinsley *et al.* 1995) but only the following few studies have examined birds over a wide range of heterogeneous landscapes: Andrén (1992), Balent and Courtiade (1992), Farina (1993), Farina (1995), McGarigal and McComb (1995), and Villard *et al.* (1995). The need for studies that are directed at the scale of the landscape has become apparent (Fry 1991, Andrén 1994, Wiens 1994).

In this study, I examined changes in habitat composition in landscapes along an agricultural land-use gradient and the effect that these changes have on different aspects of the bird species assemblage. Quantitatively, the bird assemblage responses I measured were species richness, diversity and evenness. Qualitatively, I also assessed species turnover and the rank-order of abundant species.

The ecology of the urban-rural gradient has been largely unexplored (McDonnell and Pickett 1990). Changes in variables such as landscape configuration, composition and connectivity are primary factors affecting the agricultural gradient (Merriam 1990), a segment of the urban-rural gradient. This gradient can be viewed as a gradient of agricultural intensity. Agricultural intensity is defined by two main components: (1) the proportion of an area that is actively farmed, and (2) where actively farmed, the nature of the agricultural practices. For example, if two areas have similar amounts of land devoted to agriculture but one is predominately devoted

to corn production whereas the other is dominated by pasture, then the corn growing area would be considered to have a higher agricultural intensity. Therefore, the gradient ranges from landscapes that are almost fully wooded (little to no agriculture) to landscapes that are largely crops (intensive agriculture).

Conserving biodiversity is a priority in most ecosystems (Noss 1983). In agroecosystems, conserving or optimizing habitat diversity is thought to translate into conserving or optimizing biodiversity (Pimentel *et al.* 1992, Barrett and Peles 1994). Recent studies have advocated a landscape approach to conserving biodiversity (Noss 1983, 1992). In this study I look at bird assemblage responses to increasing agricultural intensity and the implications that these relationships have for the conservation of avian biodiversity in agroecosystems.

Methods and Materials

Study Area

The study was conducted within a 60 km radius of Ottawa, Ontario, Canada (Figure 1). This area contains a wide range of agricultural land-use systems (Huffman 1983). Areas varying in percentage forest cover with access via primary and/or secondary roads were identified from maps at the 1:50 000 scale. I drove through these areas and stopped at 5 km intervals to ask the closest landowner for permission to include their property as a study site. A minimum of 5 km between sites was employed to avoid pseudoreplication (Hurlbert 1984); most bird species territories do not overlap at this separation (Schoener 1968). Twenty-nine sites were chosen, consisting of five routes with five sites apiece and one route with four sites.

A site was defined as the largest continuous area over 30 ha owned by the landowner not bisected by barriers (i.e. roads). Sites ranged in sizes from 30 to 86 ha (Mean=44.6 ha, Sd=15.2 ha). A minimum of 30 ha was required to adequately conduct the bird census for the required period of time. For three sites, the landowner's property did not meet the minimum area requirement and therefore an adjacent property was included to permit an adequate bird census.

A site was composed of three groups of habitat elements: actively farmed habitats, non-farmed habitats and edge habitats. Actively farmed habitat elements included corn, small grain (oats or barley), soyabean, hay (grasses or alfalfa), and pasture. I did not distinguish between different types of small grain or hay because

often a field was composed of a mixture of these crop types. As well, the disturbance regime (e.g. planting, cutting, cultivating) was similar for all crops of one type.

Non-cultivated habitat elements were woodlots and old fields. Edge habitats (e.g. fencerows) were the interfaces between any adjacent habitat elements.

Bird Census

Birds were censused using a variation of the variable line transect method (Emlen 1971, 1977) in 10 m wide bands parallel to the transect line (see Box 4.3 in Bibby *et al.* 1992). I chose a line-transect method for censusing birds for a number of reasons. First, this was not strictly a breeding bird census as I was interested in all birds using the study site (breeding, transients, juveniles, foraging only). Second, this method allowed me to census linear habitats (i.e. edge habitat). Finally, it allowed me to cover a large area relatively quickly. Transect lines were located a minimum of 200 m apart to avoid double counting of birds. Each site had transects totalling 1.5 km which were walked at 1 km/h. For each site, the transect length for each habitat type was proportional to each habitat's area in the site. Within any given habitat element, transects were a minimum of 100m. Transect lines were located along the edges of the different habitat elements with the exception of forest, so that on one side of the transect line, birds were counted in the one habitat element while on the other side of the transect line, birds were counted in the adjacent edge habitat to a depth of 10 m. Censusing at edges between habitats is thought to produce different results from censusing at the center of a habitat (Best *et al.* 1990), but some studies have modified traditional bird census techniques to count birds from habitat

edges (e.g. Freemark and Rogers 1993).

Edges rather than field centres were censused for a number of reasons. Some farmers were unwilling to allow me to walk through growing crops. In many instances due to the shape of the habitat (i.e. a narrow field), my detection of birds would have been limited by the edge habitat (e.g. wooded fencerow), rather than the distance from observer to the birds. Forest habitats were generally censused so that the transect line ran through the habitat rather than along one side of it. Edges of woodlots were sampled at sites where woodlots were less than 100 m wide. This sampling procedure resulted in the overcensusing of edge habitats, but this was compensated for by the fact that these are important habitats for birds in the agricultural landscape (Arnold 1983) and have proportionally higher bird densities than any other farmland habitat (Best *et al.* 1995).

Each site was censused for approximately 1.5 h per visit. Censusing was divided into two blocks: morning and evening. The morning census block began a 0.5 h before sunrise and took approximately 5 to 5.5 h to complete and covered three sites. The evening block took approximately 3.5 h and was finished around sunset and covered two sites. Most researchers (e.g. Freemark and Merriam 1986) census birds in the early morning only. I included an evening census block as bird activity increases towards the evening after the midday period of inactivity (Robbins 1981), and this study was concerned with not just breeding birds. Each site was censused on 5 occasions. Sites were rotated through the different starting times to reduce the potential bias arising from the census starting time (Shields 1979). Censusing did not

take place during rainy or windy ($> 30\text{km/h}$) conditions. Censusing took place between 9 May and 12 July 1994. Bird species that were migrants or whose geographic range did not include all the study sites (Godfrey 1986) were excluded from the analyses.

Measuring Agricultural Intensity

Agricultural intensity was defined by two main criteria: (1) the areal percentage that was actively farmed, and (2) the nature of the agricultural practices within the farmed area.

To devise a single measure that combines these two criteria, various landscape variables were measured in a 1 km radius from the center of each study site. This scale was large enough to provide a general picture of the agricultural practices of the area, yet small enough so as not to distort the relationships between the area sampled and surrounding habitats. The variables were percentage cover of corn, small grains, soyabean, hay, pasture, old field, woods, tilled land (corn + small grains + soyabeans), and untilled land (hay + pasture), number of silos, and length of agricultural edge. Agricultural edge was defined as the length of the edge of agricultural fields along wooded fencerows and woodlots. Habitat types were mapped within the 1 km radius on recent air photos and checked by landowner interviews and personal observation. Percentage cover of the various habitat types was then measured from the air photos using a digital planimeter.

A principle components analysis (PCA) was done on these landscape variables to identify a single variable representing agricultural intensity. PCA is a useful

technique for determining the underlying pattern of a dataset as it concentrates the variance into relatively few axes, as opposed to the original dimensionality of the dataset (Gauch 1982). Principle component axes were examined for 1) the amount of variance explained and 2) whether the loadings of the variables on an axis satisfied the two previously stated components of agricultural intensity. Specifically, an axis representing agricultural intensity was expected to have positive signs for the loadings of farmed landscape variables and negative loadings for non-farmed landscape variables. Different magnitudes for the various farmed landscape variables would be expected and would indicate the agricultural practices taking place. The associated principle component scores for each site for the axis representing agricultural intensity became my independent variable in subsequent analyses.

Landscape diversity was examined to provide a comparison with the generated agricultural intensity gradient using the Shannon-Weiner index (Shannon 1949), $H' = -\sum p_i \log p_i$, where p_i is the importance of each habitat type in the landscape. The potential habitats included corn, soyabean, grain, hay, pasture, forest, old field and other crops. Landscape diversity was modelled against agricultural intensity using simple linear and polynomial regression.

Bird Assemblage Structure and Composition

The bird assemblage was examined quantitatively using standard indices of diversity (species richness, evenness and diversity). Bird species richness (S) was the cumulative number of species per site over the 5 visits. Bird species diversity was $H' = -\sum p_i \log p_i$, where p_i is the proportion of individuals of the i th species per site per

census averaged over the 5 visits (Shannon 1949). Bird species evenness was calculated as $J' = H'/H'_{max}$, where H'_{max} is $\log_e S$ (i.e. the equal distribution of individuals among species). J' was also based on the average of 5 visits per site. All individuals detected were included in the calculations for H' and J' . This may introduce a bias into these indices if my ability to detect birds in open habitats was greater than in forests. I tested this by comparing the effective detection distances (see Emlen 1971, 1977) of abundant species at each end of the agricultural intensity gradient using a t-test. The relationships between the standard indices of diversity and agricultural intensity were modelled using simple linear regression.

Qualitative changes in the bird assemblage with increasing agricultural intensity were examined using species turnover along the gradient, and changes in the rankings of abundant species. Species turnover which I define as the rate of change in species composition, was calculated as $turnover = ((a-c) + (b-c))/2$ (Cody 1983), where a is the number of species at site a , b is the number of species at site b , and c is the number of species in common between the two sites. I compared turnover between adjacent sites along the intensity gradient with the midpoint between the two principle component scores of the two sites as the independent variable ($n=28$). The relationship between species turnover and agricultural intensity was modelled using simple linear regression.

Species turnover was also examined using agricultural intensity as a class variable. Sites were grouped into six agricultural intensity classes based on their principle component scores as follows: wooded, low, midlow, mid, midhigh, and

high. The wooded class contained 4 sites while the remaining 5 classes contained 5 sites apiece. Species turnover was calculated for each site within an agricultural class compared with each site in the adjacent agricultural class. This produced a mean species turnover between 2 adjacent classes ($n=20$ or 25). A one-way analysis of variance (ANOVA) and a Scheffe's test were used to test for significant differences between classes.

A rank-order table was created using the same agricultural intensity classification system as above to examine species composition of the bird assemblage. The ten most abundant species based on cumulative number of individuals were ranked in order of abundance for each end of the intensity gradient (wooded and high intensity classes). I then tracked the ranking of the top ten species at each end of the gradient through the 5 remaining agricultural intensity classes. The total number of individuals detected for four bird species that are known to be either brood parasites, predators or competitors on the bird assemblage, were plotted against the different agricultural intensity classes to provide relationships between abundances of these species and agricultural intensity. As well, the total number of birds detected over five censuses was modelled against agricultural intensity using simple linear and polynomial regression. All statistical analyses were performed using SAS (1990) and hypotheses were tested at the 5% level of significance.

Results

Agricultural Intensity

Based on the variable loadings, the first principle component (PC1) appears to be a measure of agricultural intensity (Table 1). PC1 accounted for 45.3 % of the variance in the dataset (Table 1). Both non-farmed habitats (FOREST and OLD FIELD) had negative loadings and all the farmed variables had positive loadings (Table 1). FOREST was the variable with the highest loading contributing to PC1 which relates negatively to the area being farmed. The next two highest loadings (TILL and SILOS) represent high levels of agricultural activity within these actively farmed areas (Table 1). Therefore, PC1 scores for all sites were used as the measure of agricultural intensity in subsequent analyses (see Appendix 1 for range of scores).

Figures 2-12 present scatter plots of the landscape variables plotted against PC1 scores and were as follows: FOREST decreased with agricultural intensity (Figure 2); TILL, SILOS, HAY, CORN, UNTILL, SOYABEAN, GRAIN, and PASTURE (Figures 3-10) all increased; and the scatter plots of OLD FIELD and EDGE were quadratic in shape (Figures 11 and 12).

Bird Assemblage Structure and Composition

Bird species richness, evenness and diversity all decreased significantly with increasing agricultural intensity (Figures 13, 14, and 15). Bird species richness and diversity had the strongest relationships followed by evenness (Figures 13, 14, and 15). Potential bias as a result of including all detections in calculating H' and J' is minimal. Effective detection distances (see Emlen 1971, 1977) for abundant species

were not significantly different between the wooded ($n_1=7$) and high ($n_2=6$) agricultural intensity classes ($t=0.83$, $p>0.4$). However, personal observation suggests that I was able to detect birds at greater distances in open habitats than in forest habitats. Therefore, the potential bias would be that sites with more open habitats, and hence higher agricultural intensity, might have slightly inflated diversity indices. Thus the observed relationships between these diversity indices and agricultural intensity would only be stronger if this hypothetical bias were removed.

Species turnover decreased significantly as agricultural intensity increased (Figure 16) when intensity was examined as a continuous variable. When intensity was examined as a class variable using ANOVA, the model was also significant (Figure 17). A Scheffe's test indicated that the wooded-low and low-midlow intensity class comparisons had similar turnovers, yet significantly higher turnovers than the midlow-mid, mid-midhigh and midhigh-high class comparisons (Figure 17).

Six of the ten most abundant species in the lowest intensity class (wooded) (Ovenbird (*Seiurus aurocapillus*), Black-and-white Warbler (*Mniotilta varia*), Nashville Warbler (*Vermivora ruficapilla*), Black-capped Chickadee (*Parus atricapillus*), and Common Yellowthroat (*Geothlypis trichas*)) essentially disappeared or were infrequent in the highest intensity class (Table 2). Furthermore, most species became infrequent rapidly as agricultural intensity increased (Table 2). Three of the species (American Robin (*Turdus migratorius*), Song Sparrow (*Melospiza melodia*), and European Starling (*Sturnus vulgaris*)) were quite common throughout the whole gradient (Table 2 and 3). Seven of the eleven (two species had the same relative abundance) most

abundant species in the highest intensity class (Red-winged Blackbird (*Agelaius phoeniceus*), Savannah Sparrow (*Passerculus sandwichensis*), Horned Lark (*Eremophila alpestris*), Barn Swallow (*Hirundo rustica*), Brown-headed Cowbird (*Molothrus ater*), Ring-billed Gull (*Larus delawarensis*), and Vesper Sparrow (*Pooecetes gramineus*)) are essentially absent from the lowest intensity class (Table 3). In contrast to the pattern exhibited by the abundant species found at the wooded end of the gradient, four of these seven abundant species which have essentially disappeared at the low end of the gradient are still fairly common across the remainder of the gradient (Table 3). Only three species (Horned Lark, Ring-billed Gull, and Vesper Sparrow) became infrequent or absent rapidly as intensity decreased (Table 3). The plots of total number of individuals detected for each of the following species: red-winged blackbird, brown-headed cowbird, european starling, and ring-billed gull, show that the maximum number of detections of these species was at high agricultural intensities (Figure 18). Total birds detected did not significantly change along the gradient of agricultural intensity ($p=0.33$) even when higher order terms were added to the regression model (Figure 19).

Landscape diversity had a quadratic relationship with agricultural intensity, with the highest landscape diversity occurring at a mid-intensity range (Figure 20).

Discussion

This study demonstrates that many characteristics of the bird assemblage change along an agricultural intensity gradient. Quantitatively, as agricultural intensity increased from a largely wooded landscape to a largely monoculture landscape, all three standard indices of species diversity (richness, diversity and evenness) significantly decreased. Qualitatively, the bird assemblage is composed mainly of a large pool of forest associated species at the low end of the gradient. As intensity increases, a smaller pool of habitat generalists replaces the rapidly diminishing pool of forest species in the landscape, at a rate below that of the disappearance rate of forest species, resulting in an overall decrease in species turnover along the agricultural intensity gradient.

Loss of native habitat in the form of deforestation, and introduction of non-native habitat in the form of various crop types are two main characteristics of the agricultural intensity gradient. These are also probably two of the main landscape changes driving the observed quantitative and qualitative changes in the bird assemblage.

Wooded habitats in North America generally have higher bird species richness and abundance compared to crop habitats (Freemark *et al.* 1991, Best *et al.* 1995). The structural complexity and plant species diversity of a habitat partially determine its bird assemblage (Rotenberry 1985). Forested habitats have higher within-habitat heterogeneity than crops. Increased within-habitat heterogeneity is important in increasing the bird species richness at the habitat level in forest patches (Freemark

and Merriam 1986). These habitats can also be highly variable in species composition as different types of forest can have different complements of species (May 1982, Howe 1984, Freemark and Merriam 1986, Best *et al.* 1995). I did not distinguish among different forest types (e.g. different seral stages). The high species turnover among the lower intensity classes suggests a unique complement of species in the landscapes containing a high percentage of forest.

Most crop types have low species richness and abundance for a number reasons. Actively farmed habitats are subjected to repeated, often synchronous, anthropogenic disturbances at various spatial scales (Hanski and Tiainen 1988, Best *et al.* 1995). These disturbances (e.g. tillage, planting, cultivation, fertilizer and pesticide application) result in the destruction of nests, individuals and food sources (Rodenhouse and Best 1983, Basore *et al.* 1986, Freemark and Boutin 1995), and produce habitats having low within-habitat heterogeneity (Hanski and Tiainen 1988, Best *et al.* 1995).

Forest patches are also used exclusively by more breeding bird species than are actively farmed habitats (Best *et al.* 1995). Many of these species are area sensitive and/or forest interior species (Freemark and Collins 1989, Best *et al.* 1995), and thus a continued decrease in available forested habitat along this gradient of increasing agricultural intensity results in a decrease in the species pool found in this habitat type. This is further supported by examining the abundant species at the low intensity end of the gradient. Half of these species become infrequent rapidly along the gradient suggesting a low tolerance to forest loss. These species are all associated

with the forest interior (Freemark and Collins 1989). In contrast, the loss of actively farmed habitats as agricultural intensity decreases negatively affects a very small pool of agricultural habitat specialists (Best *et al.* 1995). Only three of the abundant species (horned lark, ring-billed gull, vesper sparrow) in the highest intensity class could be classified as agricultural specialists. The majority of the abundant species at the high intensity end of the gradient are habitat generalists; they are able to persist in relatively high numbers throughout a wide range of the gradient. A low species turnover among the higher intensity classes suggests a relatively constant set of species in landscapes containing a high percentage of actively farmed habitats. Balent and Courtiade (1992) drew similar conclusions; they found that the niche breadths of bird species increased along a forest to corn gradient in France.

Therefore, the observed decrease in species richness, diversity and turnover is largely a result of (i) a decrease in a heterogeneous habitat, forest, and (ii) an increase in relatively homogeneous habitats, crops, in the agricultural landscape. My result for species richness is also in agreement with Best *et al.* (1995) who predicted an increase in the number of nesting bird species as the farm landscape went from a monoculture state to a more heterogeneous state in Iowa. Balent and Courtiade (1992) also found decreasing species richness along a forest to corn gradient. Similarly, Arnold (1983) found an increase in bird species richness as non-crop habitat elements were added to the landscape, though this was conducted for a limited number of habitats. In terms of species turnover, my results are in agreement with Thiollay (1995) who found primary forest to have quite different bird communities

than agroforests, and that within different agroforests, there was high turnover in the bird communities.

The insertion of crops as novel resources in the landscape has not had a negative impact on all species. In agricultural habitats, there are far fewer nesting species than in native habitats (Freemark *et al.* 1991, Best *et al.* 1995) and most species occur in low abundances (Best *et al.* 1995) for reasons mentioned previously. Many species do use these agricultural habitats however (Best *et al.* 1995), presumably for foraging. For example, the red-winged blackbird, common grackle (*Quiscalus quiscula*), european starling, brown-headed cowbird, and mourning dove (*Zenaidura macroura*) are some of the species that have incorporated waste grain left on crop fields after harvest as a component of their diet (Dyer and Ward 1977, Armstrong and Noakes 1981, McNichol *et al.* 1982, Clark *et al.* 1986). This phenomenon is known as landscape complementation (Dunning *et al.* 1992, Taylor *et al.* 1993), where an organism makes use of non-substitutable resources in other patches of different types. Thus these actively farmed habitats are providing resources for some species (e.g. red-winged blackbirds). Therefore a significant decrease in species evenness as agricultural intensity increased may have been a result of increased abundance of generalists in response to the insertion of novel resources, crops, in the landscape, and consequent decrease in the abundance of forest dwelling species. The observed relationship between evenness and increasing agricultural intensity may also be influenced by some species using these areas for foraging only (e.g. ring-billed gull), and a higher incidence of gregarious, polygamous species (e.g.

red-winged blackbird) and a decrease in forest species that exhibit well-developed intraspecific territoriality (Tramer 1969).

Associated with changes in habitat composition are changes in habitat configuration (Andrén 1994, McGarigal and McComb 1995). Though not specifically measured in this study, as forest habitat decreases along the intensity gradient, average forest patch size and forest interior/edge ratios will decrease, and forest interpatch distance will increase (Hanski and Tiainen 1988). These changes may have contributed to the bird assemblage responses to agricultural intensity. For example, less isolated forest patches have a higher species richness than more isolated patches (Freemark and Collins 1989). Both the composition and configuration of a landscape influence connectivity, which is the probability of an organism moving between resource patches in the landscape (Merriam 1984, Fahrig and Merriam 1985, Fahrig and Paloheimo 1988). Often, connectivity is the most important component of landscape structure affecting species survival (Henein 1995). My study focused on changes in composition only, though configuration and connectivity, the other two components of landscape structure (Taylor *et al.* 1993) can be important in determining the distribution and abundance of bird species (Freemark 1995).

Agricultural activity in eastern Ontario began only about 200 years ago (Middleton and Merriam 1983). Prior to European settlement, eastern North America was largely temperate forest (Rowe 1977). In contrast, large scale agricultural activity has occurred in Europe over a much longer period (Murray 1970). The effects on birds of changes in habitat composition and configuration differ between

North America and Europe. This may be attributed to behavioural adaptations of species at different historical scales to temporal changes in landscape structure (Merriam 1988). For example, Farina (1993, 1995) concluded that abandonment of agriculture and the subsequent increase in woodlands in rural Italy, are expected to result in reduced diversity and abundance of the bird fauna. This is the opposite of my conclusions. Therefore, my results may not be applicable to areas having undergone different historical scales of landscape change (but see Balent and Courtiade 1992).

Several species have benefitted from changes in the agricultural landscape and have become quite abundant as agricultural intensity increased (Tables 2 and 3, Figure 18). The impacts that these abundant species have on less adaptable species could be devastating (Garrott *et al.* 1993). Though not explicitly tested, brood parasitism, interspecific competition, and predation by certain abundant bird species may be among the forces driving the observed changes in the bird species assemblage along the agricultural intensity gradient. Brown-headed Cowbirds, a brood parasite, are a common species along the agricultural gradient, attaining highest numbers in areas dominated by agriculture. They are only infrequent at the low intensity end of the gradient, as these areas are low in edge habitat and actively farmed habitats which serve as breeding patches and foraging patches respectively for this species (Cook *et al.* in press). Brood parasitism has been found to increase with forest fragmentation (Robinson *et al.* 1995).

Though generally recognized as important, the impact of competition on

community structure is still poorly understood (Kelt *et al.* 1995). Both the red-winged blackbird and the introduced european starling are abundant ubiquitous species along the agricultural intensity gradient, reaching their highest numbers at high agricultural intensities. Their impacts in the form of crop losses are well documented (Dyer and Ward 1977, Tyler and Kannenbury 1980) but their potential influence as competitors is less well known. European starlings are known to compete aggressively for nest sites and can limit the abundance of cavity-nesting species (Kerpez and Smith 1990, Ingold 1994). The impact of red-winged blackbird competition has only been investigated between this species and other icterid species in marsh habitats (Orians and Collier 1963, Miller 1968). The potential for the red-winged blackbird as an important competitor in agricultural landscapes has not been examined. Red-winged blackbirds are aggressive intraspecific competitors (Searcy 1979) and can nest in a variety of habitats in the agricultural landscape (Best *et al.* 1995), often in very high densities (e.g. Basore *et al.* 1986, Warner 1992, Camp and Best 1994). Camp and Best (1994) found that red-winged blackbirds had the highest nest density in grassy roadsides adjacent to rowcrop fields, while other species that commonly nest in grassland habitats were absent. Although not demonstrated, it is possible that red-winged blackbirds were excluding other species from nesting in these linear grassy habitats.

Ring-billed gulls are a highly adaptable, opportunistic species. Currently, this species frequents landfills and urban and agricultural areas in addition to their traditional aquatic habitats (Blokpoel and Tessier 1986). This is another example of

landscape complementation (Dunning *et al.* 1992, Taylor *et al.* 1993). As a result, ring-billed gull populations have increased markedly. In agricultural areas, ring-billed gulls are often found in large numbers and are known to prey on invertebrates, small mammals, and birds in agricultural fields (Bent 1921, Blokpoel and Tessier 1986). The impact that these birds have as predators and competitors on the faunal diversity and abundance in agricultural landscapes is poorly understood. In my study, ring-billed gulls were found only at the high end of the intensity gradient. This is probably because these areas contained the highest percentage cover of foraging patches (actively farmed habitats) and the lowest percentage cover of non-foraging patches (forest) for gulls in the landscape. These sites typically had low bird species richness, diversity and evenness. Thus the addition of a predator/competitor such as the ring-billed gull in large numbers could have serious impacts on an already diminished bird assemblage.

The association of ring-billed gulls with only high intensity agricultural areas along the gradient should be interpreted with caution. The spatial scale of this study is much smaller than the spatial scale of daily ring-billed gull movements (Belant *et al.* 1993, Potter unpublished manuscript) and gulls tend to use agricultural areas near landfills or along flight paths between landfills and the breeding colonies more frequently than other agricultural areas (Horton *et al.* 1983, Potter unpublished manuscript). Extrapolating across scales can lead to erroneous interpretation of results (Wiens 1989) and hence the usefulness of multiscale studies directed at answering questions concerning adaptable species (e.g. Clergeau 1995, Pedlar 1995).

Therefore in addition to the stresses imposed on the bird assemblage through anthropogenic landscape changes, species that have benefitted from such changes may be exerting a strong influence on the structure of the bird assemblage along the agricultural gradient. This study serves as a scale specific starting point for more research focused on the effects of potentially overabundant or rapidly expanding species on the faunal composition in agricultural landscapes, and the effects of landscape structure on the distribution and abundance of these species.

Studies that have varied the proportions of different habitat types have concluded that highest species richness and diversity occur when habitats are in equal proportions in the landscape (Franklin and Forman 1987, Andrén 1992). Other studies have taken this one step further by claiming that maintaining a high habitat diversity in the landscape translates into high biodiversity at the species level (Pimentel *et al.* 1992, Andrén 1994, Barrett and Peles 1994). In contrast, my study demonstrated that the largest number of bird species was *not* found in landscapes containing the highest landscape diversity (determined by the Shannon-Wiener index, H'), rather the number of species reached a maximum in low intensity, heavily wooded landscapes with low landscape diversities (forest was considered as one habitat type only, see methods for definition of habitat types). Balent and Courtiade (1992) came to a similar conclusion for birds in an agricultural landscape in France.

I am not advocating a particular approach to conserving biodiversity in agroecosystems. Rather, I am stressing that a generalization such as "conserving habitat diversity will conserve biodiversity" needs to be qualified with specific

references to the scale and manner in which heterogeneity is measured, the definition of biologically relevant habitat types and the landscape system to be examined. .

Thus, the way one defines and measures habitat diversity may influence the relationship with biodiversity. Diversity can be divided into three components: alpha (within habitat), beta (between habitats) and gamma (regional), and these components are often defined differently by various authors (Noss 1983, Harrison 1993). In my study, my measures of habitat (landscape) diversity and species diversity would be considered indices of gamma diversity as they incorporated a series of habitats within a landscape (*sensu* Noss 1983). As well, the term diversity may simply mean the number of habitat types, or the number of habitat types and their relative proportions. My measure was a reflection of the latter. Balent and Courtiade (1992) found that species richness generally decreased from the forested end (low ecological diversity) to the corn end of their gradient, whereas ecological diversity displayed a quadratic relationship to the forest-to-corn gradient and reached a maximum at some mid-point along the gradient. In this case, ecological diversity (see Figure 2 in Balent and Courtiade (1992)) measures community structure, and is roughly equivalent to grain size diversity (i.e. landscape complexity) which can be used to measure landscape structure . However, Andrn (1994) predicts that the insertion of new habitats into a landscape will result in a higher species richness in the landscapes even if these new habitats are human-made. Pimentel *et al.* (1992) imply that increasing biodiversity can be achieved by increasing habitat diversity, which was defined as the number of different physical habitat types. Barrett and Peles (1994) suggest using methods to

measure landscape (gamma) diversity that incorporate the number of different patch types and the connectivity of these patches in the landscape, in order to maximize biodiversity in agroecosystems.

Defining ecologically relevant habitat types is also important when examining the relationship between habitat diversity and biodiversity. By delineating different patch types, I am implying that each type is discreet and internally homogeneous (Kotliar and Wiens 1990). Forest was considered a habitat type in my study, but Freemark and Merriam (1986) have demonstrated the positive relationship between within-habitat heterogeneity (a measure of alpha diversity) in forest patches and bird species richness. This would suggest that my scale of defining patches may suffice for actively farmed areas but not for non-crop habitats as birds appear to respond to patchiness at a finer scale than that of the forest patch. This is further supported by a study in the Swedish agricultural landscape, where Robertson *et al.* (1986) found that a more heterogeneous landscape with roughly the same percentage cover of arable land as a less heterogeneous landscape, contained more bird species. In this study, they differentiated among non-crop habitats but not among crop habitats. Perhaps a more detailed look at the heterogeneity of the non-crop habitats in my studied landscapes would have provided clearer insights into the observed changes in the bird assemblage along the agricultural intensity gradient and their relationship to habitat diversity.

The relationship between habitat diversity and biodiversity may also depend on the landscape system that is under study. For example, examining species diversity in

a managed forest versus an agricultural system may not produce the same pattern in relation to habitat diversity. Both systems have undergone anthropogenic disturbances but the agricultural landscape is subjected to a higher frequency of disturbance through the management of various actively farmed habitats (Best *et al.* 1995). My study has shown that increased land use for agriculture and subsequent loss of native forest habitat results in a bird assemblage with decreasing species richness, diversity and evenness. Conversely, forests managed for timber have been found to have increased bird species richness as fragmentation increased (Rosenberg and Raphael 1986). Also, McGarigal and McComb (1995) found the abundance of species associated with late seral stages generally to be highest in the more heterogeneous landscapes. In both of these studies, seral conditions found within forests were treated as different patches. Therefore, landscapes having undergone different degrees of human disturbance may show different relationships between species richness and habitat diversity.

Agricultural intensity is a term that is often used (e.g. Hanski and Tiainen 1988) but generally lacks any clear ecological measure. Intensity can be defined from an anthropocentric viewpoint or from the organism-of-interest viewpoint. In the latter view, the amount of historic or natural habitat left in the landscape can be used as a measure of intensity (Pedlar 1995). This would suffice for a single or few species study, but I was interested in the whole bird assemblage, including species having different habitat requirements in these landscapes (Best *et al.* 1995). From a purely anthropocentric point of view, intensity can be measured by cultural energy (Pimentel

1980, Anderson 1991), a measure of the human-derived energy inputs into production of various crop types. My measure of agricultural intensity is a balance of both ecological and anthropogenic points of view. I incorporate the relative proportions of the various habitat types in the landscape and yet I distinguish between the various crop types as separate habitats that have undergone varying levels of energy and resource inputs.

This study demonstrates the need for more studies done at a spatial scale greater than that of the individual patch (Wiens 1989, Fry 1991, Andrén 1994, Freemark 1995). Although simplistic in its approach, the gradient of agricultural intensity is useful for examining general patterns of the bird species assemblage at the landscape scale and elucidating possible hypotheses at the assemblage and species level in relation to landscape structure. A hierarchical approach examining interactions at various spatial scales is required for better management of agroecosystems in the future (Freemark 1995). This study is a start in that direction.

CONCLUSIONS

In summary, landscape change brought about by agriculture has had effects on the bird assemblage along a gradient of agricultural intensity. Bird species richness, diversity and evenness all decreased significantly as agricultural intensity increased. This was largely related to loss of a species-rich habitat, forest, and the gain of species-depauperate habitats, crop types, along the gradient.

Concurrent with these quantitative changes in the bird assemblage were qualitative changes. Species associated with the forest interior dominated the

assemblage at low agricultural intensities. As intensity increased through habitat loss (forest) and novel habitat introduction (actively farmed habitats), the forest species pool rapidly decreased and was replaced by habitat generalists that persisted along the gradient while the forest species continued to decline. In areas of high intensity, the assemblage was dominated by habitat generalists. The ability of these species to supplement their resources in agricultural habitats was a likely reason for their success.

Some of these abundant species are known to be either brood parasites, predators or competitors on the existing bird assemblage. This study serves as a starting point for research focused on these potentially damaging species. The implications that my results have for conserving avian biodiversity in agroecosystems oppose a commonly held view that conserving habitat diversity translates into conserving biodiversity at the species level. Such a generalization must be qualified with more relevant ecological information. This study is a scale-specific study of general patterns in the bird assemblage at a spatial scale larger than is traditionally examined in agroecosystems.

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Table 1 - Principal components derived from landscape variables measured within a 1 km radius at 29 sites in agricultural areas in eastern Ontario. Landscape variables are ordered according to their absolute loading on the first principle component.

PC variables	Principal Components	
	PC1	PC2
Eigenvalue	4.98	2.52
% variance	45.3	22.9
Cumulative % variance	45.3	68.2
Component loadings		
FOREST	-0.43	-0.02
TILL	0.37	-0.30
SILOS	0.37	-0.19
HAY	0.35	0.30
CORN	0.34	-0.34
UNTILL	0.34	0.38
GRAIN	0.26	0.08
SOYABEAN	0.20	-0.28
PASTURE	0.20	0.38
OLD FIELD	-0.16	0.17
EDGE	0.08	0.51

Table 2 - Bird species ranking along classes of increasing agricultural intensity based on cumulative abundances. Sites are grouped into agricultural classes according to first principle component scores.

Bird Species	Agricultural Intensity Class					
	Wooded	Low	Midlow	Mid	Midhigh	High
Ovenbird	1	3	25	22	31	31
American Robin	2	8	5	5	5	7
Black-and-White Warbler	3	14	23	42	50	44
Nashville Warbler	4	26	A	40	43	A
Black-capped Chickadee	5	9	13	15	32	24
White-throated Sparrow	6	18	48	A	37	46
Blue Jay	7	24	14	26	34	16
Common Yellowthroat	8	12	9	39	25	35
Song Sparrow	9	2	2	2	4	4
European Starling	10	5	3	1	3	3

* A = Absent

Table 3 - Bird species ranking along classes of decreasing agricultural intensity based on cumulative abundances. Sites are grouped into agricultural classes according to first principle component scores.

Bird Species	Agricultural Intensity Class					
	High	Midhigh	Mid	Midlow	Low	Wooded
Red-winged Blackbird	1	1	3	1	1	33
Savannah Sparrow	2	2	4	4	7	34
European Starling	3	3	1	3	5	10
Song Sparrow	4	4	2	2	2	9
Horned Lark	5	9	9	22	A	A
Bobolink	6	7	12	7	4	18
American Robin	7	5	5	5	8	2
Barn Swallow	8	15	8	6	13	46
Brown-headed Cowbird	9	6	7	17	14	54
Ring-billed Gull	10	A	A	A	A	A
Vesper Sparrow	10	11	13	27	55	A

* A = Absent

Figure 1 - Locations of 29 study sites near Ottawa, Ontario.

Figure 2 - Scatter plot of percent cover of forest within a 1 km radius from the center of each study site (n=29) along a gradient of agricultural intensity. See methods for definition of agricultural intensity.

Figure 3 - Scatter plot of percent cover of tilled land within a 1 km radius from the center of each study site (n=29) along a gradient of agricultural intensity. See methods for definition of agricultural intensity.

Figure 4 - Scatter plot of number of silos within a 1 km radius from the center of each study site (n=29) along a gradient of agricultural intensity. See methods for definition of agricultural intensity.

Figure 5 - Scatter plot of percent cover of hay within a 1 km radius from the center of each study site ($n=29$) along a gradient of agricultural intensity. See methods for definition of agricultural intensity.

Figure 7 - Scatter plot of percent cover of untilled land within a 1 km radius from the center of each study site (n=29) along a gradient of agricultural intensity. See methods for definition of agricultural intensity.

Figure 8 - Scatter plot of percent cover of grain within a 1 km radius from the center of each study site ($n=29$) along a gradient of agricultural intensity. See methods for definition of agricultural intensity.

Figure 9 - Scatter plot of percent cover of soyabean within a 1 km radius from the center of each study site ($n=29$) along a gradient of agricultural intensity. See methods for definition of agricultural intensity.

Figure 10 - Scatter plot of percent cover of pasture within a 1 km radius from the center of each study site (n=29) along a gradient of agricultural intensity. See methods for definition of agricultural intensity.

Figure 11 - Scatter plot of percent cover of old field within a 1 km radius from the center of each study site (n=29) along a gradient of agricultural intensity. See methods for definition of agricultural intensity.

Figure 12 - Scatter plot of length of edge within a 1 km radius from the center of each study site (n=29) along a gradient of agricultural intensity. See methods for definition of agricultural intensity.

Figure 13 - Bird species richness along a gradient of agricultural intensity (n=29) modelled using simple linear regression. See methods for definition of agricultural intensity.

Figure 14 - Mean bird species evenness (J') along a gradient of agricultural intensity (n=29) modelled using simple linear regression. See methods for definition of agricultural intensity.

Figure 15 - Mean bird species diversity (H') along a gradient of agricultural intensity ($n=29$) modelled using simple linear regression. See methods for definition of agricultural intensity.

Figure 16 - Species turnover between adjacent sites along a gradient of agricultural intensity ($n=28$) modelled using simple linear regression. See methods for definition of agricultural intensity.

SCHEFFE'S TEST FOR CLASS VARIABLES

w-l l-ml ml-m m-mh mh-h

Figure 17 - Mean species turnover between adjacent agricultural intensity classes. Sites were grouped into the following classes based on first principle component scores: W=wooded, l=low, ml=midlow, m=mid, mh=midhigh, and h=high. The significance of the model was examined using a one-way ANOVA, and differences between classes were tested using a Scheffe's test.

Figure 18 - Cumulative number of individuals detected over five censuses along the different agricultural intensity classes. See methods for definition of agricultural intensity classes. RWBL - red-winged blackbird, BHCO - brown-headed cowbird, EUST - european starling, RBGU - ring-billed gull.

Figure 19 - Total number of birds detected for five censuses along a gradient of agricultural intensity. See methods for definition of agricultural intensity.

Figure 20 - Landscape diversity (H') along a gradient of agricultural intensity ($n=29$) modelled using polynomial regression. See methods for definition of agricultural intensity.

Appendix 1 - Principal component scores for 29 sites based on landscape variables measured at a 1 km radius from the centre of each site.

Site	Principal Component Score
6	-3.92
7	-3.92
9	-3.73
13	-3.60
47	-2.50
5	-2.35
53	-2.21
21	-1.92
4	-1.63
20	-1.05
8	-0.67
14	-0.31
2	-0.03
11	0.08
34	0.63
15	0.95
16	1.17
26	1.41
48	1.43
18	1.83
19	1.87
27	1.95
24	1.95
3	1.98
49	2.09
17	2.38

52	2.52
28	2.52
1	3.09

END

0 6-0 6-9|6

FIN