corresponding author:

Alec R. Lindsay
3015A Museum of Zoology
University of Michgian
1109 Geddes Avenue
Ann Arbor, MI 48109-1079

Avian assemblage differences between developed and undeveloped lakeshores in a mixed northern forest.

Alec R. Lindsay, Museum of Zoology and Department of Biology, 1109 Geddes Avenue, The University of Michigan, Ann Arbor, MI 48109-1079: arlindsa@umich.edu

Sandra S. Gillum, Michael W. Meyer, Wisconsin Department of Natural Resources, 107 Sutliff Avenue, Rhinelander WI, 54501

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Abstract

We report findings of a two-year study (1996-1997) surveying breeding birds in lacustrine habitats of northern Wisconsin, USA. This area has seen marked increases in lakeshore housing development in recent years, and other studies have indicated significant shoreland habitat alteration. We paired developed and undeveloped lakes of similar physical characteristics and performed point-counts around the perimeter of each to assess avian assemblages. Our results showed no significant differences between developed and undeveloped lakes in avian abundance, richness or species diversity. Several species and some resource-guilds were commonly associated with one lake-type or the other. We did find a significantly higher diversity of diet guilds on developed lakes whereas undeveloped points had significantly lower diversity of foraging guild diversity. Seed-eaters were significantly associated with developed lakes, and insectivores showed marked declines on developed lakes. We propose that levels of development on lakeshores in northern Wisconsin are high enough to alter breeding bird habitats, and furthermore that observed decreases in numbers of insectivores on developed lakes may be of concern.

Introduction

Studies of avian community changes due to anthropogenic influences in temperate regions of North America have focused largely on the effects of forestry practices (e.g. Hagan et al., 1997; Merrill et al., 1998; Drolet and Desrochers, 1999). Studies have also assessed the effect of human habitation on the avifauna of urban parks (Tilghman, 1987; Friesen et al., 1995), showing declines in bird diversity and abundance as human development increases. Lakeshore habitats with nearby timber harvest were found to have more birds near undisturbed lakeshores and buffer strips than harvested land (Johnson and Brown, 1990). Forested lacustrine landscapes are under increasing development pressure as more people are building homes and cottages on lakeshores in northern forested areas. Despite the rapid rate of lakeshore development the effects of lakeshore development on breeding bird assemblages remain largely unstudied. Here we report results of a study that examined the differences in avian assemblages between developed and undeveloped lakeshores, and we further consider the ramifications of these observations to the future health of lakeshore habitats.

Although differences in avian abundances and diversities are often considered indicative of significant habitat change (Boulinier et al., 1998; Marsden, 1998), analyses of ecological guild composition are sensitive to more subtle differences in vegetation structure and avian habitat suitability (Croonquist and Brooks, 1991). The utility of the guild concept (sensu Root, 1967) has been debated at length in the literature (i.e. Verner, 1984; Szaro, 1986, etc.), but guild assessment has proven helpful in many studies of changes in avian assemblages (O’Connell et al., 1998; Canterbury et al., 2000). More than simply indicating significant habitat alteration, changes in avian guild composition may have larger implications for the ecological health of entire lakeshore communities, especially given the roles birds play as insect predators.

Marquis and Whelan (1994) found increased insect damage and consequent declines in plant biomass associated with the loss of insectivorous birds, and Sipura (1999) detailed the complex multi-trophic interaction between avian predators, defoliating insects and woody plant productivity. The injury and mortality of native plants caused by populations of phytophagous insects (i.e. elm spanworm *Ennomus subsignarious* on red maple *Acer rubrum* (Haney, 1999), budworms *Choristoneura spp.* on firs and pines (Miller and Rusnock, 1993; Radeloff et al., 2000)) can be considerable for environmental managers and lakeshore homeowners alike. Northern Wisconsin has seen marked increases in the numbers of defoliating insects such as: tent caterpillars *Malacosoma disstria*, large aspen tortrix *Choristoneura conflictana*, aspen blotch miner *Phyllonorycter spp*, basswood thrips *Thrips calcaratus*, forest hemlock borer *Melanopila fulvoguttata* and several others (WDNR, 1999). Population increases of insect pests may be of special concern if avian resource-guilds are altered by anthropogenic changes.

Forested lacustrine landscapes provide habitats for breeding birds, but are also increasingly valuable commodities for human residential development. Lakeshore properties in northern Wisconsin have seen significant increases in subdivision and residential development over recent decades (WDNR, 1996), placing shoreline habitats under increasing stress. This development has produced significant differences in the vegetation structure of these habitats (Elias and Meyer *in prep*) and declines in amphibian abundance have also been documented (Woodford and Meyer, *in prep*). As part of a comprehensive study of residential development pressure in northern Wisconsin, we assessed the effect of lakeshore development on avian assemblages, with particular reference to differences in both species diversity and ecological guild composition. This assessment was undertaken using avian census data collected at point-count sites around lakes with varying degrees of residential development. To associate differences in bird assemblages with residential development, we examined (1) avian abundance, richness and diversity values, (2) ecological guild diversity and dominance, and (3) species/guild associations with lake type.

Methods

Study area and site selection

This study was conducted in a forested landscape of northeastern Wisconsin, USA. This area is characterized by a high density of kettle lakes surrounded by mixed deciduous/coniferous forests. Forests are dominated largely by paper birch *Betula papyrifera*, quaking aspen *Populus tremuloides*, red oak *Quercus rubra*, sugar maple *Acer saccharum*, white pine *Pinus strobus*, and red pine *P. resinosa*, and to a lesser degree, hemlock *Tsuga canadensis*, yellow birch *B. alleghaniensis*, and red maple *A. rubrum* (see Elias and Meyer, *in prep* for further description). Study sites were located largely on privately owned lands subject to development guidelines set by state statute and local county zoning codes, although several study lakes were located within the Chequamegon-Nicolet National Forest, where shoreland is managed by the U.S. Forest Service.

Development on study lakes was indexed (*Dv*=shoreline development index) by the number of developed properties (determined by GIS database) per 100 meters of shoreline; a completely developed lake by Wisconsin Shoreline Management regulations (NR115) could have 3.3 houses per 100 meters of shoreline (*Dv*=3.3). Lakes in Vilas, Oneida and Forest counties were selected for censuses and were of two types: those with high levels of shoreline development (developed *Dv*: μ_d= 0.98, SD=0.457) and those with low levels/no shoreline development (undeveloped *Dv*: μ_u= 0.058, SD=0.108). Lake selection was not random, but instead such that each undeveloped lake was paired with a developed lake based on similarities in surface area, shoreline length, water chemistry, water color and water source. Apart from the 17 pairs of developed and undeveloped lakes, four large lakes with high concentrations of development were also sampled. These four lakes (Little and Big St. Germain Lakes, Lost Lake, Lake Minocqua) were larger than most other lakes, and not paired with undeveloped lakes, as there were no comparable undeveloped lakes of similar geophysical characteristics. These lakes were used in regression analyses described below, but in none of the paired tests.

Bird Sampling and Habitat Classification

From 2-27 June 1996-97 each lake was censused once between the hours of 0500 and 1000 EST by two observers. Surveys did not occur on days with moderate/heavy wind or rain. For each of the 34 paired lakes, locations of point-counts were evenly spaced around lakeshores, as determined by the following process: observers first canoed to the center of each lake and identified the first shore landing site by random compass bearing (from 0-360°N) generated from a random number table. From the first shore reference, five more landing sites were demarcated around the lakeshore at 60° intervals. Starting with a random landing site of the six and continuing around the lake, counts would begin at points fifty meters inland from each shore landing, using unlimited-radius counts of 10-minute duration recording all birds seen and heard (after Howe et al., 1993; Gillum, 1995). In the event a bird was not identified to species (e.g. an unknown woodpecker drumming), we included it in our calculations as long as no other taxonomically similar bird of known identity was detected at that point. On the four high-development lakes, locations of nine point-count sites were determined around each lake with assistance of maps to better cover the larger, more irregular shorelines of these lakes. At each point habitats were classified following the scheme of the Wisconsin Breeding Bird Atlas (WSO, 1995) and estimates of the percentage cover of the canopy, sub-canopy and shrub layer were also recorded.

Data analyses

From data collected at each point, abundance (number of birds), richness (number of species) and diversity measures were calculated. In an effort to circumvent shortcomings of different diversity indices, all analyses were conducted using both Shannon's (1948) and Simpson's (1949) indices. Results from both analyses were similar and thus we only report analyses using Shannon's index. We calculated Shannon's index of diversity as:

$$H' = -\sum_{i=1}^{s} (p_i)(\log p_i)$$

where s= number of species p_i= proportion of total sample belonging to the i^{th} species. We also calculated the above metrics for entire lakes, rather than just points.

To further assess differences in assemblages of birds, we evaluated differences in three types of avian resource-guild (sensu Wilson, 1999) classes of association: foraging, diet and nesting classes. Guild assignment within each class followed Ehrlich et al., (1988), recognizing 14 foraging (*f*) guilds, 9 diet (*d*) guilds and 9 nesting (*n*) guilds. For each of these resource-guild classes, diversity indices were calculated with the same equation as above, but using guild associations as the primary unit of measure. Instead of using the number of individuals of each species to calculate diversity indices, the number of individuals of each guild were used to calculate guild-class diversity indices. In essence this suspends the significance of species, and instead looks at ecological groups of birds, considering one bird occupying a niche no different from another bird occupying the same niche, regardless of species. In this view, a ground-nesting ovenbird *Seiurus aurocapillus* is counted with a ground-nesting hermit thrush *Catharus guttatus*. We use the convention of reporting the diversity index as (H'_x), where x can take the value of s, f, d, and n, corresponding to species, foraging-class, diet-class and nesting-class indices, respectively. All statistical tests mentioned in the following section were performed using species diversity indices as well as guild diversity indices; for clarity, they are only described in the form of species diversity comparisons.

To compare Shannon indices (H'_1) and (H'_2) of two assemblages, a test statistic was calculated by

$$t = \frac{H_1 - H_2}{\sqrt{s_1^2 + s_2^2}}$$

and the variance estimated as

$$s^2 = \frac{\sum_{i=1}^{s} p_i \log^2 p_i - (\sum_{i=1}^{s} p_i \log p_i)^2 / n}{n^2}$$

compared to the Student’s t distribution for degrees of freedom calculated by

$$df = \frac{[s_1^2 + s_2^2]^2}{(s_1^2)^2 / N_1 + (s_2^2)^2 / N_2}$$ (see Hutcheson, 1970).

Values of abundance, richness and diversity indices were also compared between the 34 lakes of the two development types using a simple two-tailed paired t-test. Unless otherwise noted below, p-values given in results which compare all developed and undeveloped lakes were generated by two-tailed paired *t*-tests. Since some developed lakes had points without any nearby developments (and *vice versa*), we also compared diversity measures between all undeveloped points and all developed points, regardless of lake-type, using two-tailed unpaired *t*-tests. For all statistical tests we set α=0.05.

The relationships of habitat variables to bird diversity estimates at individual points were evaluated using regression techniques. Simple linear regressions of each habitat variable (%'s of canopy, sub-canopy and shrub cover) and each avian community measure (abundance, richness, H'_x) were examined to detect habitat characteristics which correlate with diversity estimates. Simple linear regressions were also used to assess the effect of lakeshore development on avian assemblages by regressing dependent bird variables of entire lakes on shoreline development indices (*Dv*).

Log-likelihood (*G* tests: Zar, 1984) tests were used to evaluate associations of individual species (or guilds) with particular lake types. After generating a typical contingency table

species Y	DEVELOPED	UNDEVELOPED
PRESENT	a	b
ABSENT	c	d

values for the *G*-statistic were calculated as

$$G = 4.60517[\sum_i \sum_j f_{ij} log f_{ij} - \sum R_i log R_i - \sum C_j log C_j + nlogn]$$

where f_{ij} are the values of each cell in rows i and columns j, R_i are row totals, C_j are column totals, n are the total observations. G-statistics were then compared to a χ^2 table for one degree of freedom (Zar, 1984).

Results

Shoreline development indices were significantly higher on developed lakes than on undeveloped lakes ($p<0.01$) and average estimated percentages of canopy, sub-canopy and shrub cover were also significantly lower on developed lakes than undeveloped lakes ($p<0.05$). Point-count locations on developed lakes were often located near human structures and were classified as upland rural residential (URR: n=57), upland rural resort (URRr: n=2), upland rural commercial (URC: n=1), upland rural open space (URO: n=2) and upland small town residential (USR: n=6) for a total of 68 developed sites. There were 26 sites on developed lakes that were designated as upland forest types as there were no developments within sight of those points (@100-150m). Nearly all sites on undeveloped lakes were classified as upland forest types (n=82) but 2 were near homes and classified as upland rural residential (URR). Due to the random placement of points along lakeshores, several points (n=16) on 10 lakes (7 undeveloped, 3 developed) were unapproachable due to floating bogs, swamps or other obstacles.

A total of 3114 individual birds representing 107 species were identified across 224 point counts on 38 lakes (see Appendix). The 12 most commonly observed species (>75 individuals and present at >50 point-count sites) were, in decreasing frequency: red-eyed vireo *Vireo olivaceus*, american crow *Corvus brachyrynchos*, ovenbird *Seiurus aurocapillus*, american goldfinch *Carduelis tristis*, american robin *Turdus migratorius*, black-capped chickadee *Poecile atricapilla*, song sparrow *Melospiza melodia*, blue jay *Cyanocitta cristata*, chipping sparrow *Spizella passerina*, red-winged blackbird *Agelaius phoenicus*, chestnut-sided warbler *Dendroica pensylvanica* and black-throated green warbler *Dendroica virens*. On average 13.1 birds (5.5 species) were observed per undeveloped site and 13.9 birds (5.1 species) were observed per developed site ($p>0.05$ for both metrics). Measures of species diversity (H'_s), foraging-guild diversity (H'_f) and nesting guild diversity (H'_n) were not significantly different between developed and undeveloped lakes (Table 1: $p>0.05$), although 11 of 17 individual lake pairs showed significant differences in species diversity by Shannon diversity measures (H'_s: see Table 2). There were no significant relationships between shoreline development and avian: abundance (R^2=0.029), richness (R^2=0.070), species diversity (H'_s: R^2=0.034), foraging guild diversity (H'_s: R^2=0.003) or nesting guild diversity (H'_s: R^2=0.007).

Diet-guild diversity measures (H'_d) showed significant differences between developed lakes (Dev μ_{Hd}=0.43) and undeveloped lakes (Undev μ_{Hd}=0.31) ($p<0.01$). Diet-guild measures were also significantly higher at developed points (Dev μ_{Hd}=0.32) than at undeveloped points (Undev μ_{Hd}=0.22) ($p<0.01$), while foraging-guilds were significantly less diverse at developed points (Dev μ_{Hd}=0.48) than at undeveloped points (Undev μ_{Hd}=0.54) ($p<0.01$). In regression analyses, diet-guild diversity measures (H'_d) were the only indices to show significant effects of shoreline development (R^2=0.45, $p<0.01$: Fig. 1). However, values for each lake appeared to more clearly indicate a bipartite response to development depending on a threshold of ~ 0.35 *Dv* (see Fig. 1). A regression of lakes with development indices less than 0.35 *Dv* showed no significant correlation between diet-guild diversity and development (Fig 1*c*: $R^2<0.01$). Similar results were obtained for those lakes with development indices higher than 0.35 (Fig 1*b*: R^2<0.02). It is notable that one of our developed lakes fell below the *Dv*~0.35 threshold (Taylor Lake: *Dv*=0.18), and one of the undeveloped lakes fell above that value (Razorback Lake: *Dv*=0.42), yet each was appropriately paired with a lake of opposite development (Sunfish Lake: *Dv*=0.00 and Found Lake: *Dv*=1.56, respectively). The significance of these lakes will be noted later in the Discussion. Values of avian richness, abundance and diversity at each point did not correlate (R^2<0.10) with any of the three measures of habitat structure (% canopy, % sub-canopy, % shrub cover) in simple linear regressions, or in multiple regression analyses including combinations of all three variables.

Several species showed significant associations with developed or undeveloped lakes. The american crow *Corvus brachyrhynchos*, american robin *Turdus migratorius*, american goldfinch *Carduelis tristis*, eastern phoebe *Sayornis phoebe*, great crested flycatcher *Myiarchus crinitis*, baltimore oriole *Icterus galbula* and the red-winged blackbird *Agelaius phoeniceus* were all associated with developed lakes (p<0.05; G-test). The black-and-white warbler *Mniotilta varia*, black-throated blue warbler *Dendroica caerulescens*, common loon *Gavia immer*, golden-crowned kinglet *Regulus satrapa*, hermit thrush *Catharus guttatus*, ruffed grouse *Bonasa umbellus* and the warbling vireo *Vireo gilvus* were associated with undeveloped lakes (p<0.05; G-test). Several guilds were also significantly associated to different lake types, with surface-divers to undeveloped lakes and seed-eaters to developed lakes (p<0.05; G-test). Birds which typically nest on manmade structures were also associated with developed lakes (p<0.05; G-test). Given the significant association of seed-eating species with developed lakes, we removed the seven species classified as seed-eaters (see Appendix) from all point-counts for a separate analysis. Although diversity/abundance/richness metrics were different from those generated from the original data set, there were no observed differences between developed and undeveloped lakes/points for an measures except diet-guild diversity (points and lakes) and foraging-guild diversity (points only).

Figure 2 shows the contributions of each guild (within each of the three classes: foraging, diet, nesting) to the assemblages observed at developed and undeveloped lakes. Most guilds showed negligible difference between lake types, but several differences are worth note. Among foraging guilds (Fig. 2a), ground gleaners increased (34→42%) on developed lakes while hover and gleaners (17→13%) and bark gleaners (8→5%) both declined on developed lakes. Within diet guilds, insectivores declined on developed lakes (79→69%), whereas omnivores (9→15%) and seed-eaters (5→9%) increased on developed lakes. Finally, developed lakes had marked increases in deciduous tree-nesting birds (26→37%) and declines ground-nesters (27→17%) and coniferous-tree nesters (21→17%).

Discussion

Habitat fragmentation is a well-studied cause of avian community change, especially drastic habitat change such as that generated by timber harvest (Bosakowski, 1997; Thiollay, 1997; Merrill et al., 1998). Although lakeshore homeowners typically make less dramatic changes to the structure of forests, human development does have notable effects on lakeshore vegetation structure (Elias and Meyer, *in prep*). The increases in development rates are alarming (WDNR, 1996) – two out of every three lakes which were undeveloped in 1965 are now developed in northern Wisconsin. In our study area, avian species abundance, richness and diversity measures appear to be similar between developed and undeveloped lakes as well as individual points. However, assessments of ecological guild structure show some changes in response to anthropogenic disturbance. Effects appear largely to be limited to differences in the composition of diet guilds (Table 1); seed-eaters increase on developed lakes and although not significant, the data also indicate some association of insectivores to undeveloped lakes (Fig. 2b). On a more local scale, undeveloped points had more diverse foraging guilds than developed points, along with decreased diet-guild diversity. These data indicate lakeshore development does have some effect on the structure of native avian assemblages.

Regressions of each community measure against lakeshore development yielded insignificant relationships, except for diet-guild diversity measures (Fig. 1). However, the results for diet-guild regressions are clearly bipartite, where lakes with low development also show lower diet-guild diversity, and vice versa. The difference in response occurs around a development level of 3-4 lakeshore improvements per 1000m of shoreline (*Dv*~0.35). This effect may be confounded by the experimental set-up of pairing developed and undeveloped lakes, which would arguably partition the data into two groups. However, the two lakes which do not fall into their appropriate groups (undeveloped Razorback Lake (*Dv*=0.43) and developed Taylor lake (*Dv*=0.18)), provide some confirmation of the observed development threshold. Razorback Lake was classified as undeveloped by our protocol as it was paired with Found Lake (*Dv*=1.56), yet the diet-guild diversity of Razorback falls clearly within the group of developed lakes. Likewise the developed Taylor lake (*Dv*=0.18), which was paired with the undeveloped

Sunfish lake (*Dv*=0), has a diet-guild diversity index which is clearly within the group of other undeveloped lakes (see Fig. 1). These observations provide some indication of a development threshold (around 3-4 lakeshore improvements per 1000m) which affects avian assemblages.

Several species show significant associations with developed lakes (see Appendix); some of which are typically regarded as insensitive to, or even positively affected by disturbance. Brown-headed cowbirds *Molothrus ater* can affect the reproductive output of other species (Robinson et al., 1995) and their presence may have significant consequences for other breeding birds around these lakeshores. Cowbirds were observed at 8 of 17 developed lakes as well as at 4 of 17 undeveloped lakes, which is a non-significant association ($p>0.05$). Common Loons were significantly associated with undeveloped lakes ($p<0.01$), which is not unexpected as they are considered sensitive to human disturbance (Jung, 1991; Caron and Robinson, 1994). Although ground-nesters were not associated with either lake type ($p>0.05$), none of the seven species associated with developed lakes are ground-nesters, but four of the seven species associated with undeveloped lakes are ground-nesters.

Although few ecological guilds showed significant associations with either lake type, there were discernible differences in the composition of avian assemblages on developed and undeveloped lakes. A conservative interpretation of the data presented in Figure 2 confirms the observation that lakeshore development can both enhance and depreciate the quality of habitats for birds, depending on the ecological requirements of individual species. Although we have no data correlating factors like nest predators with developed or undeveloped lakes, prior studies (i.e. Schmidt and Whelan, 1998) found increased effects of nest predators like raccoons *Procyon lotor* and domestic cats (Dunn and Tessaglia, 1994) associated with human habitat alteration. Factors like these may be responsible for the decline in ground-nesters on developed lakes, as well as direct anthropogenic disturbance from landscape maintenance (mowing, clearing, etc.). Supplemental bird feeding by human residents is likely responsible for the significant increase in seed-eaters on developed lakes, but other causal factors involved in the observed guild changes are less obvious.

Our tests of guild associations indicate only that seed-eaters are significantly preferring developed lakes, but the comparisons between developed and undeveloped lakes of the diet-guild composition are still worth noting. Defoliating insects can cause modest-to-severe damage on forests (Syme, 1990; Bell and Whitmore, 1997), and insectivorous birds can play a significant role in the biological control of defoliating pests (Loyn et al., 1983; Haney, 1999). The observed decline of insectivorous birds on developed lakes (Fig. 2) may prove to be significant for the future health of lakeshore forests – a commodity of interest to wildlife managers and lakeshore homeowners alike.

Most of the metrics (abundance, richness, species diversity, foraging-guild diversity, nesting-guild diversity) describing breeding bird assemblages are similar between developed and undeveloped lakes in northern Wisconsin. However, lakeshore development does correlate with increases in diet-guild diversity, and there is some evidence that insectivores and ground-nesters prefer lower development levels. In particular, changes in diet guild diversity appear to occur near a development threshold of 3-4 improvements per 1000m of shoreline – a level that is much lower than the current regulatory guidelines of 3 developments per 100 meters of shoreline (NR 115). Several species are significantly associated with undeveloped lakes, but none of these species are listed as being of particular conservation concern (Thompson et al., 1993). These results do not show drastic effects of lakeshore development on breeding bird assemblages, but they do indicate trends worth considering for the continued health of northern Wisconsin lakeshore habitats.

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Table 1. Mean values of species (H'_s), diet (H'_d), foraging (H'_f) and nesting (H'_n) diversity indices for developed and undeveloped lakes.

	Developed Mean	(var)	Undeveloped Mean	(var)	p-value
Species diversity					
H's	1.33	0.008	1.32	0.017	p>0.05
Diet-guild diversity					
H'd	0.43	0.007	0.31	0.005	**p<0.05**
Foraging-guild diversity					
H'f	0.62	0.003	0.65	0.004	p>0.05
Nesting-guild diversity					
H'n	0.62	0.003	0.61	0.003	p>0.05

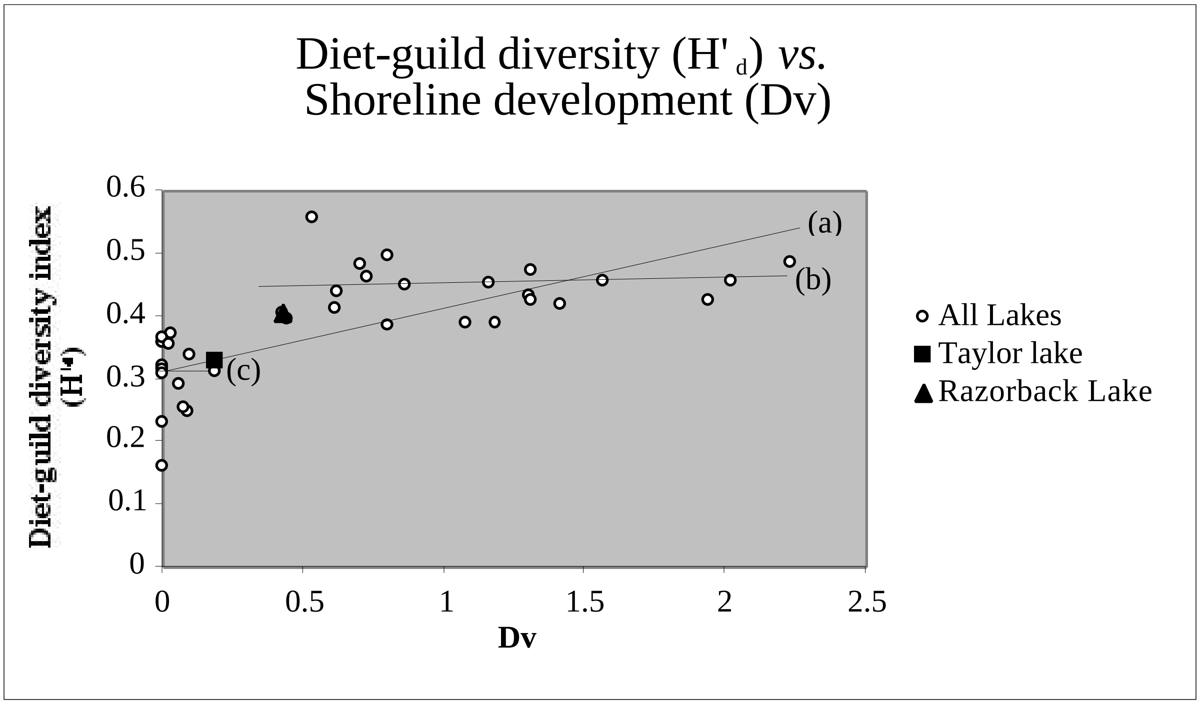
Table 2. Average abundance (*N*) and richness (*Sp*) per point for each lake. Species (H'_s) and diet-guild (H'_d) diversity indices for each lake, and development indices (*Dv*) for each lake. (*=significant differences between lakes of each pair).

pair	Undeveloped Lake	Developed Lake	N per point	Sp per point	H_s		H_d	*Dv*
A	FOUR DUCKS		10.00	5.50	1.25	*	0.25	0.09
		SQUASH	15.50	5.17	1.33		0.39	1.08
B	SUNFISH		13.83	4.50	1.29	*	0.16	0.00
		TAYLOR	18.17	5.67	1.36		0.33	0.18
C	WOLF		8.00	6.00	1.04	*	0.32	0.00
		TORCH	10.00	3.80	1.19		0.39	0.44
D	WHISPERING		9.00	3.60	1.10	*	0.36	0.00
		LOON	14.50	5.67	1.40		0.39	0.80
E	THREE JOHNS		11.00	4.83	1.33	*	0.36	0.00
		SILVER	12.50	3.83	1.14		0.47	1.31
F	WHITE DEER		10.17	4.83	1.32		0.23	0.00
		HEART	13.00	4.83	1.35		0.43	1.30
G	IMOGENE		8.17	3.17	1.10	*	0.31	0.19
		DEER	8.67	3.33	1.19		0.44	0.62
H	LUNA		15.50	5.33	1.38	*	0.32	0.00
		DOLLAR	10.80	5.20	1.31		0.45	0.86
I	UPPER NINEMILE		15.60	6.60	1.40		0.34	0.09
		FINGER	12.00	5.80	1.40		0.39	1.18
J	HOWELL		15.17	6.17	1.46	*	0.37	0.03
		TAMBLING	12.83	5.17	1.38		0.43	1.94
K	SHALLOW		10.75	5.75	1.28		0.31	0.00
		HEIRESS	9.00	4.00	1.26		0.46	0.73

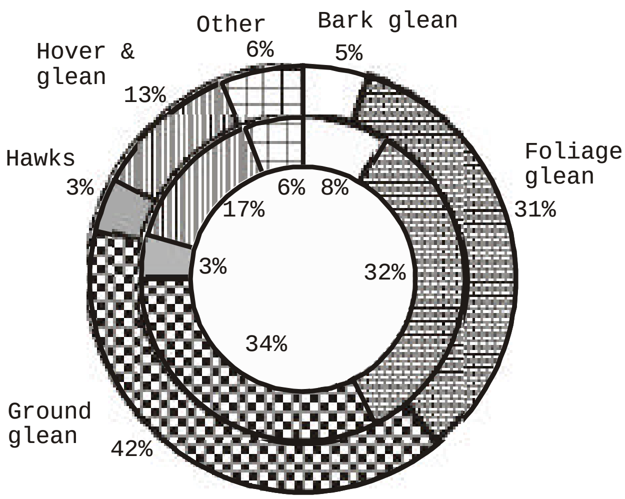
L	CUNARD		11.83		4.67		1.38	*	0.29		0.06	
		MUSKIE		17.50		6.17		1.45		0.50		0.80
M	MCGRATH		16.00		6.75		1.32		0.26		0.07	
		BUCK		19.00		4.67		1.29		0.56		0.53
N	TRILBY		18.20		7.40		1.45	*	0.31		0.00	
		BIRD		15.33		5.83		1.40		0.41		0.61
O	FRANK		17.00		6.33		1.42	*	0.37		0.00	
		MOON		13.50		4.67		1.31		0.43		1.31
P	RAZORBACK		17.50		5.67		1.39		0.41		0.43	
		FOUND		11.33		4.83		1.34		0.46		1.56
Q	CARROLL		15.00		6.50		1.46		0.35		0.02	
		BEARSKIN		22.00		7.50		1.49		0.42		1.41
		mean	13.10	13.86	5.51	5.07	1.32	1.33	0.31	0.43	0.06	0.98
		var	11.6	13.6	1.28	1.04	0.017	0.008	0.004	0.003	0.012	0.209

Figure 1. Simple linear regression plots of diet-guild diversity (H'_d) against shoreline development (*Dv*): (a) all lakes considered together (R^2 = 0.4493), (b) lakes with *Dv*>0.35 (R^2 = 0.0197), (c) lakes with *Dv*<0.35 (R^2 = 7x10^{-5}).

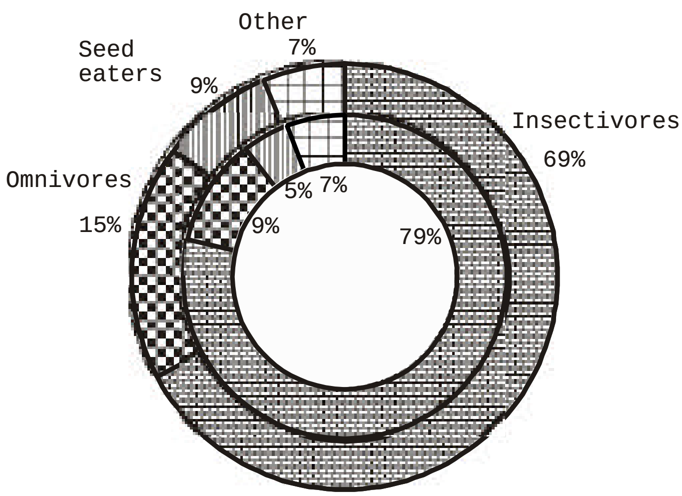
Figure 2. Compositions of each of the three resource guild classes (a) foraging guilds, (b) diet guilds, (c) nesting guilds. Values given are the percentages of each guild within the resource guild class across all developed or undeveloped lakes. Inner rings are values for undeveloped lakes, outer rings are for developed lakes.


Diet-guild diversity (H'd) vs.
Shoreline development (Dv)
Diet-guild diversity index (H'd)
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.5
1
1.5
2
2.5
Dv
(a)
(b)
(c)
All Lakes
Taylor lake
Razorback Lake

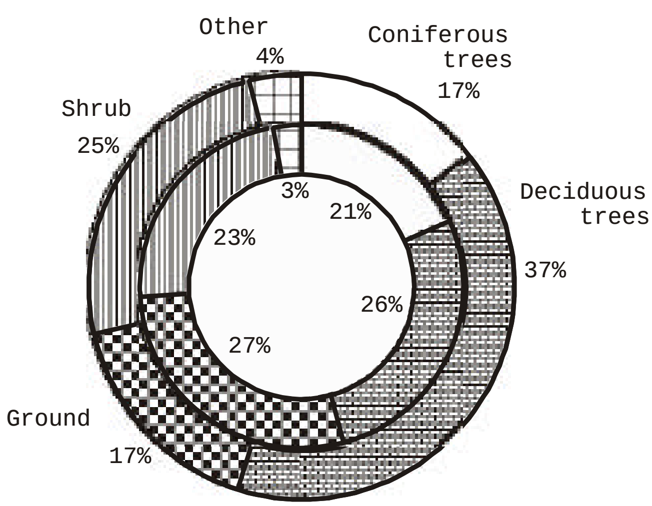
a) Foraging guilds



b) Diet guilds



c) Nesting guilds



Appendix

		Guild associations			
Common names	*Species*	*Foraging*	*Diet*	*Nesting*	*Individuals*
Alder Flycatcher	Empidonax alnorum	HA	IN	Sb	4
American Bittern	Botaurus lentiginosus	SS	FI	G	1
American Crow[d]	Corvus brachyrhynchos	GG	OM	D	216
American Goldfinch[d]	Carduelis tristis	FG	SE	Sb	161
American Kestrel	Falco sparverius	HO	IN	Sg	1
American Redstart	Setophaga ruticilla	HG	IN	D	16
American Robin[d]	Turdus migratorius	GG	IN	D	149
Bald Eagle	Haliaeetus leucocephalus	HP	FI	C	13
Baltimore Oriole[d]	Icterus galbula	FG	IN	D	14
Belted Kingfisher	Ceryle alcyon	HD	FI	B	8
Black-and-white Warbler[u]	Mniotilta varia	BG	IN	G	50
Black-capped Chickadee	Poecile atricapilla	FG	IN	D	141
Black-throated Blue Warbler[u]	Dendroica caerulescens	HG	IN	Sb	19
Black-throated Green Warbler	Dendroica virens	FG	IN	C	84
Blackburnian Warbler	Dendroica fusca	FG	IN	C	30
Blue Jay	Cyanocitta cristata	GG	OM	C	110
Blue-winged Teal	Anas discors	SU	SE	G	2
Blue-winged Warbler	Vermivora pinus	FG	IN	G	8
Bobolink	Dolichonyx oryzivorus	GG	IN	G	2
Broad-winged Hawk	Buteo platypterus	SW	SM	D	2
Brown Creeper	Certhia americana	BG	IN	C	6
Brown-headed Cowbird	Molothrus ater	GG	IN	P	28
Canada Goose	Branta canadensis	SU	GR	G	1
Canada Warbler	Wilsonia canadensis	HG	IN	G	4
Cedar Waxwing	Bombycilla cedrorum	FG	FR	D	71
Cerulean Warbler	Dendroica cerulea	FG	IN	D	1
Chestnut-sided Warbler	Dendroica pensylvanica	FG	IN	Sb	93
Chimney Swift	Chaetura pelagica	AF	IN	Hu	2
Chipping Sparrow	Spizella passerina	GG	IN	C	108

Clay-colored Sparrow	Spizella pallida	GG	IN	Sb	1
Common Grackle	Quiscalus quiscula	GG	OM	D	47
Common Loon[u]	Gavia immer	SD	FI	G	61
Common Merganser	Mergus merganser	SD	AI	D	2
Common Raven	Corvus corax	GG	OM	D	9
Common Yellowthroat	Geothlypis trichas	FG	IN	Sb	30
Connecticut Warbler	Oporornis agilis	GG	IN	G	2
Dark-eyed Junco	Junco hyemalis	GG	SE	G	3
Downy Woodpecker	Picoides pubescens	BG	IN	Sg	10
Eastern Kingbird	Tyrannus tyrannus	HA	IN	D	10
Eastern Phoebe[d]	Sayornis phoebe	HA	IN	Hu	10
Eastern Wood-Pewee	Contopus virens	HA	IN	D	49
European Starling	Sturnus vulgaris	FG	IN	Sb	8
Evening Grosbeak	Coccothraustes vespertinus	GG	SE	C	3
Field Sparrow	Spizella pusilla	GG	IN	G	1
Golden-crowned Kinglet[u]	Regulus satrapa	FG	IN	C	4
Golden-winged Warbler	Vermivora chrysoptera	FG	IN	G	4
Gray Catbird	Dumetella carolinensis	GG	IN	Sb	6
Great Blue Heron	Ardea herodias	SS	FI	D	16
Great Crested Flycatcher[d]	Myiarchus crinitus	HA	IN	D	26
Green Heron	Butorides virescens	SS	FI	D	1
Hairy Woodpecker	Picoides villosus	BG	IN	D	12
Hermit Thrush[u]	Catharus guttatus	GG	IN	G	28
Herring Gull	Larus argentatus	GG	OM	G	2
Hooded Merganser	Lophodytes cucullatus	SD	FI	Sg	2
House Wren	Troglodytes aedon	GG	IN	D	2
Indigo Bunting	Passerina cyanea	FG	IN	Sb	3
Least Flycatcher	Empidonax minimus	HG	IN	D	53
LeConte's Sparrow	Ammodramus leconteii	GG	IN	G	1
Lesser Scaup	Aythya affinis	SD	AI	G	1
Lincoln's Sparrow	Melospiza lincolnii	GG	IN	G	2

Magnolia Warbler	Dendroica magnolia	HG	IN	C	15
Mallard	Anas platyrhynchos	DA	SE	G	65
Mourning Dove	Zenaida macroura	GG	SE	D	8
Mourning Warbler	Oporornis philadelphia	FG	IN	G	2
Nashville Warbler	Vermivora ruficapilla	FG	IN	G	27
Northern Flicker	Colaptes auratus	GG	IN	Sg	4
Northern Parula	Parula americana	FG	IN	D	30
Olive-sided Flycatcher	Contopus cooperi	HA	IN	C	2
Osprey	Pandion haliaetus	HD	FI	D	6
Ovenbird	Seiurus aurocapillus	GG	IN	G	161
Philadelphia Vireo	Vireo philadelphicus	HG	IN	D	1
Pileated Woodpecker	Dryocopus pileatus	BG	IN	Sg	7
Pine Siskin	Carduelis pinus	FG	SE	C	29
Pine Warbler	Dendroica pinus	BG	IN	C	11
Purple Finch	Carpodacus purpureus	GG	SE	C	5
Purple Martin	Progne subis	AF	IN	Sg	2
Red-breasted Nuthatch	Sitta canadensis	BG	IN	C	50
Red-eyed Vireo	Vireo olivaceus	HG	IN	Sb	273
Red-headed Woodpecker	Melanerpes erythrocephalus	HA	OM	Sg	1
Red-winged Blackbird[d]	Agelaius phoeniceus	GG	IN	Sb	101
Ringed-neck Duck	Aythya collaris	UN	UN	UN	1
Rose-breasted Grosbeak	Pheucticus ludovicianus	FG	IN	D	27
Ruby-crowned Kinglet	Regulus calendula	FG	IN	C	4
Ruby-throated Hummingbird	Archilochus colubris	HG	NE	D	34
Ruffed Grouse[u]	Bonasa umbellus	GG	OM	G	3
Rufous-sided Towhee	Pipilo erythrophthalmus	GG	IN	G	2
Savannah Sparrow	Passerculus sandwichensis	GG	IN	G	1
Scarlet Tanager	Piranga olivacea	HG	IN	D	8
Sedge Wren	Cistothorus platensis	GG	IN	Gr	1
Blue-headed Vireo (Solitary)	Vireo solitarius	FG	IN	C	30
Song Sparrow	Melospiza melodia	GG	IN	G	122

Spotted Sandpiper	Actitis macularia	GG	IN	G	1
Swainson's Thrush	Catharus ustulatus	FG	IN	Sb	22
Swamp Sparrow	Melospiza georgiana	GG	IN	Sb	1
Tennessee Warbler	Vermivora peregrina	FG	IN	G	6
Tree Swallow	Tachycineta bicolor	AF	IN	Sg	24
Trumpeter Swan	Cygnus buccinator	SU	GR	G	2
Veery	Catharus fuscescens	GG	IN	G	15
Warbling Vireo[u]	Vireo gilvus	FG	IN	D	6
White-breasted Nuthatch	Sitta carolinensis	BG	IN	D	18
White-throated Sparrow	Zonotrichia albicollis	GG	IN	G	41
Winter Wren	Troglodytes troglodytes	GG	IN	Sg	12
Wood Duck	Aix sponsa	DA	AI	Sg	4
Yellow Warbler	Dendroica petechia	FG	IN	Sb	5
Yellow-bellied Flycatcher	Empidonax flaviventris	HA	IN	G	2
Yellow-bellied Sapsucker	Sphyrapicus varius	BG	IN	D	14
Yellow-rumped Warbler	Dendroica coronata	FG	IN	C	130
Yellow-throated Vireo	Vireo flavifrons	FG	IN	D	6
Unknown Gull	-	UN	UN	UN	1
Unknown Swallow	-	AF	IN	UN	1
Unknown Thrush	-	UN	UN	UN	1
Unknown Warbler	-	UN	UN	UN	1
Unknown Woodpecker	-	BG	IN	D	13
Unknown Wren	-	BG	IN	D	1

Superscript denotes lake-type association: U= undeveloped lakes, D=developed lakes

Guild abbreviations (UN=Unknown):

Foraging: AF=Aerial foraging, BG=Bark glean, DA=Dabbles, FG=Foliage glean, GG=Ground glean, HA=Hawks, HD=High dives, HG=Hover and glean, HO=Hover and Pounce, HP=High patrol, SD=Surface dives, SS=Stalk and strike, SU=Surface dips, SW=Swoops

Diet: AI=Aquatic Inverts, FI=Fish, FR=Fruits, GR=Greens, IN=Insects, NE=Nectar, OM=Omnivore, SE=Seeds, SM=Small Mammals

Nesting: B=Bank, C=Conifer, D=Deciduous, G=Ground, Gr=grass, Hu=Human structures, Sb=Shrub, Sg=Snag, P=Brood Parasite

All specific names listed as in the AOU Checklist, 7th Edition (1998).