

Influence of lakeshore development on breeding bird communities in a mixed northern forest

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Abstract

We report findings of a 2-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 indicate significant lakeshore habitat alteration. We paired developed and undeveloped lakes of similar physical characteristics and performed point-counts around the perimeter of each to assess bird community structure. Our results showed no significant differences between developed and undeveloped lakes in bird abundance, richness or species diversity. However, several species and some resource-guilds were commonly associated with one lake-type or the other. We found a significantly higher diversity of diet guilds on developed lakes. Significant declines in the prevalence of insectivorous and ground-nesting birds were documented on developed lakes, contrasting with increased prevalence of seed-eating birds and deciduous-tree nesting birds. Levels of development on lakeshores in northern Wisconsin appear to affect the composition of avian communities, which is of concern for the health of these forested lacustrine habitats. We outline several factors associated with development which may be linked to these observed bird community changes and suggest measures landowners might take to minimize impact on native breeding bird communities. © 2002 Published by Elsevier Science Ltd.

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1. 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. Johnson and Brown (1990) found that lakeshore habitats in Maine with nearby timber harvest have higher bird species richness near undisturbed lakeshores and buffer strips than harvested land. Forested lacustrine landscapes are under increasing development pressure as homes and cottages are being built at increased rates in these areas. Despite this trend, 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 consider the ramifications of these observations for the health of forested lakeshore habitats.

Although differences in bird 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 asso-

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ciated 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 subsignarius* 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 both environmental managers and lakeshore homeowners. 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, 1996–1999). Future population increases of insect pests may be of special concern if the composition of resident avian resource-guilds is 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, 2002). 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 attention to differences in 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 developed and undeveloped points and lakes.

2. Methods

2.1. Study area and site selection

This study was conducted in a forested landscape in Forest, Oneida and Vilas counties of northeastern Wisconsin, USA. This area is marked by the physiographic dominance of pitted outwash, extensive glacial lakes and wetlands. Gravelly, sandy soils and lower alkalinity values of lakes make this area sensitive to acidification (Omernik et al., 2000). Forests are dominated largely by

paper birch *Betula papyrifera*, quaking aspen *Populus tremuloides*, red oak *Quercus rubra*, sugar maple *Acer saccharum*, eastern white pine *Pinus strobus*, and red pine *Pinus resinosa*, and to a lesser degree, eastern hemlock *Tsuga canadensis*, yellow birch *Betula alleghaniensis*, and red maple *Acer 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 county zoning codes, although several study lakes were located within the Chequamegon-Nicolet National Forest, managed by the US Forest Service.

Development on study lakes was described by a shoreline development index (Dv) based on the number of developed properties (determined by GIS database) per 100 m of shoreline; a completely developed lake by Wisconsin Shoreline Management regulations (Wisconsin DNR Administrative Rule #NR 115) could have 3.3 houses per 100 m of shoreline ($Dv=3.3$). Lakes for censuses were selected to satisfy a paired study design and thus were of two types: those with high levels of shoreline development (developed Dv : $\mu_d = 0.98$, $SD=0.457$) and those with low levels/no shoreline development (undeveloped Dv : $\mu_u = 0.058$, $SD=0.108$). Each undeveloped lake was paired with a developed lake based on similarities in surface area, shoreline length, water chemistry, water color and water source.

2.2. Bird sampling and habitat classification

From 2 to 27 June 1996–1997 two observers sampled each lake once between the hours of 0500 and 1000 CDT. 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 approximate center of each lake and identified a shore landing site by random compass bearing (from 0 to 360°N) generated from a random number table. From this 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 began at points 50 m inland from each shore landing, using unlimited-radius counts of 10-min 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. At each point, we classified habitats following the scheme of the Wisconsin Breeding Bird Atlas (WSO, 1995) and made estimates of the percentage cover of the canopy, sub-canopy and shrub layer. We estimated canopy cover as a percentage of the area occupied by foliage in the top-most layer of

forest. We estimated sub-canopy and shrub layer coverages as forest volume occupation by vegetation from below the canopy to 4 m height and below 4 m height, respectively.

2.3. Data analyses

From data collected at each point, abundance (number of birds), richness (number of species) and diversity measures were calculated. Both Shannon's (1948) and Simpson's (1949) indices were used for diversity measurements, but results from both analyses were similar and thus we only report analyses using Shannon's index. We calculated the above metrics for entire lakes as well as single points.

To further assess differences in assemblages of birds, we evaluated differences in three classes of avian resource-guilds (*sensu* Wilson, 1999): foraging, diet and nesting. Guild assignment within each class followed Ehrlich et al. (1988), recognizing 13 foraging (*f*) guilds, eight diet (*d*) guilds and nine nesting (*n*) guilds. For each of these resource-guild classes, we calculated diversity indices similar to species diversity calculations mentioned earlier, but using guild associations as the primary unit of measure. In place of the number of individuals of each species we used the number of individuals in each guild 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. 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-guild, diet-guild and nesting-guild 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 *t* statistic was calculated as

$$t = \frac{H'_1 - H'_2}{\sqrt{s_1^2 + s_2^2}}$$

with 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

$$df = \frac{[s_1^2 + s_2^2]^2}{(s_1^2)/N_1 + (s_2^2)/N_2}$$

(see Hutcheson, 1970).

We also compared values of abundance, richness, and diversity indices with paired two-tailed *t*-tests between the 34 lakes of the two development types. To compare the prevalence of guilds at lakes, we calculated the proportion of each guild within its class (foraging, diet or nesting) at each lake and performed similar two-tailed paired *t*-tests. For all statistical tests we set $\alpha=0.05$, although when multiple comparisons were performed simultaneously α -levels were Bonferroni corrected.

We evaluated the relationships of habitat variables to bird diversity estimates at individual points 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. We also used simple linear regressions to assess the effect of lakeshore development on avian assemblages by regressing dependent bird variables of entire lakes on shoreline development indices (*Dv*). We used log-likelihood tests (*G* tests: Zar, 1984) to evaluate associations of individuals species (or guilds) with developed or undeveloped points/lakes.

3. Results

Point-count locations on developed lakes were often located near human structures and were classified (as in WSO, 1996) 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), upland small town residential (USR: *n*=6) and open upland uncropped (OUU: *n*=2) for a total of 70 developed sites. Although located on lakes classified as developed, some 27 sites on developed lakes were classified as upland forest (FUM, FUH, FUC: *n*=27) and as open upland (OLU, OUA: *n*=2) as there was no development within sight (100–150 m) of those points. Nearly all sites on undeveloped lakes were classified as upland forest types (FUM, FUH, FUC: *n*=82) but two were near homes and classified as upland rural residential (URR). The remaining points on undeveloped lakes were forested lowland (FLM, FLC: *n*=3) and open upland (OUU: *n*=1). Due to the random placement of points along lakeshores, several points (*n*=16) on 10 lakes (seven undeveloped, three developed) were unapproachable due to floating bogs, swamps or other obstacles. 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 at points were also significantly lower on developed lakes than undeveloped lakes ($P < 0.05$; Table 1).

We identified 2410 individual birds representing 93 species across 187 point counts on 34 lakes (see Appendix). The 12 most commonly observed species (> 70 individuals and present at > 50 point-count sites) were, in decreasing frequency: red-eyed vireo *Vireo olivaceus*, American crow *Corvus brachyrhynchos*, ovenbird *Seiurus aurocapillus*, American goldfinch *Carduelis tristis*, black-capped chickadee *Poecile atricapilla*, American robin *Turdus migratorius*, yellow-rumped warbler *Dendroica coronata*, song sparrow *Melospiza melodia*, red-winged blackbird *Agelaius phoeniceus*, blue jay *Cyanocitta cristata*, chestnut-sided warbler *Dendroica pensylvanica* and black-throated green warbler *Dendroica virens*. On average we observed 13.0 birds (10.2 species) per site on undeveloped lakes and 13.5 birds (9.9 species) per site on developed lakes ($P > 0.05$ 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 (H'_s ; see Table 2). There were no significant relationships between shoreline development (Dv) and avian: abundance ($R^2 = 0.029$), richness ($R^2 = 0.070$), species diversity (H'_s ; $R^2 = 0.034$), foraging guild diversity (H'_f ; $R^2 = 0.003$) or nesting guild diversity (H'_n ; $R^2 = 0.007$).

Diet-guild diversity measures (H'_d) were significantly different between developed lakes (Dev $\mu_{H'd} = 0.43$) and undeveloped lakes (Undev $\mu_{H'd} = 0.31$; $P < 0.01$). 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, these values appeared to more clearly indicate a bipartite response to development depending on a threshold of $\sim 0.35 Dv$ (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. 1c: $R^2 < 0.001$). We obtained similar results for those lakes with development indices higher than 0.35 (Fig. 1b: $R^2 < 0.02$). It is notable that one of our developed lakes fell below the $Dv \sim 0.35$ 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). 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 (%s canopy, sub-canopy, shrub cover) in simple linear regressions, or in multiple regression analyses including combinations of all three variables. Similarly, none of the measures of guild composition were correlated with habitat structure.

Several species showed significant associations with developed or undeveloped lakes. The American crow *Corvus brachyrhynchos*, American goldfinch *Carduelis tristis*, American robin *Turdus migratorius*, eastern phoebe *Sayornis phoebe*, great crested flycatcher *Myiarchus crinitis*, Baltimore oriole *Icterus galbula* and 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 with different lake types; surface-divers with undeveloped lakes and seed-eaters with 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).

Fig. 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 differences between

Table 1

Mean diversity indices of species (H'_s) and diet (H'_d), foraging (H'_f), and nesting (H'_n) guilds, and development indices for developed and undeveloped lakes^a

	Developed mean	(\pm var)	Undeveloped mean	(\pm var)	P-value
Species diversity (H'_s)	1.33	0.008	1.32	0.017	> 0.620
Foraging-guild diversity (H'_f)	0.62	0.007	0.65	0.005	> 0.139
Diet-guild diversity (H'_d)	0.43	0.003	0.31	0.004	< 0.001
Nesting-guild diversity (H'_n)	0.63	0.003	0.61	0.003	> 0.271
% Canopy cover	47.4	578.7	64.2	664.9	< 0.001
% Sub-canopy cover	25.2	373.9	33.7	618.7	< 0.011
% Shrub cover	32.5	707.3	42.7	916.0	< 0.016
shoreline development index (Dv)	0.98	0.209	0.06	0.012	< 0.001

^a Mean values given for habitat measures were calculated from points at each lake type. Significance measures (P -values) were calculated using two-tailed paired t -tests for the diversity measures, and two-tailed unpaired t -tests for habitat measures.

Table 2

Values listed for each lake studied are: average abundance (N) and richness (Sp) per point, species (H'_s) and diet-guild (H'_d) diversity indices, and lake development indices (D_V)^a

Pair	Undeveloped lake	Developed lake	N per point		Sp per point		H'_s		H'_d		D_V	
1	Four ducks (4)	Squash (6)	10.00	15.50	5.50	5.17	1.25	*	0.25	0.39	0.09	1.08
2	Sunfish (6)	Taylor (6)	13.83	18.17	4.50	5.67	1.29	*	0.16	0.33	0	0.18
3	Wolf (2)	Torch (5)	8.00	10.00	6.00	3.80	1.04	*	0.32	0.39	0	0.44
4	Whispering (5)	Loon (6)	9.00	14.50	3.60	5.67	1.10	*	0.36	0.39	0	0.80
5	Three johns (6)	Silver (6)	11.00	12.50	4.83	3.83	1.33	*	0.36	0.47	0	1.31
6	White deer (6)	Heart (6)	10.17	13.00	4.83	4.83	1.32		0.23	0.43	0	1.30
7	Imogene (6)	Deer (6)	8.17	8.67	3.17	3.33	1.10	*	0.31	0.44	0.19	0.62
8	Luna (6)	Dollar (5)	15.50	10.80	5.33	5.20	1.38	*	0.32	0.45	0	0.86
9	Ninemile (5)	Finger (5)	15.60	12.00	6.60	5.80	1.40		0.34	0.39	0.09	1.18
10	Howell (6)	Tambling (6)	15.17	12.83	6.17	5.17	1.46	*	0.37	0.43	0.03	1.94
11	Shallow (3)	Heiress (6)	10.75	9.00	5.75	4.00	1.28		0.31	0.46	0	0.73
12	Cunard (6)	Muskie (6)	11.83	17.50	4.67	6.17	1.38	*	0.29	0.50	0.06	0.80
13	Mcgrath (4)	Buck (6)	16.00	19.00	6.75	4.67	1.32		0.26	0.56	0.07	0.53
14	Trilby (5)	Bird (6)	18.20	15.33	7.40	5.83	1.45	*	0.31	0.41	0	0.61
15	Frank (6)	Moon (6)	17.00	13.50	6.33	4.67	1.42	*	0.37	0.43	0	1.31
16	Razorback (6)	Found (6)	17.50	11.33	5.67	4.83	1.39		0.41	0.46	0.43	1.56
17	Carroll (6)	Bearskin (6)	15.00	22.00	6.50	7.50	1.46		0.35	0.42	0.02	1.41
		Mean	13.10	13.86	5.51	5.07	1.32	1.33	0.31	0.43	0.06	0.98
		Variance	11.6	13.6	1.28	1.04	0.017	0.008	0.004	0.003	0.012	0.209
		P -value	>0.46		>0.17		>0.62		<0.01		<0.01	

^a The number of points visited on each lake is listed in parentheses after each lake name.

* Significant differences in species diversity between lakes of each pair.

lake-types, but several significant differences are worth note. Among foraging guilds (Fig. 2a), ground-gleaners increased (35→42%: $P < 0.044$) while hover-and-gleaners (16→13%: $P > 0.10$) and bark-gleaners (8→3%: $P < 0.032$) declined on developed lakes, none of which were significant (Bonferroni-corrected $\alpha = 0.0038$). Within diet guilds, insectivores significantly declined on developed lakes (80→68%: $P < 0.0001$), whereas omnivores (9→15%: $P < 0.0028$) and seed-eaters (4→10%: $P < 0.0052$) significantly increased (Bonferroni-corrected $\alpha = 0.0063$). Finally, developed lakes showed marked increases in deciduous tree-nesters (24→36%: $P < 0.0006$) and declines ground-nesters (29→18%: $P < 0.0001$; Bonferroni-corrected $\alpha = 0.0055$).

4. 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—two out of every three lakes that were undeveloped in 1965 are now developed in northern Wisconsin, and housing density on developed lakes has nearly doubled (WDNR, 1996). In our

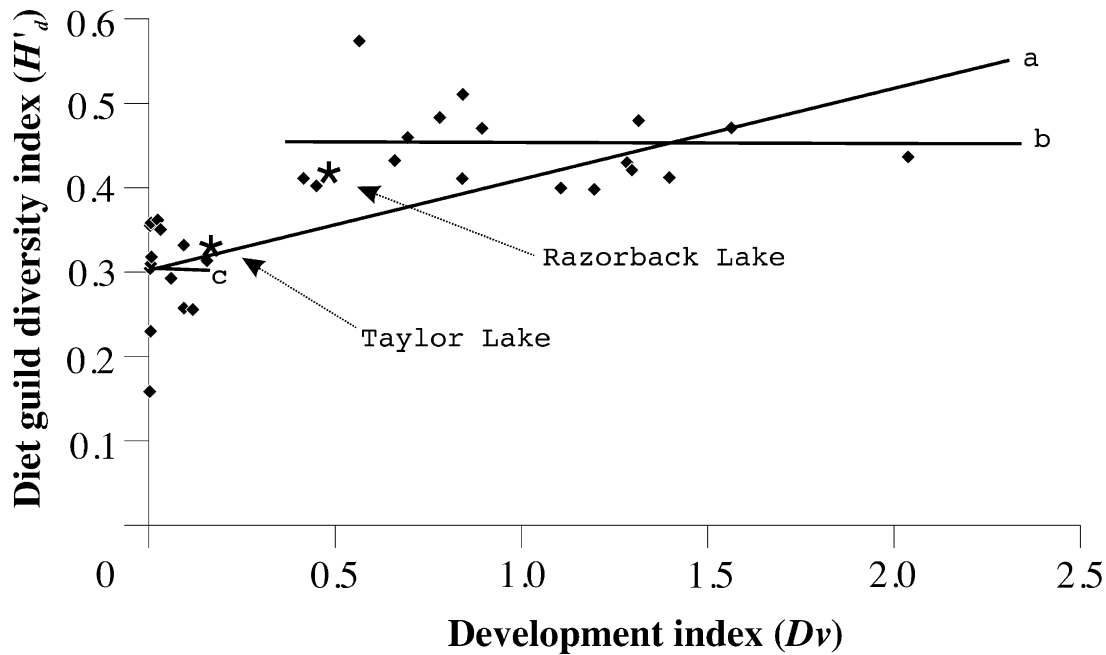


Fig. 1. Simple linear regression plots of diet-guild diversity (H'_d) against shoreline development (Dv): (a) all lakes considered together ($R^2 < 0.02$), (b) lakes with $Dv > 0.35$ ($R^2 = 0.0197$), (c) lakes with $Dv < 0.35$ ($R^2 < 0.001$).

study area, avian species abundance, richness and diversity measures appear to be similar between developed and undeveloped lakes. However, assessments of ecological guild structure and examinations of individual species associations show some significant changes in response to anthropogenic disturbance. Effects appear largely to be limited to differences in the composition of diet and nesting guilds (Fig. 2); seed-eaters increase on developed lakes and insectivores and ground-nesters tend to increase near undeveloped lakes (Fig. 2b). These data indicate lakeshore development does have some effect on the structure of native 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. We observed cowbirds at eight of 17 developed lakes as well as at four of 17 undeveloped lakes, which is a non-significant association ($P > 0.05$). However, when we looked at points on developed lakes only, we found that cowbirds were significantly associated with developed points over undeveloped points ($P < 0.05$). Habitats at these points are marked by forest/development habitat edges, a characteristic that these brood parasites prefer when seeking out host species. 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 traditional ecological measures of bird communities (abundance, richness and species diversity) showed no significant differences between undeveloped and developed lakes, our analysis of guild structure indicates that those metrics may fail to uncover more subtle, yet significant, habitat change. Although our data do not address with fine detail the specific types of habitat change caused by lakeshore development, we can infer from the predominance and deficits of various guilds on developed lakeshores several factors which may be of significant conservation importance. Fig. 2 confirms that lakeshore development can both enhance and depreciate the quality of habitats for birds, depending on the ecological requirements of individual species. None of the seven species associated with developed lakes are ground-nesters, but four of the seven species significantly associated with undeveloped lakes are ground-nesters. 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 such as raccoons *Procyon lotor* and domestic cats (Dunn and Tessaglia, 1994) associated with human habitat alteration. Such factors, as well as direct anthropogenic disturbances from landscape maintenance (mowing, clearing, etc.) may be responsible for the decline in ground-nesters on developed lakes. Points on developed lakes had significantly lower levels of

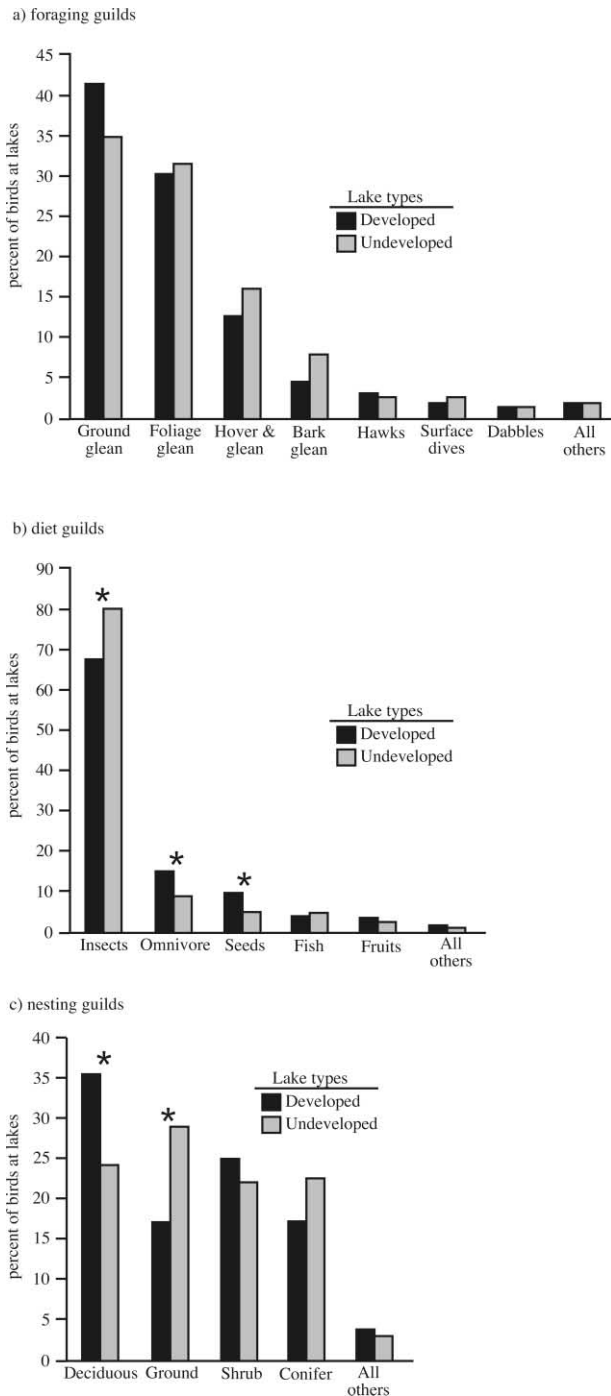


Fig. 2. Compositions of each of the three resource guild classes [(a) foraging guilds, (b) diet guilds, (c) nesting guilds] observed on developed and undeveloped lakes. Values given are the percentages of each guild within the resource guild class across all developed or undeveloped lakes. Light bars are values for undeveloped lakes, dark bars are for developed lakes.

cover in the forest shrub layer than points on undeveloped lakes (Table 1), cover that is essential for the successful breeding of ground-nesters.

On the surface, the observed increase in diet-guild diversity may appear to be beneficial for lakeshore habitats, but closer inspection of the changes in guild

composition indicates otherwise. Two major factors are implicated in the increase diet-guild diversity on developed lakes: (1) seed-eaters and omnivores clearly prefer developed lakes, doubling their presence in the bird communities there when compared to undeveloped lakes (Fig. 2), and (2) the dominance of insectivores is likewise decreased on developed lakes. Although we collected no data on supplemental feeding by lakeshore homeowners, this undoubtedly increases the attractiveness of developed lakeshores to seed-eating birds, which are generally not associated with forested lakeshore habitats. We do not necessarily propose that seed-eaters and omnivores that are benefiting from supplemental feeding are supplanting or replacing insectivores, but only that this largely explains the increases in diet-guild diversity on developed lakes.

The declining dominance of insectivores (Fig. 2) may not be only of cursory importance. 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). Furthermore, saplings of sugar maple *Acer saccharum*, an economically important tree of northern forests, showed significant increases in damage from herbivory when insectivorous birds were excluded from study areas (Strong et al., 2000). The observed decline of insectivorous birds on developed lakes may prove to be significant for the future health of lakeshore forests—a commodity of interest to both wildlife managers, lake users and shoreline landowners.

The bipartite response of diet-guild diversity regressed on development (Fig. 1) indicates that a development level of 3–4 lakeshore improvements per 1000 m of shoreline ($Dv \sim 0.35$) approximates something of a ‘development threshold.’ This effect may be confounded by the experimental set-up that paired developed and undeveloped lakes, arguably partitioning the data into two groups. However, the two lakes which do not fall into their appropriate partitions (Fig. 2), undeveloped Razorback Lake ($Dv = 0.43$) and developed Taylor lake ($Dv = 0.18$), provide support for the proposed development threshold. Razorback Lake was considered 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 (Fig. 1). These observations provide some support of this proposed development threshold (around 3–4 lakeshore improvements per 1000 m) which adversely affects avian assemblages.

In conclusion, 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 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 1000 m of shoreline—a level that is much lower than the current regulatory guidelines of three developments per 100 m of shoreline (Wisconsin DNR Administrative Rule #NR 115). Not all lakes have similar bird communities, and not all lakeshore development is similar in the degree of habitat alteration. Lakeshore development could likely diminish the negative effects on native breeding bird communities and enhance the health of the surrounding environment by (1) decreasing the density of development, and (2) minimizing the degree of clearing in the canopy, sub-canopy and especially shrub layers of forests. The results of this and companion studies should compel future research to focus on more

detailed characteristics of development, arriving at specific recommendations which can alleviate its negative effects on lakeshore habitats.

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Appendix. Guild associations

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

Appendix (continued)

Common names ^a	Species	Foraging ^b	Diet ^c	Nesting ^d	Individuals
Common Grackle	<i>Quiscalus quiscula</i>	GG	OM	D	47
Common Loon (U)	<i>Gavia immer</i>	SD	FI	G	61
Common Raven	<i>Corvus corax</i>	GG	OM	D	9
Common Yellowthroat	<i>Geothlypis trichas</i>	FG	IN	Sb	30
Connecticut Warbler	<i>Oporornis agilis</i>	GG	IN	G	2
Dark-eyed Junco	<i>Junco hyemalis</i>	GG	SE	G	3
Downy Woodpecker	<i>Picoides pubescens</i>	BG	IN	Sg	10
Eastern Kingbird	<i>Tyrannus tyrannus</i>	HA	IN	D	10
Eastern Phoebe (D)	<i>Sayornis phoebe</i>	HA	IN	Hu	10
Eastern Wood-Pewee	<i>Contopus virens</i>	HA	IN	D	49
European Starling	<i>Sturnus vulgaris</i>	FG	IN	Sb	8
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	GG	SE	C	3
Field Sparrow	<i>Spizella pusilla</i>	GG	IN	G	1
Golden-crowned Kinglet (U)	<i>Regulus satrapa</i>	FG	IN	C	4
Golden-winged Warbler	<i>Vermivora chrysoptera</i>	FG	IN	G	4
Gray Catbird	<i>Dumetella carolinensis</i>	GG	IN	Sb	6
Great Crested Flycatcher (D)	<i>Myiarchus crinitus</i>	HA	IN	D	26
Hairy Woodpecker	<i>Picoides villosus</i>	BG	IN	D	12
Hermit Thrush (U)	<i>Catharus guttatus</i>	GG	IN	G	28
House Wren	<i>Troglodytes aedon</i>	GG	IN	D	2
Indigo Bunting	<i>Passerina cyanea</i>	FG	IN	Sb	3
Least Flycatcher	<i>Empidonax minimus</i>	HG	IN	D	53
LeConte's Sparrow	<i>Ammodramus leconteii</i>	GG	IN	G	1
Lincoln's Sparrow	<i>Melospiza lincolni</i>	GG	IN	G	2
Magnolia Warbler	<i>Dendroica magnolia</i>	HG	IN	C	15
Mallard	<i>Anas platyrhynchos</i>	DA	SE	G	65
Mourning Dove	<i>Zenaidura macroura</i>	GG	SE	D	8
Mourning Warbler	<i>Oporornis philadelphia</i>	FG	IN	G	2
Nashville Warbler	<i>Vermivora ruficapilla</i>	FG	IN	G	27
Northern Flicker	<i>Colaptes auratus</i>	GG	IN	Sg	4
Northern Parula	<i>Parula americana</i>	FG	IN	D	30
Olive-sided Flycatcher	<i>Contopus cooperi</i>	HA	IN	C	2
Osprey	<i>Pandion haliaetus</i>	HD	FI	D	6
Ovenbird	<i>Seiurus aurocapillus</i>	GG	IN	G	161
Philadelphia Vireo	<i>Vireo philadelphicus</i>	HG	IN	D	1
Pileated Woodpecker	<i>Dryocopus pileatus</i>	BG	IN	Sg	7
Pine Siskin	<i>Carduelis pinus</i>	FG	SE	C	29
Pine Warbler	<i>Dendroica pinus</i>	BG	IN	C	11
Purple Finch	<i>Carpodacus purpureus</i>	GG	SE	C	5
Purple Martin	<i>Progne subis</i>	AF	IN	Sg	2
Red-breasted Nuthatch	<i>Sitta canadensis</i>	BG	IN	C	50
Red-eyed Vireo	<i>Vireo olivaceus</i>	HG	IN	Sb	273
Red-winged Blackbird (D)	<i>Agelaius phoeniceus</i>	GG	IN	Sb	101
Ringed-neck Duck	<i>Aythya collaris</i>	UN	UN	UN	1
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	FG	IN	D	27
Ruby-crowned Kinglet	<i>Regulus calendula</i>	FG	IN	C	4
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	HG	NE	D	34
Ruffed Grouse (U)	<i>Bonasa umbellus</i>	GG	OM	G	3
Rufous-sided Towhee	<i>Pipilo erythrophthalmus</i>	GG	IN	G	2
Savannah Sparrow	<i>Passerculus sandwichensis</i>	GG	IN	G	1
Scarlet Tanager	<i>Piranga olivacea</i>	HG	IN	D	8

(Table continued on next page)

Appendix (continued)

Common names ^a	Species	Foraging ^b	Diet ^c	Nesting ^d	Individuals
Sedge Wren	<i>Cistothorus platensis</i>	GG	IN	Gr	1
Blue-headed Vireo (Solitary)	<i>Vireo solitarius</i>	FG	IN	C	30
Song Sparrow	<i>Melospiza melodia</i>	GG	IN	G	122
Swainson's Thrush	<i>Catharus ustulatus</i>	FG	IN	Sb	22
Tennessee Warbler	<i>Vermivora peregrina</i>	FG	IN	G	6
Tree Swallow	<i>Tachycineta bicolor</i>	AF	IN	Sg	24
Trumpeter Swan	<i>Cygnus buccinator</i>	SU	GR	G	2
Veery	<i>Catharus fuscescens</i>	GG	IN	G	15
Warbling Vireo (U)	<i>Vireo gilvus</i>	FG	IN	D	6
White-breasted Nuthatch	<i>Sitta carolinensis</i>	BG	IN	D	18
White-throated Sparrow	<i>Zonotrichia albicollis</i>	GG	IN	G	41
Winter Wren	<i>Troglodytes troglodytes</i>	GG	IN	Sg	12
Yellow Warbler	<i>Dendroica petechia</i>	FG	IN	Sb	5
Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	HA	IN	G	2
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	BG	IN	D	14
Yellow-rumped Warbler	<i>Dendroica coronata</i>	FG	IN	C	130
Yellow-throated Vireo	<i>Vireo flavifrons</i>	FG	IN	D	6
Unknown Thrush	–	UN	UN	UN	1
Unknown Warbler	–	UN	UN	UN	1
Unknown Woodpecker	–	BG	IN	D	13
Unknown Wren	–	BG	IN	D	1

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

^a U = undeveloped lakes, D = developed lakes.

^b 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, UN = Unknown.

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

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

References

- AOU (American Ornithologist's Union), 1998. Check-list of North American Birds, seventh ed. American Ornithologist's Union, Washington, DC. Allen Press, Inc, Lawrence, Kansas.
- Bell, J.L., Whitmore, R.C., 1997. Bird populations and habitat in *Bacillus thuringiensis* and dimlin-treated and untreated areas of hardwood forest. *American Midland Naturalist* 137, 239–250.
- Bosakowski, T., 1997. Breeding bird abundance and habitat relationships on a private industrial forest in the western Washington Cascades. *Northwest Science* 71, 244–253.
- Boulinier, T., Nichols, J.D., Hines, J.E., Sauer, J.R., Flather, C.H., Pollock, K.H., 1998. Higher temporal variability of forest breeding bird communities in fragmented landscapes. *Proceedings of the National Academy of Sciences, USA* 95, 7491–7501.
- Caron, J.A., Robinson, W.L., 1994. Responses of breeding common loons to human activity in upper Michigan. *Hydrobiologica* 279/280, 431–438.
- Canterbury, G.E., Martin, T.E., Petit, D.R., Petit, L.J., Bradford, D.F., 2000. Bird communities and habitat as ecological indicators of forest condition in regional monitoring. *Conservation Biology* 14, 544–558.
- Croonquist, M.J., Brooks, R.P., 1991. Use of avian and mammalian guilds as indicators of cumulative impacts in riparian-wetland areas. *Environmental Management* 15, 701–714.
- Drolet, B., Desrochers, A., 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. *The Condor* 101, 699–704.
- Dunn, E.H., Tessaglia, D.L., 1994. Predation of birds at feeders in winter. *Journal of Field Ornithology* 65, 8–16.
- Ehrlich, P.R., Dobkin, D.S., Wheye, D., 1988. *The Birders Handbook: A Field Guide to the natural History of North American Birds*. Simon and Schuster, Inc, New York.
- Elias, J., Meyer, M.W., (in prep). Comparisons of undeveloped and developed shorelands, northern Wisconsin, and recommendations for restoration. *Restoration Ecology*.
- Friesen, L.E., Eagels, P.F., Mackay, R.J., 1995. Effects of residential development on forest-dwelling neotropical migrant songbirds. *Conservation Biology* 9, 1408–1414.
- Gillum, S.S., 1995. Estimated densities of breeding birds: a comparison of fixed-radius and unlimited-radius point counts in the Nicolet National Forest of northern Wisconsin. MA thesis, Northeastern Illinois University, Chicago.

- Hagan, J.M., McKinley, P.S., Meehan, A.L., Grove, S.L., 1997. Diversity and abundance of landbirds in a northeastern industrial forest. *Journal of Wildlife Management* 61, 718–735.
- Haney, C.J., 1999. Numerical response of birds to an irruption of elm spanworm (*Ennomos subsignarius*[Hbn.]; Geometridae: Lepidoptera) in old-growth forest of the Appalachian Plateau, USA. *Forest Ecology and Management* 120, 203–217.
- Howe, R.W., Wolf, A.T., Rinaldi, T., 1993. Monitoring birds in a regional landscape: lessons from the Nicolet National Forest Bird Survey. In: Ralph, C.J., Sauer, J., Droege, S. (Eds.), *USDA Forest Service General Technical Report PSW-GTR-149*. Pacific Southwest Research Station, Albany, CA.
- Hutcheson, K., 1970. A test for comparing diversities based on the Shannon formula. *Journal of Theoretical Biology* 29, 151–154.
- Johnson, W.N., Brown, P.W., 1990. Avian use of a lakeshore buffer strip and an undisturbed lakeshore in Maine. *Northern Journal of Applied Forestry* 7, 114–117.
- Jung, R.E., 1991. Effects of human disturbance and lake characteristics on the behavior and breeding success of Common Loons. *Passenger Pigeon* 53, 207–218.
- Krebs, C.J., 1978. *Ecology: the Experimental Analysis of Distribution and Abundance*. Harper & Row, New York.
- Loyn, R.H., Runnalls, R.G., Forward, G.Y., 1983. Territorial bell miners and other birds affecting populations of insect prey. *Science* 221, 411–413.
- Marquis, R.J., Whelan, C.J., 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75, 2007–2014.
- Marsden, S.J., 1998. Changes in bird abundance following selective logging on Seram, Indonesia. *Conservation Biology* 12, 605–611.
- Merrill, S.B., Cuthbert, F.J., Oehlert, G., 1998. Residual patches and their contribution to forest-bird diversity on northern Minnesota aspen clearcuts. *Conservation Biology* 12, 190–199.
- Miller, A., Rusnock, P., 1993. The rise and fall of the silvicultural hypothesis in spruce budworm (*Choristoneura fumiferana*) management in eastern Canada. *Forest Ecology and Management* 61, 71–189.
- O'Connell, T.J., Jackson, L.E., Brooks, R.P., 1998. A bird community index of biotic integrity for the mid-atlantic highlands. *Environmental Monitoring and Assessment* 51, 145–156.
- Omernik, J.M., Chapman, S.S., Lillie, R.A., Dumke, R.T., 2000. Ecoregions of Wisconsin. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 88, 77–103.
- Radeloff, V.C., Mladenoff, D.J., Boyce, M.S., 2000. Effects of interacting disturbances on landscape patterns: budworm defoliation and salvage logging. *Ecological Applications* 10, 233–247.
- Robinson, S.K., Rothstein, S.I., Brittingham, M.C., Petit, L.J., Grzybowski, J.A., 1995. Ecology and behavior of cowbirds and their impact on host populations. In: Martin, T.E., Finch, D. (Eds.), *Ecology and Management of Neotropical Migratory Birds*. Oxford University Press, New York, pp. 428–460.
- Root, R.B., 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* 37, 317–350.
- Schmidt, K.A., Whelan, C.J., 1998. Predator-mediated interactions between and within guilds of nesting songbirds: experimental and observational evidence. *The American Naturalist* 152, 393–402.
- Shannon, C.E., 1948. A mathematical theory of communication. *Bell System Technical Journal* 27, 379–423, 623–656 (as in Krebs, 1978).
- Simpson, E.H., 1949. Measurement of diversity. *Nature* 163, 688.
- Sipura, M., 1999. Tritrophic interactions: willows, herbivorous insects and insectivorous birds. *Oecologia* 121, 537–545.
- Strong, A.M., Sherry, T.W., Holmes, R.T., 2000. Bird predation on herbivorous insects: indirect effects on sugar maple saplings. *Oecologia* 125, 370–379.
- Syme, P.D., 1990. Insect pest problems and monitoring in Ontario conifer plantations. *Revue D'Entomologie du Quebec* 35, 25–30.
- Szaro, R.C., 1986. Guild management: an evaluation of avian guilds as a predictive tool. *Environmental Management* 10, 681–688.
- Thiollay, J.M., 1997. Disturbance, selective logging and bird diversity: a Neotropical forest study. *Biodiversity and Conservation* 6, 1155–1173.
- Tilghman, N.G., 1987. Characteristics of urban woodlands affecting breeding bird diversity and abundance. *Landscape and Urban Planning* 14, 481–495.
- Verner, J., 1984. The guild concept applied to management of bird populations. *Environmental Management* 8, 1–14.
- Wilson, J.B., 1999. Guilds, functional types and ecological groups. *Oikos* 86, 507–522.
- WDNR (Wisconsin Department of Natural Resources), 1996. Northern Wisconsin's lakes and shorelands: a report examining a resource under pressure. Wisconsin Department of Natural Resources.
- WDNR (Wisconsin Department of Natural Resources), 1996–1999. *Forest Health Conditions in Wisconsin Annual Reports: 1996–1999*. WDNR, PO Box 7921, Madison, WI 53707.
- WSO (Wisconsin Society of Ornithologists), 1995. *Wisconsin Breeding Bird Atlas: Atlasing Handbook 1995–1999*. Wisconsin Society of Ornithologists, Inc. (Available: <http://wso.uwgb.edu/birds/wbba/>).
- Woodford, J.E., Meyer, M.W., 2002. Impact of lakeshore development on green frog (*Rana clamitans*) abundance. *Biological Conservation* (in press).
- Zar, J.H., 1984. *Biostatistical Analysis*, second ed. Prentice Hall, Inc, New Jersey.