
Effects of Residential Development on Forest-Dwelling Neotropical Migrant Songbirds

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Abstract: *Many bird species are in local or regional decline because of habitat loss or degradation. We attempted to disentangle the effects of residential development from the effects of forest size on forest-bird communities, with particular emphasis on Neotropical migrant species. Two variables were examined for their influence on avian diversity and abundance: forest size and the number of houses outside a forest within 100 m of the edge. We found that Neotropical migrants consistently increased in number and abundance as forest size increased. Of greater interest, we found that the number of houses surrounding a forest severely undermined its suitability for Neotropical migrants. Neotropical migrants consistently decreased in diversity and abundance as the level of adjacent development increased, regardless of forest size. The effects of development were striking: 4-ha woodlots without any nearby houses had on average a richer, more abundant Neotropical community than did 25-ha urban woodlots. No predictable pattern of change concerning development or forest size was observed for short-distance migrants or permanent residents. Current planning regulations generally permit housing right up to forest edges. This practice may prevent protection of ecological features within the forest. Threshold distances for housing developments around forests need to be determined to prevent or minimize adverse effects on features and functions within the forests.*

Efectos del desarrollo urbano sobre los bosques habitados por aves neotropicales migratorias

Resumen: *Numerosas especies de aves han disminuido a nivel local o regional debido a la pérdida del hábitat y a la degradación del ambiente. Intentamos separar los efectos del desarrollo residencial de los efectos del tamaño del bosque sobre las comunidades de aves, poniendo particular énfasis en las especies neotropicales migratorias. Se examinaron dos variables para determinar su influencia en la diversidad y abundancia de las aves: el tamaño del bosque y el número de casas fuera del bosque a menos de 100 m del borde. Encontramos que las aves neotropicales migratorias incrementaron consistentemente en número y en abundancia, en la medida en que el tamaño del bosque se incrementó. De mayor interés aún, encontramos que el número de casas que rodean al bosque disminuyó severamente su grado de adecuación para ser usado por los migrantes neotropicales. Las aves neotropicales migratorias decrecieron consistentemente en diversidad y en abundancia, a medida que el nivel de desarrollo de las áreas adyacentes se incrementó, independientemente del tamaño del bosque. Los impactos del desarrollo fueron sorprendentes: 4-ha de un rodal sin ninguna casa en las cercanías tuvo en promedio una comunidad de aves neotropicales más rica y abundante que en un rodal de 25-ha un área urbana. No se observó ningún patrón de cambio predecible en relación al desarrollo o al tamaño del bosque para aves migratorias de corta distancia o residentes permanentes. Las regulaciones actuales de planificación, permiten en general la urbanización hasta el borde mismo del bosque. Esta práctica puede ser insuficiente para proteger las características ecológicas dentro del bosque. Se necesita determinar las distancias umbrales que debe guardar el desarrollo urbano alrededor de los bosques, para prevenir o minimizar los impactos adversos sobre las características y las funciones dentro del bosque.*

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1408

Introduction

Rural landscapes have changed dramatically in recent decades as settlement and new development have spilled into the countryside. Natural areas have come under increased human pressures that may exacerbate the negative effects of fragmentation. We attempted to disentangle some of the effects of residential housing and forest-fragment size on forest birds, particularly long-distance (Neotropical) migrants.

Considerable effort has gone to studying fragmentation effects on forest birds in eastern North America (reviewed in Hagan & Johnson 1992). Forest size has been identified as a key determinant of avian community structure: many forest-dwelling Neotropical species (hereafter Neotropical migrants) decline in number or become locally extinct when forests are subdivided (Askins et al. 1990). Factors that measure vegetation structure have proven far less important than forest area in predicting the presence and abundance of Neotropical migrants (Ambuel & Temple 1983; Askins et al. 1987; Blake & Karr 1987).

Fragmentation dynamics cannot be considered only within the context of habitat size. Remnant patches are subject to many adverse effects. Saunders et al. (1991) contend that in small patches "ecosystem dynamics are probably driven predominantly by external rather than internal forces." For example, suburbanization may not necessarily result in forest loss (woodlands are spared even as development encircles them), but the urban surroundings may negatively affect forest avifauna (Engels & Sexton 1994). Detrimental influences associated with urban sprawl may be the reason why many species of forest birds continue to decline even where forest regeneration has occurred (Herkert et al. 1993).

Forest fragments of similar size and vegetative structure may not be ecologically equal because of differences in their surroundings. This raises a number of questions with respect to housing developments. Do Neotropical migrant communities undergo change when houses are situated around but not in forests? How many houses are needed to induce a change? Are larger forests less vulnerable to effects from housing than smaller forests? Which Neotropical migrants are most sensitive to development? What are the implications for urban planning and the management of forest bird communities?

We examined the effects on Neotropical migrants of the number of houses surrounding forests for three different forest-size classes.

Methods

Study Area and Site Selection

Field research was conducted in 1992 and 1994. All study sites in 1992 and all except four in 1994 were lo-

cated in the Region of Waterloo in southwestern Ontario (43°N 80°W). The Region of Waterloo encompasses an area of 137,369 ha and has a population of 396,000 (Regional Municipality of Waterloo 1994). The four additional sites in 1994 were all within the city of Guelph (population 80,000), located 12 miles to the east of the Region of Waterloo.

The Region of Waterloo is an intensively farmed district with about 14% of the landscape remaining under forest cover (Ontario Ministry of Natural Resources 1981). Forests in this area comprise part of the Lower Great Lakes-St. Lawrence forest belt. Woodlands are small (few exceed 80 ha in size) and virtually no old-growth forest remains (Elkin 1987).

Seventy-two woodlot sites were selected for study in each of the two years. Sixty-three of the sites were studied in both years; nine different woodlots were included in 1994 either to increase sample sizes or because original sites were modified (logged, internal housing developments constructed, or site destroyed). All sites were initially identified on 1:5000 air photo maps (1990 edition), and their condition was verified by site visits. Woodlots were chosen on the basis of being discrete patches separated from other tracts by at least 100 m of open ground. Woodlands that were long and narrow, that were recently logged or grazed, or that contained streams or steep slopes were not selected.

Primary habitat at all sites was upland deciduous forest, with sugar maple (*Acer saccharum*) being the dominant tree and sapling species. Given the structural uniformity of the sites and knowing that vegetative variables have usually not been strong predictors of Neotropical forest birds, a detailed vegetation survey was not undertaken.

Woodlots were selected in one of three discontinuous size categories (Table 1): small (3–4 ha); medium (8–15 ha); large (20–50 ha). A size variable was included in the study primarily to test whether the effects of development were dependent on forest size. Woodlots were then classified according to the number of houses outside their perimeters within 100 m of the forest edge: 0 houses (no development); 1–3 houses (low development); 8–15 houses (medium development); and ≥ 25 houses (high development). Woodlots with houses inside their borders were not selected.

Bird Censusing

A single survey station was established in each forest, either in the approximate center or, if the site was sufficiently large, at least 250 m from the nearest edge. A single-point count method (Whitcomb et al. 1981) was used to sample populations of forest birds. The point counts assumed a fixed radius of 100 m (Whitcomb et al. 1981). The area surveyed was approximately 3.6 ha, which was the approximate size of the smallest wood-

Table 1. Number of woodlot sites by size and development class.

Woodlot size	Size (ha)	Development class	Number of adjacent houses	Number of sites 1992	Number of sites 1994
Small	3-4	none	0	7	6
	3-4	low	1-3	7	6
	3-4	medium	8-15	6	6
	3-4	high	≥ 25	6	6
Medium	8-15	none	0	6	6
	8-15	low	1-3	7	6
	8-15	medium	8-15	6	6
	8-15	high	≥ 25	5	6
Large	20-50	none	0	6	6
	20-50	low	1-3	5	6
	20-50	medium	8-15	6	6
	20-50	high	≥ 25	5	6

lots in the study. Sampling area for most species was therefore similar at all sites regardless of forest size.

It should be noted that radius distance was of no consequence in assessing development effects because comparisons of bird communities were made only within forest-size classes and not between them (small sites were compared to other small sites, medium sites to medium, large sites to large). Any bias in the point-count method would therefore apply equally to all of the sites in any particular size class.

The same two observers were used in each year of the study. Stations were visited twice, once in early June and again about two weeks later. Each visit was of 20 minutes duration. The order of visits was staggered so that each station was sampled once between 0530 and 0715 hours and once between 0715 and 0900 hours. All birds detected by song or sight (except flyovers and those calling from outside the forests) were recorded. The maximum number of each species detected during the two visits was taken as the measure of abundance for that species.

Statistical Methods

We summarized the raw data for each site in each year by calculating the number of individuals (abundance) and the number of species classified according to migration strategy (whether the species was a Neotropical migrant, short-distance migrant, or permanent resident according to classifications by Whitcomb et al. [1981] and Freemark & Collins [1992]).

The two summaries for Neotropical migrants were the dependent variables in the formal analysis. The independent variables were indicator variables corresponding to size class and urban development category. The data were modeled with an appropriate generalized linear

model (McCullagh & Nelder 1983). In each case, a Poisson link function was used in which the mean abundance or number of species, μ_{ij} , at a site in size class i and development class j is related to the independent variables by the model

$$\log \mu_{ij} = \mu + \partial_i + \beta_j + (\partial\beta)_{ij}$$

$$i = 1, \dots, 3, \quad j = 1, \dots, 4.$$

The models, which were fit separately for each year, correspond to those for a two-way analysis of variance with interaction. The parameter ∂_i represents the effect of size class i , β_j the effect of development class j , and $(\partial\beta)_{ij}$ the interaction between the size class and the development category. If a model with $(\partial\beta)_{ij} = 0$ fits the data, the effect of changing development category is the same within each size class.

The models were fit to the data using the SAS procedure Proc Genmod (SAS version 6.0, SAS Institute 1990) to construct an analysis of deviance (McCullagh & Nelder 1983). The order of fitting was first the full model, then the model without interaction terms, and finally the model without the main effect terms. The change in deviance was used to examine the significance of the various parameters in the models.

Results

The response of the three migratory groups to forest size and development levels was similar for the two years (Table 2). The formal analysis yielded consistent results for each year.

The number of houses near a site significantly affected Neotropical migrants. This group consistently decreased in diversity and abundance as the level of adjacent devel-

opment increased ($p < 0.001$, Fig. 1). Within each of the three size classes, woodlots with no development contained the most diverse and abundant Neotropical migrant community (the one exception being in medium-sized woodlots in 1994). Just the reverse pertained to high development sites that invariably held the lowest diversity and abundance of Neotropical migrants in all three size classes.

Differences between high and no development classes were striking: high development sites in all three size classes had less than half the average diversity and one-third to one-half the average abundance of Neotropical migrants of no development sites. In both years there was no evidence ($p > 0.10$) of an interaction between size class and development level. This means that the effects of development on abundance and diversity of the group were independent of forest-size class. Average diversity levels of Neotropical migrants dropped off most sharply at the development level of ≥ 25 houses (Fig. 1). Average abundance levels declined sooner, indicating

Table 2. Mean number of species and mean individual abundance recorded at each survey site in 1992 (first column) and 1994 (second column), grouped according to migration strategy.

Site class (no. of houses)	All species		Neo-tropical		Short-distance		Perma- nent	
	Number of Species							
Small								
0-3	17.3	15.5	5.4	4.3	5.9	5.8	6.0	5.3
1-3	15.5	15.7	4.4	3.3	6.0	6.8	5.1	5.5
8-15	14.0	15.5	4.0	3.8	5.8	6.5	4.2	5.2
≥ 25	14.1	14.0	2.5	1.5	5.3	6.2	6.3	6.3
Medium								
0	19.0	18.7	7.8	6.2	6.2	7.2	5.0	5.3
1-3	21.6	16.5	6.3	6.3	8.4	5.7	6.9	4.5
8-15	19.7	17.7	5.7	5.2	8.2	6.8	5.8	5.7
≥ 25	17.0	13.8	3.8	2.5	5.8	5.2	7.4	6.2
Large								
0	18.3	17.0	7.5	6.8	5.2	5.0	5.7	5.2
1-3	17.6	16.7	6.8	6.3	4.8	5.7	6.0	4.7
8-15	20.5	17.5	7.3	5.5	6.0	5.8	7.2	6.2
≥ 25	15.6	14.7	4.4	3.3	5.0	5.7	6.2	5.7
	Individual Abundance							
Small								
0	20.4	21.3	6.7	7.2	7.0	7.3	6.7	6.8
1-3	20.6	19.6	6.3	4.5	8.0	8.8	6.3	6.3
8-15	18.1	19.5	4.5	4.3	8.3	8.7	5.3	5.5
≥ 25	18.0	18.7	2.5	1.7	6.5	8.3	9.0	8.7
Medium								
0	26.7	26.3	13.5	10.7	7.8	9.3	5.3	6.3
1-3	27.3	21.0	9.6	9.2	9.7	6.8	7.5	5.0
8-15	26.5	23.4	9.0	6.8	10.7	9.8	6.8	6.8
≥ 25	23.7	19.3	5.2	3.3	8.5	7.5	10.0	8.5
Large								
0	27.8	26.2	13.8	13.3	7.3	7.2	6.7	5.7
1-3	24.6	23.8	12.0	11.8	5.8	7.0	6.8	5.0
8-15	28.3	21.3	10.8	7.2	8.5	7.3	9.0	6.8
≥ 25	21.8	20.6	6.8	4.8	6.6	8.3	8.4	7.5

that, while many species were present in the low and medium development sites, they occurred in lower numbers.

Comparison of the nine most common Neotropical species (accounting for more than 91% of Neotropical, abundance each year) suggests varying sensitivities to development pressures. The Great Crested Flycatcher (scientific names of birds are given in Appendix 1) and Red-eyed Vireo were least affected by the presence of houses (Tables 3 and 4). The Eastern Wood-Pewee, the most abundant Neotropical migrant in this study and a species considered to be fairly tolerant of human activity (Cheskey 1991), displayed a clear preference for no-development as opposed to high-development forests (Table 4).

The most dramatic response to development came from the Wood Thrush. This species was common at no- and low-development sites but practically disappeared from high-development forests (Tables 3 and 4). In 1994 not one of 18 urban woodlots harbored even a single Wood Thrush. A similar disaffection for high-development sites was seen among Scarlet Tanagers, Rose-breasted Grosbeaks, and (surprisingly, give its reputation as a backyard bird) Northern Oriole.

Neotropical migrants tended to increase in diversity and abundance as forest size increased ($p < 0.001$; Table 2), consistent with findings reported elsewhere. In both years, no predictable pattern of change in response to development levels or forest size was observed for short-distance migrants or permanent residents (Table 2).

Discussion

Urban sprawl is widespread in North America and threatens to negate the benefits of forest regrowth that has occurred in many regions (Askins et al. 1990). As development reaches into rural areas, many forests, if not fragmented or obliterated outright, are enveloped by human settlement. These forests may subsequently lose parts of their avian communities not because of habitat loss but because of negative influences associated with nearby urban development.

Forman and Godron (1986: 314) noted that the importance of surroundings "is emerging as a critical issue in landscape planning and management." Our study suggests that external effects severely deflate the ecological value of adjacent forests (Neotropical migrants being an indicator of this value). Moreover, the effects are not dependent on size because large forests seem as vulnerable to development stresses as small forests. Keeping forests intact is in itself inadequate to maintaining healthy forest-bird communities. For example, 4-ha woodlots with no surrounding development contained Neotropical migrants in higher average diversity and abundance than 25-ha urban woodlots (Table 2).

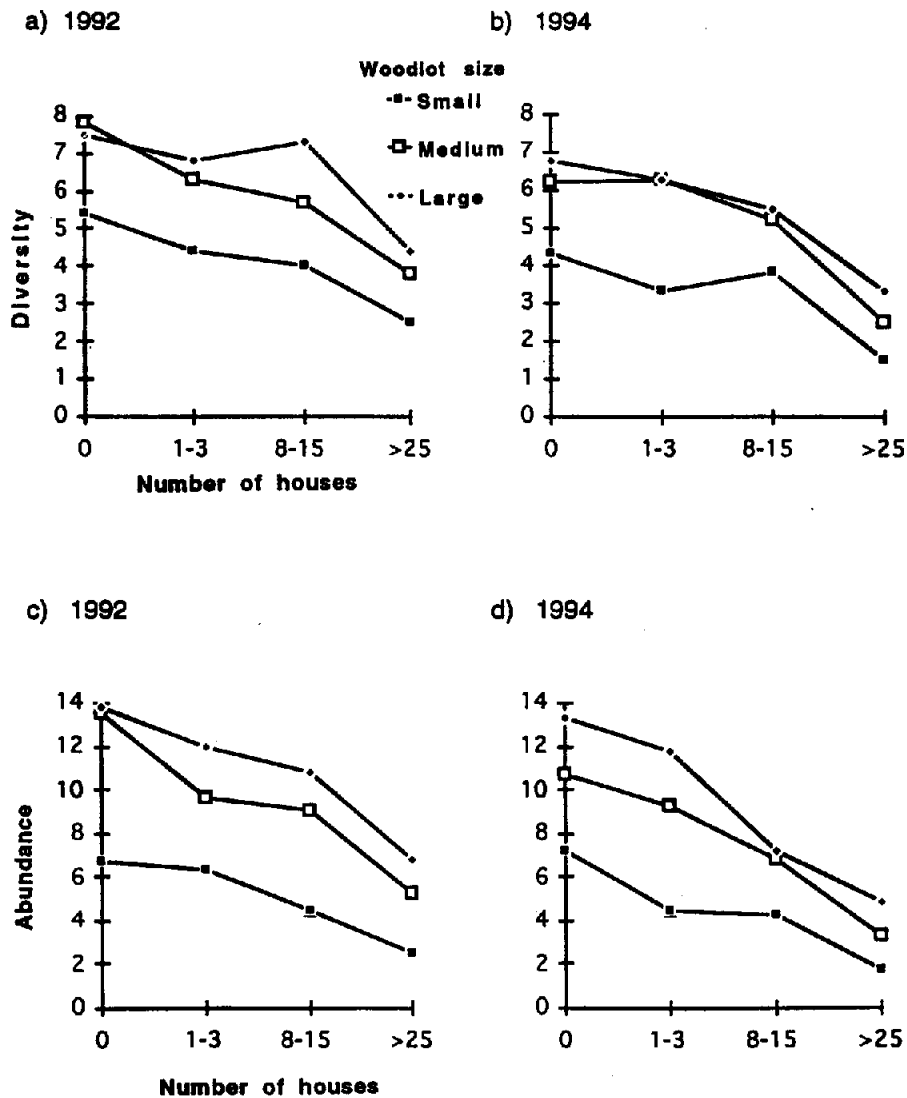


Figure 1. Average species diversity (a and b) and individual abundance (c and d) of Neotropical migrants versus surrounding development.

The Wood Thrush is in trouble throughout its breeding range (Robbins et al. 1989); the species' abundance in Ontario is estimated to be only 19% of what it was in the early 1960s (Hussell 1992). Its decline, and that of other forest birds, is difficult to explain, though it is likely that habitat alteration in both the temperate and Neotropical zones ultimately plays a role. Our study suggests that degradation of breeding habitat due to urban encroachment may be a contributing factor to the disappearance of these birds. The virtual absence of Wood Thrush from urban forests in the Waterloo Region certainly casts doubt on the contention that the species "has recently shown tolerance even of wooded areas within cities" (Sadler 1987).

The breeding success of Neotropical migrants in Illinois was almost too low to measure owing to extreme rates of nest predation and parasitism (Robinson 1992). In southern Ontario some Neotropical migrants were not present to breed (no matter how successfully) in for-

est fragments, even though apparently suitable nesting habitat was available; factors associated with urban development undermined the forests' suitability for these species.

Identifying what it is about houses that renders forest fragments unfit for Neotropical migrants was beyond the scope of this research. Several mechanisms are possible and beg further study. House cats are potent predators of small birds in urban and suburban environments and may be a factor in depressing songbird populations (Churcher & Lawton 1989). Gray squirrels (*Sciurus carolinensis*) abound in cities, subsidized in part by bird feeders, and may be important nest predators, although they have been overlooked in most passerine predation studies (Leimgruber et al. 1994). A species' psychological need for maintaining distance from houses (Whitcomb et al. 1981) and social behavior that requires the presence of conspecifics (Morton 1992) may also play a role in limiting some songbirds.

Table 3. Frequency of occurrence (expressed as a percentage of total sites at which a species was found) of the nine most common* Neotropical migrants in 1992 (first column) and 1994 (second column).

Site Class (no. of houses)	Eastern Wood- Pewee		Great Crested Flycatcher		Wood Thrush		Red- eyed Vireo		Oven- bird	Scarlet Tanager	Rose- breasted Grosbeak	Indigo Bunting	Northern Oriole					
Small																		
0	86	83	71	83	43	67	71	33	0	17	0	0	43	50	57	50	100	50
1-3	100	83	86	50	0	33	57	50	0	0	0	0	57	17	29	33	57	50
8-15	100	83	83	50	33	33	67	33	17	0	0	0	33	33	17	17	50	83
≥ 25	83	17	85	50	0	0	17	50	0	0	0	0	33	0	17	33	17	0
Medium																		
0	100	100	100	83	100	37	100	83	50	17	50	17	67	83	67	33	83	100
1-3	100	100	100	83	57	83	71	100	0	0	14	0	71	67	43	67	100	100
8-15	100	83	100	67	50	33	100	100	17	0	0	0	33	33	33	33	67	67
≥ 25	100	83	100	67	0	0	100	50	20	17	20	0	20	0	0	17	0	0
Large																		
0	100	100	100	100	83	83	100	100	33	50	50	33	83	100	50	33	67	67
1-3	100	83	100	83	100	100	100	100	20	67	40	0	80	50	40	50	80	50
8-15	100	100	100	83	67	17	83	100	0	33	17	0	50	67	67	67	100	33
≥ 25	100	83	60	50	40	0	80	100	60	0	0	0	20	17	40	17	40	17

*Found in a minimum of 10 woodlots in one of the years.

Management Implications

There is growing agreement among planners, politicians, and the public on the need for preserving and enhancing healthy ecosystems. For example, the Commission on Planning and Development Reform in Ontario has recommended that “development shall not be permitted on adjacent and related lands if it adversely affects the integrity of the natural features or ecological functions of the areas” (Ontario Ministry of Municipal Affairs 1993).

Current planning practice generally permits housing to extend right up to forest perimeters. This practice, while physically preserving forests, may fail to safeguard their ecological features. Complex interactions take place along the interface of the two very different ecosystems—urban and suburban versus forest—the effects of which seem especially harmful to Neotropical migrants. Forests cannot be expected to retain their ecological identity as the land around them is subject to ever-intensified human use.

It is time to rethink our strategies for protecting val-

Table 4. Mean individual abundance per site of the nine most common* Neotropical migrant species in 1992 (first column) and 1994 (second column).

Site Class (no. of houses)	Eastern Wood- Pewee		Great Crested Flycatcher		Wood Thrush		Red- eyed Vireo		Oven- Bird	Scarlet Tanager	Rose- breasted Grosbeak	Indigo Bunting	Northern Oriole					
Small																		
0	1.4	1.5	0.7	1.0	0.5	0.7	0.8	0.5	0	0.2	0	0	0.5	1.0	0.5	0.7	1.0	0.8
1-3	1.7	1.2	0.8	0.5	0	0.3	0.7	0.7	0	0	0	0	0.7	0.2	0.3	0.7	0.7	0.8
8-15	1.3	1.2	1.0	0.5	0.3	0.3	0.7	0.3	0.2	0	0	0	0.3	0.3	0.2	0.2	0.5	1.0
≥ 25	0.8	0.2	0.7	0.5	0	0	0.2	0.7	0	0	0	0	0.3	0	0.2	0.3	0.2	0
Medium																		
0	2.8	2.8	1.7	1.0	2.0	1.2	2.2	1.8	0.5	0.2	1.0	0.3	0.8	1.0	0.7	0.3	1.2	1.7
1-3	2.1	1.7	1.7	1.2	0.8	1.3	1.2	1.3	0	0	0.2	0	1.0	0.8	1.0	0.8	1.2	1.7
8-15	2.2	1.7	1.3	1.0	0.7	0.3	2.2	1.2	0.2	0	0	0	0.5	0.3	0.3	0.5	1.0	1.0
≥ 25	1.6	1.5	1.0	0.8	0	0	1.6	0.5	0.4	0.2	0.2	0	0.2	0	0	0.2	0	0
Large																		
0	2.8	3.0	1.5	1.3	1.8	2.0	2.2	2.7	0.8	0.5	1.3	0.7	1.2	1.5	0.5	0.3	0.8	1.2
1-3	2.4	1.8	1.5	1.3	2.0	2.0	2.2	2.2	0.2	1.0	0.4	0	1.6	1.2	0.4	0.8	0.8	0.7
8-15	2.2	1.2	1.3	1.2	1.0	0.2	1.8	2.2	0	0.3	0.2	0	1.0	0.7	0.7	0.7	1.0	0.3
≥ 25	1.8	1.3	1.4	0.7	0.4	0	1.6	1.8	0.6	0	0	0	0.2	0.2	0.4	0.2	0.4	0.2

* Found in a minimum of 10 woodlots in one of the years.

ued woodlands. In Ontario significant wetlands now receive special protection: development is unequivocally prohibited within their boundaries, and buffers of 120 m are required around them to protect their functions and features (Ontario Ministry of Municipal Affairs 1992). Threshold distances for housing developments around woodlots likewise need to be determined in order to prevent or minimize potentially adverse effects.

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Appendix 1

Neotropical migrant species recorded in the region of Waterloo in 1992 and 1994.

Common name	Scientific name
Ruby-throated Hummingbird	<i>Arachilochus colubris</i>
Eastern Wood-Pewee	<i>Contopus virens</i>
Willow Flycatcher	<i>Empidonax traillii</i>
Least Flycatcher	<i>Empidonax minimus</i>
Great Crested Flycatcher	<i>Myiarchus crinitus</i>
Eastern Kingbird	<i>Tyrannus tyrannus</i>
Blue-gray Gnatcatcher	<i>Polioptilla caerulea</i>
Veery	<i>Catbarus fuscescens</i>
Wood Thrush	<i>Hylocichla mustelina</i>
Yellow-throated Vireo	<i>Vireo flavifrons</i>
Red-eyed Vireo	<i>Vireo olivaceus</i>
Warbling Vireo	<i>Vireo gilvus</i>
Cerulean Warbler	<i>Dendroica cerulea</i>
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>
Black-throated Green Warbler	<i>Dendroica virens</i>
American Redstart	<i>Setophaga ruticilla</i>
Common Yellowthroat	<i>Geothlypis trichas</i>
Northern Waterthrush	<i>Seiurus noveboracensis</i>
Mourning Warbler	<i>Oporornis philadelphia</i>
Ovenbird	<i>Seiurus aurocapillus</i>
Scarlet Tanager	<i>Piranga olivacea</i>
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>
Indigo Bunting	<i>Passerina cyanea</i>
Northern Oriole	<i>Icterus galbula</i>