

VOLUME 18, ISSUE 1, ARTICLE 15

Heide, K. T., L. E. Friesen, V. E. Martin, E. D. Cheskey, M. D. Cadman, and D. R. Norris. 2023. Before-and-after evidence that urbanization contributes to the decline of a migratory songbird. Avian Conservation and Ecology 18(1):15. https://doi.org/10.5751/ACE-02366-180115 Copyright © 2023 by the author(s). Published here under license by the Resilience Alliance.

Research Paper

Before-and-after evidence that urbanization contributes to the decline of a migratory songbird

*Karl T. Heide*¹, *Lyle E. Friesen, Virgil E. Martin*², *Edward D. Cheskey*³, *Michael D. Cadman*⁴ and D. Ryan Norris¹ Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada, ²Regional Municipality of Waterloo, Planning (retired), Waterloo, Ontario, Canada, ³Nature Canada, Ottawa, Ontario, Canada, ⁴Canadian Wildlife Service, Environment Canada, Ottawa, Ontario, Canada

ABSTRACT. Although urbanization is widely believed to be an increasing threat to biodiversity, drawing strong inferences about its effects on wildlife has been challenging because the state of a population prior to development is rarely known. The Wood Thrush (*Hylocichla mustelina*) is a steeply declining migratory songbird that breeds in North American temperate deciduous forests and winters in Central America. From 1987 to 2001, Wood Thrush abundance and daily nest survival were measured in 72 forest fragments across Waterloo Region, Ontario, Canada. Some of these fragments have since been surrounded by urbanization while others have remained rural. In 2020 and 2021, we reassessed Wood Thrush abundance and daily nest survival in these same fragments by replicating point count and nest monitoring protocols. Our results suggest that Wood Thrush have declined most steeply in fragments with development built within 1 km during the intervening 20-year period (-79% vs. only -57% elsewhere), although experiencing no decline in daily nest survival over the same time period, regardless of development. Our findings provide rare before-and-after evidence that urbanization near breeding habitat is contributing to a pronounced localized decline of a migratory songbird, likely by mechanisms unrelated to nest survival.

Des données avant-après indiquent que l'urbanisation contribue au déclin d'un passereau migrateur

RÉSUMÉ. Même si l'on considère généralement que l'urbanisation constitue une menace croissante pour la biodiversité, il est difficile de tirer des conclusions solides quant à ses effets sur la faune sauvage, car l'état d'une population avant la construction des lotissements est rarement connu. La Grive des bois (*Hylocichla mustelina*) est un passereau migrateur en forte baisse qui se reproduit dans les forêts feuillues tempérées d'Amérique du Nord et hiverne en Amérique centrale. De 1987 à 2001, l'abondance de la Grive des bois et la survie quotidienne au nid ont été mesurées dans 72 parcelles de forêt de la région de Waterloo, en Ontario, au Canada. Certaines de ces parcelles ont depuis été entourées par des lotissements tandis que d'autres sont restées dans leur état rural. En 2020 et 2021, nous avons réévalué l'abondance de la Grive des bois et la survie quotidienne au nid dans ces mêmes parcelles en reproduisant les protocoles de dénombrement par points d'écoute et de suivi des nids. Nos résultats montrent que la Grive des bois a connu la baisse la plus marquée dans les parcelles où des lotissements ont été construits à moins d'un kilomètre au cours de la même période, peu importe si des lotissements ont été construits ou non à proximité. Nos résultats fournissent de rares données avant et après indiquant que l'urbanisation à proximité de l'habitat de nidification contribue au déclin localisé prononcé d'un passereau migrateur, probablement par des mécanismes qui ne sont pas liés à la survie au nid.

Key Words: *breeding abundance; forest fragmentation; Hylocichla mustelina*; Neotropical migrant; nest success; population dynamics; urban sprawl; Wood Thrush

INTRODUCTION

In North America, there are an estimated 29% fewer birds than there were in 1970, which represents a loss of nearly 3 billion individuals over a period of only 50 years (Rosenberg et al. 2019). Among declining North American avifauna, those facing the greatest risk of extinction are the Nearctic-Neotropical migrants (Rosenberg et al. 2019). Factors influencing the abundance of Nearctic-Neotropical migratory birds may occur during the breeding season in North America, the stationary over-wintering period in the Neotropics, or during migration (Sherry and Holmes 1995). This is further complicated by the possibility that events during one of these periods may carry over to influence nest success and abundance in a subsequent period (Norris et al. 2004, Harrison et al. 2011).

One major factor contributing to habitat loss and migratory bird declines may be urbanization. Although some studies have found urban parks and residential areas with large trees to be suitable breeding habitat for certain species (Roth et al. 1987, Strohbach et al. 2013), many more have documented negative correlations between urbanization and the abundance and diversity of Nearctic-Neotropical migrants (Friesen et al. 1995, Melles et al. 2003, Pidgeon et al. 2007, Minor and Urban 2010). In addition to habitat loss, urbanization may affect bird abundance through

Table 1. Possible hypotheses and their associated mechanisms explaining variation in Wood Thrush (*Hylocichla mustelina*) nest success considered in this study.

Hypothesis Name	Hypothesized Mechanism	Support in the Literature
Brood parasitism	Brown-headed Cowbirds (<i>Moluthrus ater</i>) lay their eggs in host nests and eject host eggs, both of which result in lower reproductive output and overall probability of success.	Hoover and Brittingham (1998) Weinberg and Roth (1998)
Sapling density	Dense vegetation around the nest deters predators, resulting in higher nest success rates.	Hoover and Brittingham (1998) Fauth (2000) Driscoll et al. (2005)
Nest height	Nests in dense understory have a lower probability of success, possibly due to poor visibility or pressure from predators that hunt mainly at low to mid levels, such as raccoons (<i>Procyon lotor</i>).	Newell and Kostalos (2007)
Urban nest predators	Presence of humans in the surroundings leads to higher abundance of raccoons and <i>Accipiters</i> , both common nest predators of Wood Thrush, resulting in lower nest success rates in proximity to development.	Wilcove (1985) Chace and Walsh (2006) Cadman et al. (2007) McCobe et al. (2018)
Urban food supply	Abundant food sources of urban areas attract predators away from Wood Thrush nests, resulting in higher nest success rates.	Friesen et al. (2013)
Initiation date	Nests initiated earlier in the season have a higher probability of success because of higher quality sites being selected first.	Price et al. (1988) Nur et al. (2004)
Fragment size	Larger forest fragments have higher nest success due to lower abundance of cowbirds and human-associated predators and decreased edge effects.	Burke and Nol (2000) Newell and Kostalos (2007)
Regional forest cover	Forest fragments within heavily forested landscapes produce more successful nests due to lower predator and cowbird abundance and because these fragments are occupied by higher quality breeding individuals.	Robinson et al. (1995) Hoover and Brittingham (1998) Weinberg and Roth (1998)
Adult mortality	Areas with more sources of adult mortality during the nesting season (such as vehicles, window strikes, and urban predators), have lower nest success rates because nests cannot fledge without parental care.	Schmidt and Whelan (2005)

a wide variety of indirect mechanisms, including disease transmission (Brittingham and Temple 1986), collisions with vehicles and structures (Klem 1989, Chace and Walsh 2006), altered predation regimes (Major et al. 1996), altered food sources (Egan and Brittingham 1994), and changes to vegetation structure (Chace and Walsh 2006). Less clear is the relationship between urbanization and reproductive success, with positive, negative, and non-significant effects reported depending on the location, species, and study design (Wilcove 1985, Driscoll et al. 2005, Friesen et al. 2005, 2013, Chace and Walsh 2006, Newell and Kostalos 2007, Vincze et al. 2017; Table 1).

The Wood Thrush (*Hylocichla mustelina*) is a Nearctic-Neotropical migratory songbird that winters in Central America and breeds in eastern North American deciduous forest (Stanley et al. 2015). Between 1970 and 2012, the Wood Thrush declined by approximately 59% across its breeding range (Partners in Flight 2021) and in Ontario by an alarming 83% (COSEWIC 2012). Although habitat loss on the wintering grounds is likely an important driver of Wood Thrush declines (Taylor and Stutchbury 2016), pressures on the breeding grounds may also pose a threat (Holmes 2007, Rushing et al. 2016). These breeding season pressures include forest loss (Freemark and Collins 1992, Robinson et al. 1995, Weinberg and Roth 1998, Driscoll et al. 2005), forest fragmentation (Robinson et al. 1995, Burke and Nol 2000), brood parasitism by Brown-headed Cowbirds (*Molothrus*)

ater; Robinson 1992, Hoover and Brittingham 1998), and the relentless expansion of urban areas across eastern North America (Friesen et al. 1995, 2005, Phillips et al. 2005, Chace and Walsh 2006, Cadman et al. 2007, McCabe et al. 2018).

Evidence suggests that urbanization may be eroding the viability of Wood Thrush breeding populations. Friesen et al. (1995) reported that the abundance of Wood Thrush and other Neotropical migratory birds breeding in forest fragments in Ontario was negatively related to the number of adjacent houses within 100 m of a fragment, independent of fragment size. However, because this study occurred over a relatively short period of three years (1992-1994), it remains unknown whether potential site-specific conditions such as forest management, alongside development may be differentially affecting the trajectory of Wood Thrush populations over time. In Michigan, Wood Thrush site occupancy was 50-75% higher in forests with a moderate relative to a high number of houses in the surrounding area (Taylor et al. 2016), but this study occurred at a single point in time. In Virginia, there was a decrease in the abundance of Wood Thrush and other Neotropical migrants at one location between 1942 and 1979, during which time the 47-ha study site transitioned from a forest-dominated landscape to a low-density residential area (Aldrich and Coffin 1980). By contrast, in another before-after study conducted at a single location in Ohio, Wood Thrush abundance increased after urbanization, presumably due to changes in vegetation structure that made the habitat more suitable for breeding (Horn 1985). Herein, while past research has provided evidence that urbanization can negatively influence Wood Thrush abundance, an even more rigorous approach would be to examine abundance both before and after urbanization at multiple sites with new surrounding development and to compare these to nearby sites in which no development occurred.

We explore the effect of urbanization on Wood Thrush population decline in Waterloo Region, Ontario, Canada, by comparing historical estimates of abundance and daily nest survival collected between 1987 and 2001 in then-rural forest fragments, with contemporary post-development estimates of the same measures from the same fragments. A suite of rural-forest fragments without recent development in their surroundings served as pseudo-control sites and structural vegetation plots allowed us to examine within-fragment habitat changes between the two time periods. Landcover layers from before and after urbanization provided estimates of the amount and proximity of development around the forest fragments within fixed-radius buffers ranging from 100 m to 4 km. We examined whether the recent observed decline in Wood Thrush abundance across Waterloo Region has been amplified by a negative response to nearby urbanization, and whether daily nest survival has also been affected by urbanization in the surrounding landscape, either positively or negatively, due to a variety of possible mechanisms (Table 1). If urbanization acted as a cumulative effect on populations, we predicted the steepest decline of Wood Thrush abundance and the greatest change in daily nest survival to have occurred in fragments that experienced new residential or commercial development in the surrounding landscape between the two time periods. We also examined whether vegetation structure changed significantly over this same time period and whether such changes were more likely to occur in forest fragments that experienced development in their surroundings between the two time periods than in those that did not.

STUDY SITES AND METHODS

Study area

Prior to European settlement, Waterloo Region (Fig. 1) was predominantly forested, with small areas burned for rotating agriculture and hunting practices of the Haudenosaunee (Iroquois) and Anishinaabe (Ojibway) tribes (Mississaugas of the New Credit First Nation [date unknown]). During the 1800s, most of the original forest was cleared by European settlers and land was converted to permanent agriculture and eventually towns (Martin 1991). By the beginning of the 20th century, little forest remained, but over the past hundred years, some areas with marginal agricultural capability have been left to regenerate, resulting in patchy landscapes of agriculture mixed with isolated fragments of forest at varying stages of succession (Larson 1999). Despite intensifying agricultural practices and ever-expanding urbanization, an analysis of recent landcover data (Potapov et al. 2022; Walmsley and Norris 2023, unpublished data) revealed that forest cover in Waterloo Region has seen a marginal increase over the past 20 years (15.4% in 2000 vs. 16.5% in 2020). This may be due to a combination of forest regeneration and strong forest protection policies in the region.

Because many forest fragments in Waterloo Region are situated on private land, management decisions can vary considerably over time from one locale to the next. Although a few forest fragments have remained relatively undisturbed for the better part of a century, most have been selectively logged on a periodical basis. Often, forest fragments dominated by sugar maple (*Acer saccharum*) are tapped for maple syrup production, a practice correlated with selective logging. Some forest fragments are intensively used for hiking, mountain biking, horseback riding, or hunting, while others are off limits to the public.

Study design

Following the basic framework of a before-after-control-impact (BACI) design, as described by Morrison et al. (2008), data were collected in 72 forest fragments across Waterloo Region during historical (1987-2001) and contemporary (2020-2021) time periods. We used aerial imagery to identify a suite of forest fragments that varied in size and isolation, then we visited any fragment for which we were able to obtain access from the landowner. The type and amount of data (nest, point count, or vegetation) collected in each forest fragment, in the contemporary period, depended on which historical data were available (Appendix 1). Historical data sources included a point count study from 1990-1994 (Friesen et al. 1995), a nest success study from 1996 and 1997 (Friesen et al. 1999), and additional point count data collected between 1987 and 2000, some through the Ontario Forest Bird Monitoring Program (FBMP; Welsh 1995) and some by the City of Waterloo (Cheskey 2017). Daily nest survival and abundance were also measured in several forest fragments between 1998 and 2001 for a study on urban pressure (Friesen et al. 2005). Nest-site vegetation components were measured at some of the nests found in the historical period and at all of the nests found in the contemporary period.

Although it is difficult to classify any of the forest fragments in this study as true "control" sites because landscape change has inevitably occurred around all of them, many of the fragments have been encroached upon by new residential and commercial development between the historical and contemporary time periods (Fig. 1), while others have either remained in a rural or urban context. Of the forest fragments with recent development, there is considerable variation in the amount and proximity of the development as well as the size of the fragment (Fig. 1; Appendix 1). Although development has occurred around many of the forest fragments, strong protection policies in Waterloo Region have prevented most instances of actual intrusion into the fragments resulting in a reduction in their size. Minor changes in forest area between time periods may reflect slight differences in classification accuracy between our two landcover layers and typically do not amount to changes greater than a few hectares (Appendix 1). Fragments that lost or gained more than 10% of their original area between time periods were excluded from all analyses.

Point counts

In both time periods, we conducted standardized 10 min point counts at the same 100 stations within 55 forest fragments. The fragments ranged in size from 2-154 ha (mean = 23.8 ha) and included both rural and urban fragments as well as some that transitioned from a rural to an urban context between the two

Fig. 1. Location of the study area and examples of development surrounding forest fragments: (A) Waterloo Region in southern Ontario, Canada, (B) location of the forest fragments surveyed, and (C and D) landcover classification around a subset of the fragments in the historical (2001) and contemporary (2019) time period. Contains information made available under Grand River Conservation Authority's Open Data License v.1.0.



time periods (Appendix 1). Because historical counts were not all collected for the same project, protocols differed slightly and the number of stations and survey years per fragment varied. The number of stations per fragment ranged from 1 to 16 (mean = 1.44) with larger fragments typically containing more stations than smaller fragments. No station was ever placed within 200 m of another station or within 50 m of a forest edge. The smallest fragment containing more than 1 station was 19.4 ha. All birds heard or seen, typically within a fixed radius of 100 m, were recorded. Stations were usually established at one location per fragment in the approximate center of the fragment and were surveyed twice a year during the month of June between 05:50 and 09:15 (Friesen et al. 1995). Forest fragments surveyed by the FBMP (Welsh 1995) and the City of Waterloo (Cheskey 2017) followed a similar protocol with the following differences: these fragments contained multiple stations as opposed to one, and counts used an unlimited radius (but differentiated between </> 100 m) and ran until 10:00.

Avian studies often use point counts to estimate abundance and incorporate visit-level information such as weather, time, and noise into a statistical model to account for differences in detectability (Ralph and Scott 1981). An inevitable limitation to our study was that our historical dataset did not include this information (although we did collect it in the contemporary period). We were, therefore, required to rely on a study design that minimized detection bias, which is a valid alternative to modeling, especially considering the difficulty of accounting for every possible factor that could affect detection (Hutto 2017). Regardless of the methodology used to count birds in the field, we only included birds detected within 100 m inside the forest margin in our analysis. Such fixed radius point counts are considered appropriate for generating indices of relative abundance in urban areas when the habitat is consistent across sites and when the number of detections is at least 60-80, both of which were true in our study (Petit et al. 1995, van Heezik and Seddon 2012). We used a 10-min duration, which has been shown to be the point when species detection rates begin to plateau in Beech-Maple dominated forests like ours (Petit et al. 1995). To ensure that the highest count reflected actual detections and not observer bias, the same observer always returned for the second visit. In most cases, the observer in the contemporary period was not the same as the observer in the historical period, but observer skill level was comparable. In both time periods, stations were randomly divided among several skilled observers to avoid observer-based detection bias. Much of the concern around detection variability has to do with interspecific variation (Johnson 2008, Hutto 2016), which was not an issue in this singlespecies study. Furthermore, being a lower-frequency vocalizer, the Wood Thrush is easy to detect regardless of the age of the observer. To minimize the impact of noise and weather, counts were not conducted in any more than a light drizzle or in wind stronger than a four on the Beaufort Scale. By conducting all counts in the morning and making sure the two visits occurred at different points in the breeding season and at different times in the morning, we attempted to control detection bias associated with time of day and time of year. As a final measure of control against erratic weather events or one-off sources of noise (such as from adjacent machinery), we used only the highest count value of the two visits. Combined, these measures only left one potential source of bias: site-specific sources of persistent noise like roads or running water. To test whether noise was related to development pressure or to forest size, we plotted our contemporary visit-level noise data (collected on a scale of 1-5 with 1 being no noise and 5 being excessive noise) against the percent cover of development (at 100 m, 1 km, and 4 km) and against fragment size.

Nest monitoring and nest success

From May to July (1996-2001 and 2020-2021), we searched for Wood Thrush nests in 35 forest fragments across Waterloo Region that ranged in size from 2 to 146 ha (mean = 21.2 ha; Friesen et al. 1999, 2005). Twenty of these fragments were the same as those used in the earlier point count study (Friesen et al. 1995; Appendix 1). To find and monitor nests, we systematically walked the entire fragment to locate territories, then if no Wood Thrush were detected, we ran playback recordings to induce singing. In each time period, we performed intensive area searches in the territories of singing males with the goal of finding every nest in the fragment. Later in the summer, we returned to each fragment, searching the remainder of the forest to uncover more secretive pairs or second-brood nests from pairs previously surveyed. Because the historical nest searching was not done with future comparisons in mind, no notes were taken on the number of visits or number of search hours. This was admittedly an unfortunate limitation. However, search effort was proportional to the size of the fragment, with larger fragments taking many more hours to thoroughly search than smaller ones. To ensure an equivalent distribution of effort between time periods, we continued to devote sufficient hours to large fragments in the contemporary period regardless of whether any Wood Thrush were detected. This accounted for the likelihood that many formerly suitable territories are no longer used because of the range-wide decline of the species.

Nests were checked on average every 3-4 days but every 1-2 days around transitions (hatch and fledge) to ensure fate could be determined accurately. Contents of nests up to 10-m high were recorded using a mirror or wireless endoscope with the aid of a 6-m extendable pole and step ladder. Nests higher than 10 m were monitored from the ground by observing parental behavior, but the contents could not be checked. Following Friesen et al. (1999), a successful nest was defined as producing at least one Wood Thrush fledgling. Young from Wood Thrush nests tend to fledge between day 12-15, and disturbances around the nest as early as day 10 can result in premature fledging (Evans et al. 2020). Following Friesen et al. (2005), once a Wood Thrush nestling reached day 10, we deemed the nest successful unless evidence of predation was observed thereafter. The limitation with this assumption is that success estimates and modeled daily survival rate were biased high because some predation events inevitably occurred after day 10 but before nestlings actually fledged. Monitoring ceased once the nest was empty or deemed inactive (cold eggs or three consecutive checks without activity). Fieldwork was approved under permit # 4369 of the University of Guelph's Animal Utilization Protocol.

We estimated daily nest survival using the Mayfield method (Mayfield 1975). Though the nestling period can range from 12-15 days and the incubation period from 12-13 days (Evans et al. 2020), a 25-day nesting cycle (beginning on the day of penultimate egg lay) was chosen as a standard at the time historical data were collected and was used for consistency throughout this study. We calculated exposure days as the total number of days during which all nests were monitored in a given time period. This approach accounted for differing observation periods between nests and the increasing probability of detecting nest failure with the length of a nest's observation period.

Vegetation sampling

In 14 forest fragments (7 urbanized and 7 rural), we measured the structure and composition of the vegetation within 12.5 m of nests found in both the historical and contemporary periods. Vegetation was always measured during the same year in which the nest was active. Along four ropes laid out in each cardinal direction from the nest, we counted the number of saplings (woody plants < 7.5 cm in diameter at breast height (DBH) and < 8 m in height) within arm's length and measured leaf litter at 5 m increments by inserting a ruler into the litter layer until it touched solid ground. Next, we tallied the number of trees of 6 size classes greater than 7.5 cm DBH within the plot. Finally, we visually estimated the percent cover of five forest strata: groundcover, shrub layer, sapling layer, subcanopy, and canopy. Wood Thrush have been found to select nest microhabitats with many small saplings (Hoover and Brittingham 1998) and the density of the sapling, subcanopy, and shrub layers around the nest may provide cover from predators (Fauth 2000, Driscoll et al. 2005). Leaf litter depth is important to the invertebrates on which Wood Thrush feed, as are canopy cover, forest age, and groundcover (Evans et al. 2020).

Landcover classification

To quantify development occurring around forest fragments between historical and contemporary sampling, we used opensourced GIS software (QGIS Development Team 2021) to create 2 spatial layers that captured landcover across Waterloo Region at a resolution of 30 m at two points in time (2001 and 2019; Fig. 1). The historical layer was based on a foundation of an existing landcover layer (Grand River Conservation Authority 1999). To enhance the accuracy of forest fragment size and shape, we augmented this layer by overlaying forest polygons that we had manually traced over physical stereo imagery in 2001 using a stereoscope. The contemporary layer was based on the most recently available annual crop inventory (ACI) data (Centre for Agroclimate, Geomatics, and Earth Observation 2019). Because ACI was often poor at differentiating land classes around the urban fringe, we improved its classification by overlaying polygons that we manually traced around all land classes (including forest fragments) over the most recently available Google Earth aerial imagery (Google Earth Pro 2019). This approach was comparable to the stereoscope digitization method used in 2001 to delineate the forest fragments, and it allowed us to complete the time-consuming process remotely during the height of the COVID-19 pandemic. Although any manually delineated polygon is subject to a certain degree of human error or bias toward inclusion/exclusion, we maximized consistency in the level of accuracy by keeping the map at the same scale (1:50,000) in both time periods while tracing the polygons. This scale was shown in preliminary tests to be effective at measuring the amount of forest cover in our landscape. A roads layer from the Southern Ontario Land Resource Information System, version 3.0 (Ontario Ministry of Natural Resources 2019), was included in both the historical and contemporary layers. New roads built since 2001 were then erased from the historical layer.

We broke down landcover into six distinct classes deemed relevant to the nesting ecology of Wood Thrush: (1) forest, (2) field (vegetation predominantly shorter than 2 m, largely comprised of annual crops), (3) residential/commercial/industrial development, (4) bare ground (no vegetation), (5) water, and (6) non-forested natural areas (NFNA), a class which included overgrown pasture, shrubby wetland, conifer plantations, abandoned orchards, and anything with a similar spectral signature. We distinguished NFNA as separate from forest because juvenile Wood Thrush have been shown to prefer early-successional habitats during postbreeding dispersal (Anders et al. 1998, Vega-Rivera et al. 1998). Isolated pixels and polygons less than 624 m² were dissolved into their nearest neighbor to eliminate spurious misclassifications resulting from noise in the original raster layers.

We calculated landcover percentages within fixed buffers of 100 m, 1 km, and 4 km. We selected these scales because of their biological relevance to Wood Thrush, consistency with previous studies, and recommendations in the literature. The 100-m radius scale is roughly equivalent to the estimated size of a Wood Thrush breeding territory (Evans et al. 2008) and was also used by Friesen et al. (1995) to look specifically at the effects of housing. Although adults typically stay within 100 m of an active nest, they are known to travel up to 1 km for extra-pair copulation and relocation to new nest sites after failed attempts (Macintosh et al. 2011). Larger still is the dispersal distance of juveniles after fledging prior to fall migration, which can be as far as 4 km (Anders et al. 1998), and this scale was also used in a 2013 study on nest predation (Friesen et al. 2013). For point count landcover analysis, buffers were concentric to the point count station, while nest survival analysis used buffers drawn within a fixed radius of the edge of the patch. This latter approach was used because the exact location within the fragment was not recorded for all historical nests.

Statistical analysis

Data were analyzed in R v.3.6.2 (R Core Team 2020). Forest fragments were only included in our analysis if data (including zeroes) were available from both time periods. Because of the high degree of variation in its amount and proximity, development was modeled as a continuous rather than a categorical variable. Model fit and validity were checked using the R package "DHARMa." Variables and interaction terms were chosen because of previous support in the literature as predictors of Wood Thrush abundance or nest success. See Table 1 for examples of mechanisms thought to affect nest success.

First, we modeled the influence of development on Wood Thrush abundance (highest value out of two visits) at the level of the individual point count station in a given year. We used generalized linear mixed-effects models (GLMMs) with a negative binomial link because our count data were over dispersed and zero inflated (Lindén and Mäntyniemi 2011). A candidate set of 29 possible models (Appendix 3, Table A3.1) included time period, development at all 3 scales (100 m, 1 km, 4 km), fragment size, and regional cover of non-forested natural areas (1 km and 4 km). The model set also included interaction terms between time period and development at each scale and between development at each scale and fragment size. Station ID and year were included in all models as random effects to account for potential short-term or highly localized fluctuations in abundance. We assessed model support based on \triangle AICc, the AIC value corrected for small sample sizes (Burnham and Anderson 2002). Models with a Δ AICc value < 2 were considered as having greatest support, with the awareness that parameters from models with a K-value greater than that of the top supported model may not be truly informative (Arnold 2010). Nevertheless, parameter estimates from all models ranking within 2 \triangle AICc were averaged using the R package "AICcmodavg" to investigate the relative significance of parameters within this set of top supported models. We then calculated 85% conditional confidence intervals of each parameter or model-averaged parameter and identified those that did not overlap zero as important predictors, recognizing that parameters not occurring in the top model may hold questionable importance. Arnold (2010) demonstrated that, because AIC selects models at p < 0.157, using 95% CIs could result in variables in best-approximating models supported by lower AIC values being unjustly discarded.

Second, we modeled the effects of 10 predictor variables on Wood Thrush daily nest survival at the level of the individual nest using logistic regression GLMMs with the "logistic exposure" link (Shaffer 2004). This approach accounted for increasing probability of success with length of exposure by raising each success or failure event to the power of the number of exposure days. Predictor variables in the candidate model set of 91 possible models (Appendix 3, Table A3.2) included time period, development at 3 scales, initiation date (Price 1988), sapling density, canopy cover, nest height, fragment size, and regional forest cover at the 4 km scale (Table 1 for hypothesis support). We also included the interaction between time period and each scale of development in the model set, as well as interactions between development and fragment size, regional forest cover, sapling density and nest height, interactions between time period and nest height, and between nest height and sapling density. Our sample size did not allow us to look at nest survival at the level of the individual fragment, but to partially account for this, fragment ID was included in the model set as a random effect. Because nest success may fluctuate on an annual basis (Fauth 2000), year was also included as a random effect. Model averaging and confidence interval estimation followed the same methods used for the abundance models.

Third, we addressed the possibility of changing vegetation as a contributor to variation in Wood Thrush abundance. Lacking historical randomized vegetation plots to compare against, we used nests from 14 forest fragments in which nest vegetation data had been collected in both time periods as our units of measurement (historical: n = 111 nests, contemporary: n = 86

nests). Of these 14 fragments, 7 had experienced development within 4 km since 2001, and 7 had not. If Wood Thrush nest site preference did not change after only a few generations, any differences in nest site vegetation characteristics between time periods or fragment types would imply a difference in habitat availability. We ran a series of non-parametric Friedman tests on the fragment-aggregated means of nine nest vegetation variables: sapling density, tree density, leaf litter depth, nest height, and the percent cover of five strata (canopy, groundcover, saplings, shrub cover, and subcanopy). Each of these 9 response variables was modeled as a function of time period (a binary categorical predictor) for 3 separate sets of tests: (1) across all 14 fragments, (2) within 7 fragments that experienced development within 4 km, and (3) within 7 fragments that did not experience development within 4 km. A significant effect of time period on a given vegetation variable in fragments that experienced development would suggest that development affected that vegetation variable over time. We also included fragment ID as a blocking factor to account for repeated measures within a fragment. We did not analyze development at the other two scales (1 km and 100 m) because only two fragments with nest vegetation data from both time periods experienced development < 1 km away. To minimize the probability of false detection from running multiple (n = 27) tests, we used a Bonferroni correction to adjust the original α value of 0.05 to 0.002 (0.05/27). Vegetation was always measured later in the same season the nest was active (historical period: 1996-2001, contemporary period: 2020-2021).

RESULTS

Wood Thrush abundance

Historical mean count (individuals per station per year \pm SE, 1.14 \pm 0.07, n = 302) was almost triple that of contemporary mean count (0.33 \pm 0.05, n = 174), which translates to an overall decline of 71%. This decline was steepest (79%) in fragments that experienced development within 1 km (historical period [mean count \pm SE]: 1.25 \pm 0.10, n = 188, contemporary period: 0.26 \pm 0.06, n = 82; Fig. 2a). By contrast, the decline in fragments without recent development was 57% (historical period: 1.06 ± 0.11 , n = 100, contemporary period: 0.46 ± 0.09 , n = 78; Fig. 2a). The top model explaining Wood Thrush abundance included time period * development (within 1 km) + fragment size + nonforested natural areas (within 1 km) + a random effect of station ID (weight = 0.65). There were no other models within 2 \triangle AICc (Table 2), and \triangle AICc to the second-best model was 3.05 (Appendix 3, Table A3.1). Wood Thrush mean count was positively related to fragment size (effect size = 0.008 ± 0.002 , 85% CI = 0.006 to 0.011) and negatively related to non-forested natural areas within 1 km (effect size: -0.077 ± 0.027 , 85% CI = -0.115 to -0.038). Mean count was higher in 2021 than in 2020 across the same 78 point count stations (2021: 0.38 ± 0.08 , 2020: 0.33 ± 0.08). The same short-term fluctuation was apparent through casual observations during nest searching and while navigating between point counts. In 2021, we observed Wood Thrush in 15 forest fragments where we had not found them in 2020, compared to only 5 fragments where we observed them in 2020 but not in 2021. In our analysis of the effect of noise bias on our count values, we found no significant correlation (Pearson's product-moment) between noise and the three development scales (r = 0.26, 0.35, and 0.29, respectively, n = 288). We also did not find noise to be related to the size of the fragment in which the count was conducted (r = -0.24, n = 288).

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Fig. 2. Mean count (A) and Mayfield daily nest survival (B) of Wood Thrush (*Hylocichla mustelina*) in Waterloo Region during the historical (1987-2001) and contemporary (2021-2021) time periods. Error bars represent standard error and numbers next to dots represent sample size of point count stations (A) and nests (B). For the purposes of visualization, abundance estimates are broken down here into three groups: rural control forest fragments, fragments with new development (within 1 km) during the intervening time, and fragments with adjacent development existing before the historical period. Nest success estimates are displayed for two groups: rural controls and fragments with new development within 4 km. The effect of development was modeled as a continuous variable using a generalized linear mixed-effects model (GLMM) approach. For effect sizes, see Results.



Wood Thrush nest success

We monitored a total of 280 nests in the historical period and 90 nests in the contemporary period. In the contemporary period, we found and monitored 65 nests in fragments with development within 4 km and 25 nests in rural fragments. In the historical period, 187 of the nests monitored were located in the now-urbanized (within 4 km) fragments, and the remaining 93 nests were in fragments that have remained rural. In the historical period, we found active Wood Thrush nests in all 35 forest fragments that we searched, while in the contemporary period, nests were found in only 14 of these same 35 fragment in which an

Table 2. Model summary of parameter estimates from the best-fit negative binomial generalized linear mixed-effects model predicting Wood Thrush (*Hylocichla mustelina*) abundance, based on a candidate set of 29 model combinations of the variables: time period, fragment size, percent cover of existing development at the 100 m, 1 km, and 4 km scales, and percent cover of non-forested natural areas (NFNA) at the 1 km and 4 km scales. The model shown in this table also includes the random effects of point count station ID (variance = 0.7311 ± 0.5345) and year (variance = $2.6 \times 10^{-11} \pm 5.2 \times 10^{-6}$).

Parameter	Estimate \pm SE	z value	85% CI
Intercept [†]	-0.381 ± 0.218	-1.751	-0.694, -0.068
Time period [†]	-0.766 ± 0.198	-3.866	-1.051, -0.481
Development (1 km)	-0.004 ± 0.007	-0.586	-0.014, 0.006
NFNA $(1 \text{ km})^{\dagger}$	-0.077 ± 0.027	-2.866	-0.115, -0.038
Fragment size [†]	0.008 ± 0.002	4.391	0.006, 0.011
Time period: development (1 km) †	-0.021 ± 0.010	-2.209	-0.035, -0.007

active nest was found in the contemporary period was 7.2 ha, and the sole nest found there successfully fledged young. Mean clutch size in the historical period was 3.02 and in the contemporary period was 3.26. Contemporary nests in our sample were placed on average 3.2 m higher than historical nests (historical mean 3.3 m \pm 2.2, n = 271 nests, contemporary mean 6.5 m \pm 5.4, n = 87 nests). Mayfield daily nest survival was 0.484 ± 0.016 (n = 269 nests) during the historical period and 0.594 ± 0.028 (n = 80) during the contemporary period, which represents an estimated increase of 23%. Of failed nests in the historical period, 43% (50/117) failed in the egg stage and 45% (53/117) in the nestling stage, with the remaining 14 nests failing at an unknown stage. In the contemporary period, 45% (14/31) of failures occurred in the egg stage and 42% (13/31) in the nestling stage, with 4 nests failing at unknown stages. To explain variation in Mayfield daily nest survival, we found seven candidate models within two $\Delta AICc$ (Table 3). Nest height was included in six of these top seven models, whereas time period occurred in only two models and development at the three scales in only one model each (Table 3). When averaged across the top seven models, the only predictor variable whose 85% confidence intervals did not overlap with zero was nest height $(0.058 \pm 0.038, 85\% \text{ CI} = 0.003 \text{ to } 0.112; \text{ Appendix}$ 2).

Changes in vegetation surrounding nests over time

After aggregating nests by forest fragment and controlling for false detection rate using a Bonferroni correction (Table 4), we did not detect any significant changes in vegetation over time except for a decrease in leaf litter (P = 0.001, 95% CI). When analyzed separately, there was also no significant effect of time period on any of the vegetation variables within the seven fragments experiencing development. If development was a driving factor in vegetation change, one would expect to see a different trajectory in vegetation structure between the fragments that experienced development and those that did not, but we found no significant change in vegetation in either group of fragments (developed or undeveloped) between the two time periods. **Table 3.** Models with \triangle AICc values < 2 from a set of 91 candidate generalized linear mixed-effects models predicting Wood Thrush (*Hylocichla mustelina*) nest success (measured as Mayfield daily nest survival). All models in this table include fragment ID and year as random effects. Fixed effects are listed along with number of parameters (K), AICc, \triangle AICc, AICc weight (wi), and log-likelihood.

Model predicting nest success	K	AICc	∆AICc	W _i	LL
Nest height	4	666.58	0.00	0.28	-329.23
Nest height + time period	5	667.47	0.89	0.18	-328.65
Time period	4	668.41	1.83	0.11	-330.15
Nest height + development (1 km)	5	668.45	1.87	0.11	-329.14
Nest height + development (100 m)	5	668.47	1.89	0.11	-329.15
Nest height + sapling cover	5	668.53	1.95	0.11	-329.18
Nest height + development (4 km)	5	668.55	1.96	0.10	-329.19

DISCUSSION

Even in the context of a steep range-wide decline brought on by numerous threats throughout the annual cycle, our results clearly show that the localized breeding abundance of Wood Thrush in Waterloo Region has been negatively influenced by urbanization over a 20-year period. Among 14 forest fragments experiencing development within 1 km between 2001 and 2019, we found a 79% decline in Wood Thrush abundance versus a 57% decline in fragments that remained rural during the same period. Our study area experienced a slight increase in forest cover between the historical and contemporary periods, suggesting that habitat loss has not been an important contributor to this observed recent decline. Evidence for a strong population decline amplified by urbanization comes despite nest survival showing a nonsignificant improvement over time and no significant difference in nest survival between urbanizing and rural forest fragments.

Many studies reporting declines in the abundance of Nearctic-Neotropical migrant birds with urbanization have proposed nest predation as a possible explanation (Chace and Walsh 2006), but our results suggest that declines sometimes occur by mechanisms **Table 4.** Chi-squared values (χ 2) and p-values from 27 Friedman tests analyzing the effect of time period on 9 nest vegetation variables in 14 forest fragments. The fragment-aggregated means of each variable were compared between time periods with fragment ID specified as a blocking factor, once within all fragments (n = 14), once for fragments with development within 4 km (devel. 4 k, n = 7), and again for rural fragments (rural, n = 7).

	Effect of t (all fra	time period gments)	Effect o (devel. 4	f time period k fragments)	Effect of time period (rural fragments)		
Response variable	χ2	Р	χ2	Р	χ2	Р	
Sapling count	2.571	0.109	3.571	0.059	0.143	0.706	
Groundcover (%)	4.571	0.032	1.286	0.257	3.571	0.059	
Shrub cover (%)	2.571	0.109	0.143	0.706	3.571	0.059	
Sapling cover (%)	0.000	1.000	1.286	0.257	1.286	0.257	
Subcanopy (%)	1.143	0.285	1.286	0.257	0.143	0.706	
Canopy (%)	1.143	0.285	1.286	0.257	0.143	0.706	
Litter depth	10.286	0.001^{\dagger}	7.000	0.008	3.571	0.059	
Tree count	7.143	0.008	1.286	0.257	7.000	0.008	
Nest height	7.143	0.008	7.000	0.008	1.286	0.257	

[†]Denotes a significant p-value based on an α value of 0.05 and Bonferroni-corrected threshold of 0.05/27 = 0.002. A significant effect of time period in any of the measurements for devel. 4 k fragments, where there is no effect in rural fragments, would suggest that development has influenced the vegetation variable in question. A lack of significance does not imply a lack of effect.

unrelated to reproductive success. One possible demographic factor driving declines in urban areas may be post-fledging juvenile mortality. In Oregon, fledgling Spotted Towhees (Pipilo maculatus) that associated with urban edges were at a higher risk of predation than those that remained in the forest interior (Shipley et al. 2013). Another possible reason for declines in urban areas could be a neophobic aversion to development. Whitcomb et al. (1981) suggested that Neotropical migrants might avoid settling near housing, and Greenberg (1984) found that Chestnutsided Warblers (Setophaga pensylvanica) selected foraging microhabitats that resembled natal microhabitats over those that did not. Wood Thrush that fledge in areas without human disturbance may similarly avoid occupying habitats later in life that have unfamiliar objects, sounds, or situations. Thus, neophobia could serve to negate what would otherwise be a situation in which non-urban forest fragments would act as sources for urban sinks.

As well as contributing to mortality and neophobia, human presence in natural areas can cause changes to the vegetation that leave habitats unsuitable to species that once inhabited them (Hoehne 1981, Friesen 1998). Increased foot and bike traffic and off-leash pets in publicly accessible areas can degrade the sapling, shrub, and groundcover layers and reduce the amount of leaf litter (Whitecotton et al. 2000). In addition, poor management in urban areas can result in even-aged closed canopy forests with little to no understory (Ahlering and Faaborg 2006). The only vegetation metric we measured that changed significantly between time periods was leaf litter depth, which decreased over time regardless of urbanization, possibly due to an increase in invasive earthworms (McCay and Skull 2019). Although we found no significant changes in vegetation structure over time in urbanized vs. rural forest fragments, it remains possible that some other unmeasured aspect of forest structure may have changed as a result of increased human activity.

We sought to address the spatial scale of response by examining effects of development at the 100 m (breeding territory), 1 km (adult home range), and 4 km (juvenile dispersal) scales. Declines

in abundance have been demonstrated in other species because of adjacent development causing urban edge effects such as erosion, noise, and invasive species spread (Friesen et al. 1995, Bolger et al. 1997, Stralberg and Williams 2002). Interestingly, though, our model results show stronger support for an effect of development on abundance at the 1 km scale than the 100 m scale. We found many nests near houses, refuse piles, fences, and in invasive shrubs such as common buckthorn (Rhamnus cathartica). In one instance, a pair successfully nested in an ornamental blue spruce (Picea pungens) at the edge of a manicured lawn. These findings suggest that Wood Thrush may be able to adapt to changing conditions at the microhabitat level, perhaps even taking advantage of novel situations for possible protection against predators, but the species nevertheless responds negatively to habitat changes introduced by development in the broader landscape.

Our model results indicate that Wood Thrush daily nest survival in Waterloo Region was positively affected by nest height. Wood Thrush are known to place their nests between 0 and 30 m high, but the range-wide average is thought to be around 2-4 m (Evans et al. 2020). The upward shift in nest height we observed in our sample (nearly a 100% increase over a 20-year period) may be explained by a lack of available substrates in the lower forest strata that has manifested in certain forest fragments over time, perhaps because of poor management or increased human disturbance in those fragments. Placing nests higher as a result of a dwindling sapling layer may inadvertently serve to protect nests from predators that hunt near the ground, such as raccoons (*Procyon lotor*), the primary mammalian nest predator of Wood Thrush in Waterloo Region (Newell and Kostalos 2007, Friesen et al. 2013; Table 1).

Non-forested natural areas (NFNA) showed a negative effect on abundance, possibly because the NFNA land class included natural areas likely of little value to Wood Thrush. Post-hoc examination of the landcover layers (virtual "ground-truthing" using Google Earth) revealed that when NFNA cover within 1 km of a forest fragment exceeded 10%, the majority of these lands were made up of conifer plantations, not early successional habitats or wetlands. These same fragments also had considerably fewer Wood Thrush detections (in both time periods) than the overall average. Although Wood Thrush were observed to nest in conifer plantations adjacent to deciduous forest on at least two occasions during our study, it would seem that large amounts of these semi-natural "monocultures" may be displacing more favorable habitats and leading to lower abundance. Furthermore, Wood Thrush that do nest in these plantations may face novel predator regimes, possibly affecting the survival of nests in unknown ways. For example, it was recently shown in Ontario that Eastern Wood-Pewees (*Contopus virens*) experienced lower nesting success in conifer plantations than in deciduous forests and that these plantations had higher predator densities (Falconer and Nol 2020).

We caution that landcover classifications based on spectral signatures are prone to spurious misclassifications that could affect results of fine-scale analyses, making it difficult to rule out adjacent development as a contributing factor to declines. A previous study (Friesen et al. 2005) used a more detailed approach of mapping the locations and timing of newly built structures adjacent to a forest fragment. The study did not find evidence for an effect of the adjacent development, but because it was conducted over a relatively short period (i.e., 4 years) and involved one forest fragment undergoing significant development in its adjacent surroundings, it might not have captured the long-term effects of this development or potential management differences between fragments. Future work could attempt the same approach but in multiple fragments experiencing development and after a longer period of time post-development, to examine whether negative effects occur as a direct result of proximity to individual structures.

CONCLUSIONS

The present before-and-after study provides strong evidence that over a 20-year period, the breeding abundance of a Nearctic-Neotropical migrant songbird decreased most steeply in forest fragments with new development in the landscape within 1 km. Forest fragments already surrounded by development may never serve as prime breeding habitat, but with strategic implementation of greenbelts and high-density urban planning policy, abundance in fragments near the urban fringe could be maintained at levels comparable to more rural fragments. The Wood Thrush is only one example of species that benefits from gaps in the forest generated by natural and anthropogenic disturbances. Many of the regulations currently in place to safeguard urban forests, such as tree-cutting bylaws, may actually be detrimental to species that rely on arboreal disturbance. Future research should investigate urban forest management policies as well as the post-fledging period and neophobia among migratory birds that occupy urban forest habitats because these could be key reasons why certain species are able to adapt while others are not. That said, declines likely result from many cumulative effects, and the impacts of development on juvenile survival and nest productivity remain unclear. Recovery efforts must, therefore, occur range-wide, be contextually appropriate, and take into consideration all the needs of the declining species in question.

Acknowledgments:

This research was conducted within the territories of the Neutral, Anishinaabe, Haudenosaunee, and Ojibwayl Chippewa peoples and on the Haldimand Tract, land granted to the Haudenosaunee of the Six Nations of the Grand River, as well as Treaty #4 of the Upper Canada treaties. We are grateful for the privilege to work on these lands and recognize the enduring presence of all Indigenous Peoples. We thank the landowners who granted us permission to access their properties. We thank A. Virostek, J. Nene, E. Heisey, A. Picard, E. Grahame, K. Ong, M. Fuirst, L. Custode, N. Quarrel, and E. Gow for their assistance in the field and with statistical analysis. Funding was provided by the Natural Sciences and Engineering Research Council, the Wilson Ornithological Society, Eco-Canada, and Natural Resource Solutions Inc. This project used data maintained by the Canadian Wildlife Service, which was collected through the Ontario Forest Bird Monitoring Program.

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Editor-in-Chief: Alexander L. Bond Subject Editor: Andrew J. Campomizzi



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Appendix 1. List of forest fragments included in this study, their size, and number of point counts, nests and vegetation plots in each fragment in the historical (1987-2001) and contemporary (2020-2021) time periods. In this table, forest fragments have been grouped into categories of surrounding land use (see table footer) based on a post-hoc analysis of before-and-after landcover layers.

					Point count stations	Ne	ests	No veget plo	est ation ots
Fragment type	Forest Fragment	2001 Area (ha)	2019 Area (ha)	Percent change in area (2001- 2019)	(Both time periods)	1987 - 2001	2020 	1987 - 2001	2020
Rural ⁺									
	AM	2.8	2.8	0.0	0	4	0	0	0
	CL	10.5	10.5	0.0	0	1	0	1	0
	RN	4.0	4.0	0.0	0	3	0	3	0
	SIS	9.5	9.5	0.0	0	2	0	2	0
	SIL¶	23.4	23.5	0.4	1	4	9	1	9
	HO	3.2	3.2	0.0	1	1	0	1	0
	SNE	2.3	2.3	0.0	0	1	0	1	0
	WA	6.3	6.3	0.0	0	3	0	3	0
	CR	8.7	8.7	0.0	0	1	1	1	1
	MS	23.8	24.8	4.2	0	2	2	2	2
	0	7.2	7.2	0.0	0	4	1	4	1
	HY	10.7	10.8	0.9	0	3	2	3	2
	FB	10.4	9.7	-6.7	0	1	4	1	3
	HA	10.2	10.2	0.0	0	7	5	7	5
	CE	3.4	3.4	0.0	1	NA	NA	0	0
	ED	29.7	29.7	0.0	1	NA	NA	0	0
	GI	22.8	22.8	0.0	1	NA	NA	0	0
	HK	2.4	2.3	-4.2	1	NA	NA	0	0
	HEN	25.2	24.0	-4.8	1	NA	NA	0	0
	HES	8.7	8.7	0.0	1	NA	NA	0	0
	SC	25.3	25.3	0.0	I r	NA	NA	0	0
	342 DL #	153.1	154.2	0.7	5	NA 45	NA	0	0
	BL#	21.8	23.2	6.4	1	45	0	42	0
	BL4	6.1	6.1	0.0	1	6	0	5	0
A 11 /	GR	26.3	26.2	-0.4	0	4	1	0	0
Aajacent	DMI	22.2	20 6	0.0	1	0	0	0	0
aevelopment *	DML	32.3	32.6	0.9	1	ð	0	ð	0
	SA	6.5 0.7	6.5 0.7	0.0	0	9	0	9	0
	S15 STI	9.7	9.7	0.0	1	4	1	4	1
	SIL ED1	20.2 4.6	27.0	3.1	1	0 NIA	U	0	0
	EKI	4.0	4.0	0.0	1	NΑ	ΝA	0	0

	OS	25.4	24.5	-3.5	1	NA	NA	0	0
	WI	13.8	13.8	0.0	1	NA	NA	0	0
	479	19.4	19.7	1.5	3	NA	NA	0	0
	480	64.2	69.9	8.9	3	NA	NA	0	0
	FH	140	145.7	4.3	16	74	18	83	17
Landscape									
development §	DMS	11.3	11.5	1.8	1	3	0	3	0
-	AD	43.4	43.4	0.0	1	6	5	6	5
	EM	30.2	30.2	0.0	1	2	11	2	11
	PE	3.5	3.5	0.0	1	1	0	1	0
	SMK	11.2	11.2	0.0	0	2	0	2	0
	DE	63.8	64.4	0.9	1	NA	NA	0	0
	RE	8.2	8.2	0.0	1	NA	NA	0	0
	RG	7.2	7.2	0.0	1	NA	NA	0	0
	SM	8.0	8.0	0.0	1	NA	NA	0	0
	SP	45.0	45.0	0.0	0	12	20	12	19
	MC	24.2	24.2	0.0	1	21	0	21	0
	TR	9.8	9.8	0.0	1	16	0	16	0
	GM	34.5	34.5	0.0	1	3	2	3	2
	SD	36.0	37.8	5.0	1	12	8	10	7
	CD	103.6	109.7	5.9	10	NA	NA	0	0
	ТО	7.2	7.2	0.0	1	NA	NA	0	0
	TS	3.8	3.8	0.0	1	NA	NA	0	0
	344	57.6	59.6	3.5	3	NA	NA	0	0
	SY¶	5.5	5.5	0.0	1	NA	NA	0	0
	SHK	7.7	7.9	2.6	1	2	0	2	0
	SK2	31.4	33.5	6.7	0	1	0	1	0
	SL	55.5	54.9	-1.1	3	NA	NA	0	0
	S	50.4	54.4	7.9	4	6	0	6	0
	229	32.1	32.1	0.0	5	NA	NA	0	0
Urban	DE	15.0	15.0					0	0
	BE	17.0	17.0	0.0	1	NA	NA	0	0
	BH	7.9	8.1	2.5	1	NA	NA	0	0
	HP	23.7	23.7	0.0	1	NA	NA	0	0
	KW	2.8	2.8	0.0	1	NA	NA	0	0
		1.1	1.1 12.1	0.0	1	INA NA	NA NA	0	0
	MW	15.1	15.1	0.0	1	INA NA	NA	0	0
		2.2	2.3	4.5	1	INA NA	NA NA	0	0
	SW	24.9 10.4	20.7 10.4	1.2	1	INA	INA NA	0	0
	3U T7	10.4	10.4	0.0	1	INA NA	INA NA	0	0
		0.8	1.1	ð.ð	1	INA NA	INA NA	0	0
		4.2	4.2	0.0	1	INA NA	INA NA	0	0
		5.5	5.5	-5.7	1	INA NA	NA	0	0
Total	IA	0.1	0.1	0.0	100	280	00	272	85
i Juai					100	200	20		05

+ No new urban development built within 4 km of the site since 2001

* New urban development built within 100 m of the site since 2001

§ New urban expansion between 100 m and 4 km of the site since 2001

| Urban development has existed within 100 m of the site since prior to 2001

 \P Construction of a single home began within the woodlot during the contemporary study period

New quarry operation <100 m away built since 2001, but no urban development within 4km

Predictor	Estimate ± SE	z value	85% CI
Time period	0.301 ± 0.236	1.273	-0.039, 0.642
Nest height ⁺	0.063 ± 0.034	1.879	0.015, 0.112
Sapling cover	-0.001 ± 0.004	0.326	-0.007, 0.004
Development (100 m)	0.004 ± 0.010	0.409	-0.010, 0.018
Development (1 km)	0.005 ± 0.012	0.427	-0.012, 0.022
Development (4 km)	0.004 ± 0.012	0.305	-0.013, 0.021

Appendix 2. Conditional averaged parameter estimates and 85% confidence intervals for nest success predictors occurring in the top 7 candidate models (< $2 \Delta AICc$). Of the 6 variables retained in this subset candidate list, only nest height had an 85% averaged confidence interval that did not overlap zero.

+85% CI does not overlap zero

Appendix 3. Candidate model sets for Wood Thrush abundance (Table A3.1) and nest success (Table A3.2).

Table A3.1. List of 29 candidate generalized linear models predicting Wood Thrush abundance. All models include year and fragment ID as random effects.

Model predicting abundance	K	AICc	Δ AICc	Wi	LL
period*devel_1k+NFNA_1k+size	9	1028.94	0.00	0.65	-505.28
period+devel_1k+NFNA_1k+size	8	1031.99	3.05	0.14	-507.84
period+devel_4k+NFNA_1k+size	8	1033.93	4.99	0.05	-508.81
period*devel_100m+size	8	1034.73	5.79	0.04	-509.21
period*devel_1k+size	8	1035.07	6.13	0.03	-509.38
period+NFNA_1k+size	7	1035.70	6.77	0.02	-510.73
NFNA_100m+size	7	1035.70	6.77	0.02	-510.73
NFNA_1k+size	8	1035.98	7.05	0.02	-509.84
period+devel_100m+NFNA_1k+size	8	1037.36	8.42	0.01	-510.52
period+devel_1k+size	7	1037.85	8.91	0.01	-511.81
period+devel_1k*size	8	1038.86	9.92	0.00	-511.28
period+devel_4k+size	7	1039.46	10.52	0.00	-512.61
period+devel_4k*size	8	1040.24	11.30	0.00	-511.97
period+size	6	1042.27	13.33	0.00	-515.05
period+devel_100m*size	8	1043.32	14.39	0.00	-513.51
period+devel_100m+size	8	1044.35	15.42	0.00	-514.02
period+devel_1k+NFNA_1k	7	1046.27	17.33	0.00	-516.01
devel_4k+NFNA_1k	7	1048.48	19.54	0.00	-517.12
period*devel_4k	7	1048.82	19.89	0.00	-517.29
period*devel_1k	7	1049.16	20.22	0.00	-517.46
period+devel_1k	6	1049.81	20.87	0.00	-518.82
period+devel_4k	6	1051.72	22.79	0.00	-519.77
period+NFNA_1k	6	1052.08	23.14	0.00	-519.95
devel_100m+NFNA_1k	7	1053.85	24.91	0.00	-519.81
period	5	1056.77	27.83	0.00	-523.32
period+devel_100m	6	1058.33	29.39	0.00	-523.07
period+NFNA_100m	6	1058.48	29.54	0.00	-523.15
period*devel_100m	7	1058.99	30.05	0.00	-522.37
null	4	1077.89	48.96	0.00	-534.90

Model predicting nest success	K	AICc	Δ AICc	Wi	LL
height	4	666.58	0.00	0.08	-329.23
period+height	5	667.47	0.89	0.05	-328.65
period	4	668.41	1.83	0.03	-330.15
height+devel_1k	5	668.45	1.87	0.03	-329.14
height+devel_100m	5	668.47	1.89	0.03	-329.15
height+sapling cover	5	668.53	1.95	0.03	-329.18
height+devel_4k	5	668.55	1.96	0.03	-329.19
forest_4k	4	668.87	2.29	0.03	-330.38
period+forest_4k	5	669.06	2.47	0.02	-329.44
period+initiation date	5	669.25	2.67	0.02	-329.54
null	3	669.30	2.72	0.02	-331.62
period+height+devel_4k	6	669.46	2.87	0.02	-328.60
period+height+devel_1k	6	669.47	2.89	0.02	-328.61
period+height+devel_100m	6	669.47	2.89	0.02	-328.61
period+sapling cover+height	6	669.52	2.94	0.02	-328.64
height*devel_1k	6	669.54	2.95	0.02	-328.64
period*height	6	669.54	2.96	0.02	-328.65
initiation date+sapling cover+height	7	669.73	3.15	0.02	-327.70
height*sapling cover	6	669.84	3.26	0.02	-328.80
height*devel_100m	6	670.04	3.46	0.01	-328.90
period+size	5	670.05	3.47	0.01	-329.94
period+canopy cover	5	670.09	3.51	0.01	-329.96
height+sapling cover+size+forest_4k	7	670.16	3.58	0.01	-327.92
period*sapling cover	6	670.22	3.64	0.01	-328.99
height+sapling cover+size	6	670.25	3.67	0.01	-329.00
period+sapling cover	5	670.32	3.74	0.01	-330.07
canopy cover	4	670.34	3.75	0.01	-331.11
period+devel_1k	5	670.34	3.75	0.01	-330.08
period+devel_100m	5	670.34	3.76	0.01	-330.08
period+devel_4k	5	670.35	3.77	0.01	-330.09
height*devel_4k	6	670.51	3.93	0.01	-329.13
initiation date	4	670.60	4.02	0.01	-331.24
period+height*devel_1k	7	670.63	4.05	0.01	-328.15
size	4	670.69	4.10	0.01	-331.28
sapling cover	4	670.70	4.12	0.01	-331.29
size+forest_4k	5	670.75	4.17	0.01	-330.29
period+height*sapling cover	7	670.80	4.22	0.01	-328.24
forest_4k+devel_100m	5	670.82	4.24	0.01	-330.32

Table A3.2. List of 91 candidate generalized linear models predicting Wood Thrush nest success. All models include year and point count station ID as random effects.

forest_4k+devel_1k	5	670.87	4.29	0.01	-330.35
period+initiation date+sapling cover+height	7	670.88	4.30	0.01	-328.28
forest_4k+devel_4k	5	670.88	4.30	0.01	-330.35
devel_1k	4	670.89	4.31	0.01	-331.39
devel_100m	4	670.94	4.36	0.01	-331.41
period+size+forest_4k	6	670.98	4.40	0.01	-329.37
period+height*devel_100m	7	671.06	4.48	0.01	-328.36
period+forest_4k+devel_4k	6	671.09	4.51	0.01	-329.42
period+forest_4k+devel_100m	6	671.10	4.52	0.01	-329.43
period+forest_4k+devel_1k	6	671.12	4.54	0.01	-329.44
devel_4k	4	671.17	4.59	0.01	-331.53
period+height*devel_4k	7	671.49	4.91	0.01	-328.58
initiation date+sapling					
cover+height+size+forest_4k	8	671.76	5.18	0.01	-327.67
period+height+sapling cover+size+forest_4k	8	671.89	5.31	0.01	-327.73
period*devel_4k	6	671.94	5.36	0.01	-329.85
period+initiation date+size+forest_4k	7	671.98	5.40	0.01	-328.83
period+size+devel_1k	6	672.06	5.48	0.01	-329.91
period+size+devel_4k	6	672.10	5.52	0.01	-329.93
forest_4k+devel_4k	6	672.11	5.52	0.01	-329.93
period+size+devel_100m	6	672.12	5.54	0.01	-329.94
initiation date+size+forest_4k	6	672.15	5.57	0.01	-329.95
period+devel_1k	6	672.24	5.66	0.00	-330.00
period+devel_1k+sapling cover	6	672.25	5.67	0.00	-330.00
period+devel_4k+sapling cover	6	672.26	5.68	0.00	-330.01
period+devel_100m+sapling cover	6	672.27	5.69	0.00	-330.01
devel_1k+sapling cover	5	672.32	5.74	0.00	-331.07
devel_100m+sapling cover	5	672.38	5.80	0.00	-331.10
period*devel_100m	6	672.39	5.80	0.00	-330.07
period+forest_4k*devel_4k	7	672.46	5.88	0.00	-329.07
devel_4k+sapling cover	5	672.57	5.99	0.00	-331.20
size+devel_4k	5	672.70	6.12	0.00	-331.26
size+devel_100m	5	672.73	6.15	0.00	-331.28
size+devel_1k	5	672.74	6.16	0.00	-331.28
forest_4k*devel_1k	6	672.80	6.22	0.00	-330.28
forest_4k*devel_100m	6	672.82	6.24	0.00	-330.29
period+forest_4k*devel_1k	7	673.18	6.60	0.00	-329.42
period+forest_4k*devel_100m	7	673.19	6.61	0.00	-329.43
period+initiation date+sapling					
cover+height+size+forest_4k	9	673.38	6.79	0.00	-327.42
period+size*devel_4k	7	673.92	7.33	0.00	-329.79
period+devel_100m*sapling cover	7	673.97	7.39	0.00	-329.82
period+size*devel_100m	7	674.04	7.46	0.00	-329.86

period+size*devel_1k	7	674.07	7.48	0.00	-329.87
period+devel_1k*sapling cover	7	674.17	7.59	0.00	-329.92
devel_100m*sapling cover	6	674.18	7.60	0.00	-330.97
devel_1k*sapling cover	6	674.28	7.70	0.00	-331.02
period+devel_4k*sapling cover	7	674.34	7.76	0.00	-330.01
devel_4k*sapling cover	6	674.64	8.06	0.00	-331.20
size*devel_4k	6	674.72	8.14	0.00	-331.24
size*devel_100m	6	674.79	8.21	0.00	-331.27
size*devel_1k	6	674.81	8.23	0.00	-331.28
height+devel_1k+sapling					
cover+size+period+forest_4k+initiation date	10	675.39	8.81	0.00	-327.37
height+devel_100m+sapling					
cover+size+period+forest_4k+initiation date	10	675.49	8.91	0.00	-327.42
height+devel_4k+sapling					
cover+size+period+forest_4k+initiation date	10	675.50	8.91	0.00	-327.42