

## EFFECTS OF DISTANCE TO EDGE AND EDGE TYPE ON NESTLING GROWTH AND NEST SURVIVAL IN THE WOOD THRUSH

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**Abstract.** Many studies investigating edge effects on forest-nesting birds have focused on nest success. Fewer have examined edge effects on other components of fitness. Nestling growth rates have been positively correlated with food availability, which may differ at edges compared to the forest interior. However, previous work has not examined growth as a function of distance to edge and edge type. We investigated whether edge type, distance to edge, hatching date, brood size, brood parasitism, year, and site influenced growth rates of wings, tarsi, and mass of nestling Wood Thrushes (*Hylocichla mustelina*) using regression tree analyses. Simultaneously, we examined edge effects on daily nest survival. We conducted our study in southwestern Michigan in 2002 and 2003. We located 175 nests and measured nestlings from 61 nests. Contrary to expectations, tarsal and mass growth rates were more rapid near edges than in the forest interior and tarsal growth rates were more rapid near gradual edge types than near abrupt edge types. Wing chord growth rates were more rapid in the forest interior than at edges. Mass and tarsal growth rates were more rapid later in the breeding season, when brood sizes were smaller. We found no effect of edge type or distance to edge on nest survival. The influence of edge on nestling growth rate but not nest survival suggests nestling growth rates may indicate edge-interior and edge type differences in habitat quality, even when high regional fragmentation levels overwhelm potential edge-interior differences in nest survival.

**Key words:** distance to edge, edge effects, edge type, *Hylocichla mustelina*, nest survival, nestling growth rates, Wood Thrush.

### Efectos de la Distancia al Borde y el Tipo de Borde en el Crecimiento de los Pichones y en la Supervivencia de los Nidos en *Hylocichla mustelina*

**Resumen.** Muchos de los estudios que investigan los efectos de borde en las aves que nidifican en bosques se han enfocado en el éxito de los nidos. Menos estudios han examinado los efectos de borde en otros componentes de la adecuación biológica. Las tasas de crecimiento de los pichones han sido positivamente correlacionadas con la disponibilidad de alimentos, la cual puede diferir entre los bordes y el interior del bosque. Sin embargo, los trabajos previos no han examinado el crecimiento en función de la distancia al borde y del tipo de borde. Usando análisis de árboles de regresión, investigamos si el tipo de borde, la distancia al borde, la fecha de eclosión, el tamaño de la nidada, el parasitismo de la nidada, el año y el sitio influenciaron las tasas de crecimiento de las alas, el tarso y el peso de los pichones de *Hylocichla mustelina*. Simultáneamente, examinamos los efectos de borde en la supervivencia diaria de los nidos. Realizamos nuestro estudio en el sudoeste de Michigan en 2002 y 2003. Localizamos 175 nidos y medimos pichones provenientes de 61 nidos. Contrariamente a lo que esperábamos, las tasas de incremento del tarso y del peso fueron mayores cerca de los bordes que en el interior del bosque, y las tasas de incremento del tarso fueron mayores cerca de bordes de tipo gradual que cerca de bordes de tipo abrupto. Las tasas de incremento de la cuerda alar fueron mayores en el interior del bosque que en los bordes. Las tasas de incremento del peso y el tarso fueron mayores al final de la estación reproductiva, cuando el tamaño de la nidada fue más pequeño. No encontramos un efecto del tipo de borde y de la distancia al borde en la supervivencia de los nidos. La influencia del borde en la tasa de crecimiento de los pichones, pero no en la supervivencia de los nidos, sugiere que la tasa de crecimiento de los pichones podría indicar diferencias en la calidad de hábitat entre borde e interior y entre tipos de borde, aún cuando los altos niveles de fragmentación regionales

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tengan efectos superiores a las diferencias potenciales en la supervivencia del nido entre borde e interior.

## INTRODUCTION

Previous work investigating the impact of fragmentation on forest-nesting birds in eastern North America has focused on nest success, as influenced by nest predator and Brown-headed Cowbird (*Molothrus ater*) responses to edges (Brittingham and Temple 1983, Askins et al. 1990). Our knowledge of edge effects on fitness components besides nest success is much more limited.

Nestling growth rates are useful measures with which to examine the influence of environmental factors on the potential fitness of organisms, because they are associated with variables like final nestling mass (Ricklefs and Peters 1981) and postfledging survival (McCarty 2001). In addition, they can sometimes provide more information than, for example, final nestling mass about potential mechanisms through which environmental factors operate. Growth curves can show when body mass or a body structure is increasing in size most quickly (Massemin et al. 2002) and thus when an environmental factor like food limitation is most likely to be important.

Most environmental influences on growth variability that have been identified in the literature relate to food abundance (Gebhardt-Henrich and Richner 1998). Edge habitat can experience modified microclimatic conditions (Chen et al. 1993, Murcia 1995), which can affect the abundance of invertebrates, the primary food source of many forest-nesting species (Schowalter et al. 1981). Thus, territories in edge habitat may have different food supplies than territories in the forest interior (Burke and Nol 1998, Duguay et al. 2000).

Wood Thrush (*Hylocichla mustelina*) nestling growth rates have been positively correlated with the available biomass of their primary food source, soil invertebrates (Duguay et al. 2000), indicating that nestling growth rates may reflect differences in nesting habitat quality. Wood Thrushes, which primarily forage for soil invertebrates in leaf litter on the forest floor, prefer nest sites with canopies of mature trees (Hoover and Brittingham 1998), moist soils, shade, and decaying leaf litter (Roth et al. 1996, Artman and Downhower 2003). Nest sites in

the forest interior are more likely to have these conditions than nest sites near forest edges, where there is a greater amount of secondary forest regrowth composed of shrubs and immature trees (Hoover and Brittingham 1998).

Species may vary in their responses to different edge types (Sisk and Battin 2002). Ries et al. (2004) found that species' edge responses are generally predictable and consistent only when edge type remains constant. Specifically, edge type may influence the success of individuals in accessing habitat, gaining resources, escaping predation, and avoiding cowbird parasitism (Ries et al. 2004).

The Wood Thrush is a Neotropical migrant that has declined throughout most of its range (Robbins, Sauer et al. 1989, Peterjohn et al. 1995). It often nests near habitat edges and in small woodlots (Roth et al. 1996), but has been classified as area-sensitive (Robbins et al. 1989, Weinberg and Roth 1998). Some studies have reported lower nest success for Wood Thrushes in smaller forest patches (Hoover et al. 1995, Burke and Nol 2000). However, other studies have found no effect of patch size on nest success (Weinberg and Roth 1998, Friesen et al. 1999, Fauth 2000). Similarly, some studies that have examined edge effects on nest predation and cowbird parasitism have found no effect (Burke and Nol 2000, Fauth 2000) while a few have found that nest success increases with distance from edge (Hoover et al. 1995, Ford et al. 2001).

The objectives of our study were to: 1) estimate and compare tarsal, mass, and wing chord growth rate constants of nestling Wood Thrushes among edge types and with distance from edge, and 2) estimate and compare annual nest survival among edge types and sites, and with distance from edge. We also examined the influence on nestling growth of year, site, and three factors previously found to affect nestling growth: brood size (Kunz and Ekman 2000), date of hatching (McCarty and Winkler 1999), and cowbird parasitism (Dearborn et al. 1998). Effects of distance to edge and edge type on growth of nestling Wood Thrushes could act additively or synergistically with edge effects on nest survival to influence reproductive success

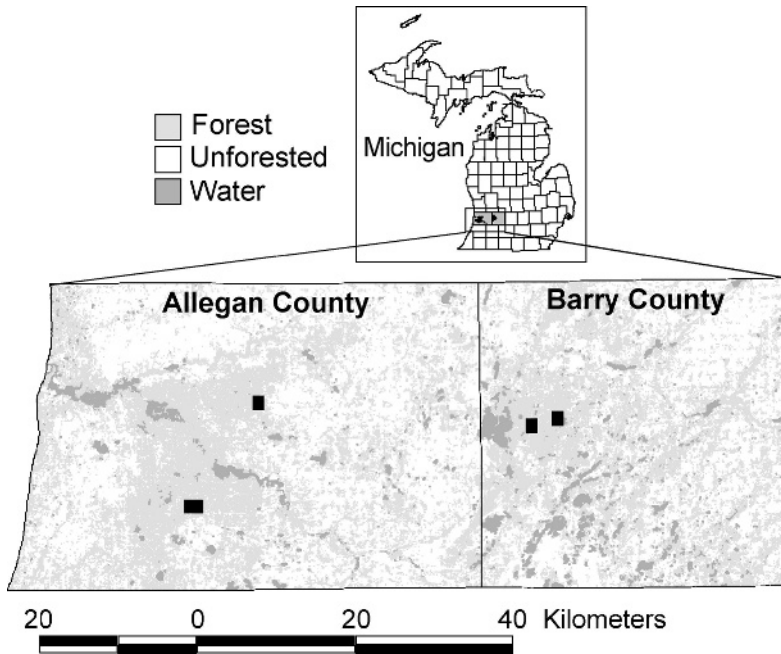


FIGURE 1. Location of the two study sites in southwestern Michigan: Allegan State Game Area (Allegan) in Allegan County and Barry State Game Area and Yankee Springs Recreational Area (Barry) in Barry County. Forest cover in southwestern Michigan is fragmented. 'Unforested' land includes all cover types other than forest and water (barren, developed, shrubland, herbaceous, and wetlands). The four study plots are represented by the four black rectangles.

(Smith and Andersen 1982, De Santo et al. 2002).

Habitat edges influence invertebrate movement and abundance (Crist et al. 2006). Some evidence suggests that edges have lower invertebrate abundance than forest interiors (Schowalter et al. 1981, Duguay et al. 2000). Hence, we predicted that nestlings from nests near edges would have reduced growth rates compared to those in nests farther from edges. We also predicted that nestling growth would vary by edge type, because edge types vary with regard to resources and environmental conditions and this variability influences biological responses (Bollinger and Gavin 2004, Ries and Sisk 2004). Because we did not have specific knowledge regarding invertebrate abundance in the edge types we examined, we did not make specific predictions about the directions of these trends. Nestlings may allocate resources differently among body structures during growth (Kunz and Ekman 2000). Because of the thermoregulatory benefit to nestlings of greater mass (Dawson et al. 2005), and because Wood

Thrush wing chord growth is not completed at fledging (Brown and Roth 2004), we predicted that mass and tarsal growth would be more rapid than wing chord growth.

METHODS

STUDY AREA

Our two study sites were in southwestern Michigan. Allegan State Game Area (hereafter, Allegan; 42°34'N, 85°58'W), located in Allegan County, was approximately 20 235 ha in extent. Barry State Game Area and Yankee Springs Recreational Area (hereafter, Barry; 42°36'N, 85°27'W) was located 56 km west of Allegan in Barry County and approximately 8300 ha in extent (Fig. 1).

At each site in 2002, two plots that ranged in size from 75 to 80 ha were established in contiguous, mature forest tracts >300 ha in size. Each plot was bordered on one side by a two-lane road. The four plots were chosen because they had similar vegetation composi-

tion, vegetation structure, and management history.

Forest cover at each site was fragmented (Fig. 1), but there were more residential openings at Barry. Both game areas were surrounded primarily by agricultural land. Disturbance patterns at Allegan and Barry were similar; both employed timber sales and maintained openings by cutting or mowing. Plots were in areas managed for mature forests and were undisturbed by management practices over the course of this two-year study.

Allegan plots were on poorly drained, generally flat slopes in bottomland forests on sandy lakeplain and ranged from approximately 210 to 230 m in elevation, while the Barry plots were on well-drained undulating hills in upland forests on interlobate deposits and ranged from approximately 240 to 320 m in elevation. The vegetation structure of the two sites was similar with canopy cover, mean canopy height, mean shrub height, and ground cover (<0.5 m) slightly greater on average at Allegan (93%, 17.8 m, 0.4 m, 56%, respectively) than at Barry (86%, 17.2 m, 0.3 m, 38%, respectively). Based on our vegetation measurements, Allegan plots were dominated in the canopy (>15 m) by red maple (*Acer rubrum*; 36%) and white oak (*Quercus alba*; 25%), in the midstory (6–15 m) by red maple (22%), ironwood (*Carpinus caroliniana*; 15%), and flowering dogwood (*Cornus florida*; 15%), and in the understory (0.5–5 m) by ironwood (26%) and flowering dogwood (17%). Barry plots were dominated in the canopy by black oak (*Quercus velutina*; 45%), red maple (25%), and white oak (10%), in the midstory by red maple (39%) and flowering dogwood (18%), and in the understory by red maple (31%) and sassafras (*Sassafras albidum*; 15%).

#### STUDY SPECIES

We chose the Wood Thrush as our focal species because: 1) it is considered a forest-interior species (Whitcomb et al. 1981, Robbins et al. 1989); 2) substantial populations nest in the study sites and may be important source populations in the Midwest (The Nature Conservancy and Michigan Department of Natural Resources, unpubl. data); 3) nests can readily be located and monitored in the forest understory and midstory; 4) previous studies have found that this species is negatively

affected by forest fragmentation (Hoover et al. 1995, Weinberg and Roth 1998, Burke and Nol 2000, Fauth 2000, Ford et al. 2001); and 5) data on adult body size are available (Roth et al. 1996, Brown and Roth 2004) for calculations of growth rate constants.

#### NEST SEARCHING AND MONITORING

Active Wood Thrush nests were located in 2002 and 2003 from early May through late August. Nests were found by searching plots every other day and observing singing males, listening for female vocalizations, and following birds carrying nesting material or food. Locations of nests were marked with flagging at a distance  $\geq 10$  m from the nest and their coordinates recorded using a global positioning system (GPS; Garmin 12XL, GARMIN Corporation, Olathe, Kansas) with the position averaging function to improve accuracy to within 5 m of the nest's true location. Nests were checked every two days for loss of eggs or nestlings and cowbird parasitism until the young fledged or the nest failed. We categorized nests using criteria in Ralph et al. (1993) as successful, failed because of predation, abandonment, cowbird parasitism, weather, or observer activities, or uncertain fate. Nests were considered successful if they fledged at least one Wood Thrush. Adults were unmarked, thus re-nesting attempts were not identifiable.

#### NESTLING GROWTH

Mass and measurements of tarsi and wing chords were recorded each time the nest was checked, every 2–4 days, until the last time nestlings were found in the nest, or until two days before the projected fledging date (Roth et al. 1996). Wood Thrushes typically hatch within two days of each other (Brown and Roth 2004); therefore, we waited to measure nestlings until all eggs had hatched to minimize observer effects on hatching success. Each nestling was aged separately at each visit because nestlings did not usually hatch synchronously. We identified nestlings by marking each individual on a unique toe with a nontoxic marker. The marks were not permanent and had to be reapplied at each visit. The age of a nestling was expressed in brood days, where brood day 0 was its hatching day. Nestlings were weighed with a digital scale (ProScale 250, My Weigh Scale Company, Phoenix, Arizona) to the nearest

0.1 g. The unflattened right wing chord was measured to the nearest 0.5 mm using a steel wing ruler with a feather stop, and the right tarsus was measured from the rear middle of the intertarsal joint to the distal edge of the last complete scale before the toes to the nearest 0.1 mm using dial calipers. One individual made all measurements. On the final visit to the nest, nestlings were fitted with U.S. Fish and Wildlife Service metal bands. Only nestlings from nests that could be reached with a 3 m stepladder were measured; typically these nests were  $\leq 6$  m high. The reachable nests constituted 58% (61 of 105) of the active nests that survived the incubation period.

#### DISTANCE TO EDGE

We considered edges to occur where there was a clearly defined change in vegetation structure between forest and adjacent land (Flaspohler et al. 2001). We differentiated five forest edge types: 1) a two-lane road edge showed an abrupt change from a two-lane country road  $\sim 10$  m wide to mature forest, with a  $> 5$  m wide opening in the forest canopy over the road; 2) a marsh edge showed an abrupt change from marsh to mature forest and the marsh had a diameter three times the height of the adjacent forest canopy (Paton 1994); 3) a wildlife opening edge showed an abrupt change from cropland field, typically alfalfa planted to sustain local wildlife and maintained by mowing, to mature forest and the opening had a diameter three times the height of the adjacent forest canopy; 4) a powerline corridor edge showed a gradual change from a corridor  $\sim 10$  m wide to mature forest with an opening in the forest canopy  $> 5$  m; and 5) a recent clearcut edge showed a gradual change from an opening that was clearcut  $\sim 5$  years prior and the opening had a diameter three times the height of the adjacent forest canopy. A recent clearcut edge also contained shrub-level vegetation  $< 2.5$  cm dbh (diameter at breast height) that extended  $> 2$  m from the forest. Edge types were classified as abrupt (two-lane road, marsh, wildlife opening) or gradual (powerline corridor, recent clearcut) based on whether the edge transition was stark (e.g., forest to road) and whether the transition zone containing shrub-level vegetation between the mature forest and the open land extended  $\leq 2$  m (abrupt edges) or  $> 2$  m (gradual edges).

The shortest distance from each nest to the nearest forest edge was determined using GPS locations of nests and 1 m resolution 1998 Digital Orthophoto Quadrangles in ArcView version 3.2 (ESRI, Redlands, California). Aerial imagery was obtained from the Michigan Department of Natural Resources. We ground-truthed all plots and determined that land cover had not changed significantly between 1998 and 2001, which was later verified by state land managers. We treated distance to the nearest forest edge as a continuous variable.

#### STATISTICAL ANALYSES

Logistic growth curves were fit to measurements of nestlings by brood day. Growth rate constants were calculated for right tarsus length, right wing chord, and mass for each brood (Ricklefs 1967, Brown and Roth 2004) after Peters (1983):

$$M(x) = \frac{A}{1 + \left[ \frac{A}{M(0)} - 1 \right] e^{(-Kx)}}$$

where  $x$  is nestling age,  $M(x)$  is the measurement at age  $x$ ,  $A$  is the asymptotic value,  $M(0)$  is the initial measurement on brood day 0, and  $K$  is the growth rate constant. We used a non-linear regression procedure (PROC NLIN; SAS Institute 2002) to fit the curves. Growth rate constants were calculated for each brood because measurements of nestlings from the same nest cannot be treated as independent (Hurlbert 1984). Curves were fit to observations of the growth of all nestlings of a brood, each aged separately, from brood days 0 to 10. We excluded broods that had  $< 5$  measurements from the analyses because no standard errors or confidence intervals could be computed for their growth rate constants (Ricklefs 1967).

Since we did not capture adults at our study sites we used asymptotic values for mass and the lengths of the tarsi and wings from measurements of after-hatching-year males and females in Newark, Delaware (Roth et al. 1996, Brown and Roth 2004). Only mass data from adults captured during the breeding season were used for calculation, since weights from postbreeding adults may be reduced and weights from migrants may be elevated (Johnson et al. 1990, Conway et al. 1994, Leberg et al. 1996). There are no reports of geographic



variation in the adult body size of Wood Thrushes (Clement 2000). The same adult asymptotic value for each measurement was entered into the logistic growth equation for every brood (Starck and Ricklefs 1998). The asymptotic adult mean mass was 49.9 g (males,  $n = 1232$ ; females,  $n = 955$ ), the asymptotic mean wing chord was 106 mm (males,  $n = 1201$ ; females,  $n = 937$ ), and the asymptotic mean tarsus length was 31 mm (males,  $n = 15$ ; females,  $n = 10$ ; Roth et al. 1996, Brown and Roth 2004).

Regression trees were used to investigate which predictor variables influenced each nestling growth variable and to identify interactions between predictor variables using CART® version 5.0 (Salford Systems, San Diego, California). Interactions between variables are identified by the structure of the regression tree when there is more than one variable split on the same “branch.” Regression trees detect two-variable interactions, partition the cases, and analyze each group separately so that variable interactions are not reflected in the variance values of the final tree models. Regression trees make no assumptions about data distributions or the relationship between predictor and response variables, while still allowing for the identification of interactions (Andersen et al. 2000, Roff and Roff 2003). Trees enable the exploration and identification of patterns that would be missed by traditional regression approaches (De’ath and Fabricius 2000).

We specified seven potential predictor variables in the regression tree models for nestling growth: year, site, distance to edge, edge type, brood size, date of hatching of the first egg, and brood parasitism. We calculated brood size by averaging the daily number of Wood Thrush and Brown-headed Cowbird nestlings observed in each nest throughout the nestling period and rounding to the nearest whole number. This allowed us to account for brood reduction when it occurred. We constructed a Pearson correlation matrix to examine correlations among variables. The data were sequentially split using the least squares fitting method based on the sum of the residual deviations. The optimal tree size was chosen using a series of 10-fold cross-validations to select the tree size with the lowest estimated relative error (Breiman et al. 1984) and to ensure the reliability of the fitted tree (Andersen et al. 2000). Cross-validation parti-

tions 90% of the data into a training dataset used to fit the tree and 10% of the data into a validation dataset. Regression trees were generated for each growth response variable, which is displayed graphically as a “hanging” mobile where each split in the data contains a test on one of the predictor variables, and we report the relative error of each model. Tree mobiles are not presented here but are available upon request from SAK. The importance of each variable was determined by the model’s improvement with the inclusion of each predictor variable as a splitter and the percent variance explained by each predictor variable for each model.

Trees were assessed for potential outliers, which were identified as terminal nodes containing a single observation (Breiman et al. 1984). The improvement to the model was compared with and without the potential outlier. Outliers may have a large influence on least-squares estimation so we removed them if they resulted in  $\geq 50\%$  reduction in the residual sum of squares (Breiman et al. 1984).

Daily survival rates (DSR) of nests were estimated for each edge type using the Mayfield method (Mayfield 1961, 1975) with exposure terminated using the midpoint approach for nests of known fate (Manolis et al. 2000). We used a 13-day incubation period and a 12-day nestling period to determine exposure days (Roth et al. 1996). Standard errors and confidence intervals for Mayfield estimates were calculated following the method of Johnson (1979). Productivity was calculated as the mean number of fledglings produced per successful nest, and we compared means of successful nests near abrupt and gradual edge types.

Cox proportional hazard regression was used to test the influence of year, site, distance to edge, and edge type on nest survival (Allison 1997). Exposure days were evaluated as risk factors. Nest fate was included as a censor variable (0 for successful and uncertain, 1 for failure). Failed nests were not censored because we knew the time interval in which they failed, whereas we censored the final nest check interval for successful nests or those with uncertain fates. In the regression model, the hazard for any nest is a fixed proportion of the hazard for any other nest and there is no underlying distribution assumption or assump-

tion of constant mortality (Allison 1997). Cox regression uses exposure days, rather than nest fate, as the response variable. Hence, nests observed for fewer days are not given the same weight as nests observed throughout the entire nesting period because they provide less information about the contribution of covariates to survival (Manolis et al. 2000). Cox regression analyses were conducted with PROC PHREG (SAS Institute 2002). We considered  $P \leq 0.05$  significant and values are reported as means  $\pm$  SE unless indicated otherwise.

Preliminary analyses revealed relatively low cowbird parasitism frequencies so we did not include brood parasitism as a potential explanatory variable in the Cox proportional hazard regression analysis. However, we noted a potential pattern of brood parasitism related to edge type, so we did an ad hoc analysis of independence to test for an association between edge type and brood parasitism using the  $G$ -statistic with Williams' correction (Sokal and Rohlf 1981).

## RESULTS

### NESTLING GROWTH

We measured 91 nestlings from 28 nests at Allegan, 35 nestlings from 11 nests in 2002 and 56 nestlings from 17 nests in 2003. At Barry, we measured 102 nestlings from 33 nests, 65 nestlings from 20 nests in 2002 and 37 nestlings from 13 nests in 2003. Nestlings from six nests, four at Allegan and two at Barry, were excluded from analyses because early depredation resulted in too few measurements ( $<5$ ) of nestlings to fit a growth curve. For the remaining nests that were included in analyses, the means and ranges of distances from the edge varied among edge types (Fig. 2). Seven of the 55 nests for which we measured nestling growth were within 100 m of more than one edge. Three of these nests were located in forest  $<5$  m from a road with a wildlife opening edge 40–50 m away. Two of those three nests were at Allegan and one at Barry.

We tested for correlations among all continuous variables and found that the brood sizes of nests included in regression analyses were negatively correlated with their hatching dates ( $r = -0.53$ ,  $F_{1,52} = 20.2$ ,  $P < 0.001$ ; Fig. 3). One observation was identified as an outlier

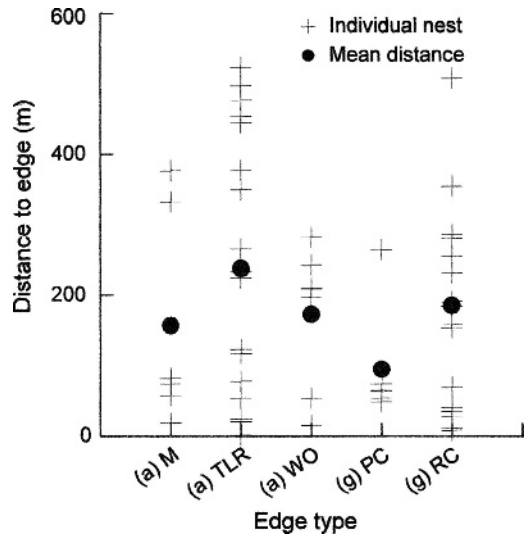


FIGURE 2. Mean distances (m) of Wood Thrush nests from the nearest edge in southwestern Michigan differed among edge types for nests for which nestlings were measured. Edge types were classified as abrupt (a; TLR = two-lane road, M = marsh, WO = wildlife opening) or gradual (g; PC = powerline corridor, RC = recent clearcut) based on whether the edge transition was stark (e.g., forest to road) and whether the transition zone containing shrub-level vegetation between the mature forest and the open land extended  $\leq 2$  m (abrupt edges) or  $>2$  m (gradual edges).

and removed from the regression tree for tarsus growth.

The regression tree for the right tarsus had a residual mean deviance of 1.0 and showed that distance to edge and date of hatching influenced tarsal growth rates (Table 1). An interaction between distance to edge and edge type was identified based on the structure of the tree. Nestlings in nests located nearest to gradual edges (powerline corridor, recent clearcut) had more rapid tarsal growth rates than those in nests farther from these edges, while growth rates did not differ for nestlings in edge and interior nests located nearest to abrupt edges (two-lane road, marsh, wildlife opening). We compared mean growth rates among edge types and found that nestlings in nests near gradual edges had more rapid tarsal growth rates than those in nests near abrupt edges ( $t_{44} = -2.9$ ,  $P = 0.007$ ; Fig. 4). In addition, nests hatching later in the season had more rapid tarsal growth rates. We averaged daily measurements of the right tarsus of all nestlings and

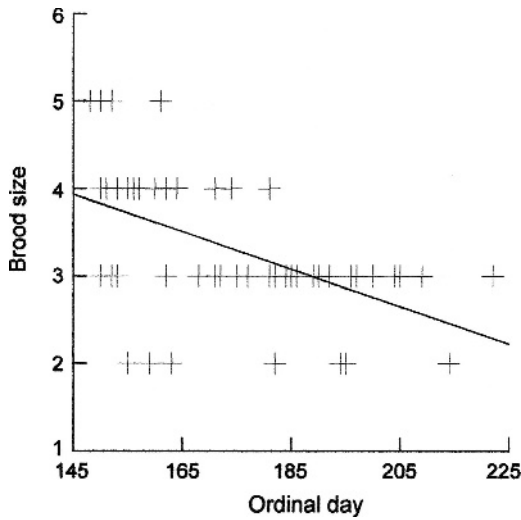


FIGURE 3. Brood sizes of Wood Thrush nests in southwestern Michigan included in nestling growth analyses were negatively correlated with the date of hatching of the first egg (in ordinal days).

plotted these daily means to illustrate the growth pattern of the tarsus (Fig. 5). Tarsi had reached adult length by brood day 10 based on the asymptotic value (31 mm) that we used.

The regression tree for mass had a residual mean deviance of 1.0 and revealed that hatching date, distance to edge, and edge type influenced mass growth rates (Table 1). Nestlings in nests that hatched later in the season had more rapid mass growth rates than those in nests that hatched earlier in the season. An interaction between distance to edge and edge type was found, and was in the same direction as in the tarsus regression tree results: nestlings in nests located closer to gradual edges (powerline corridor, recent clearcut) had more rapid mass growth rates than those farther from these

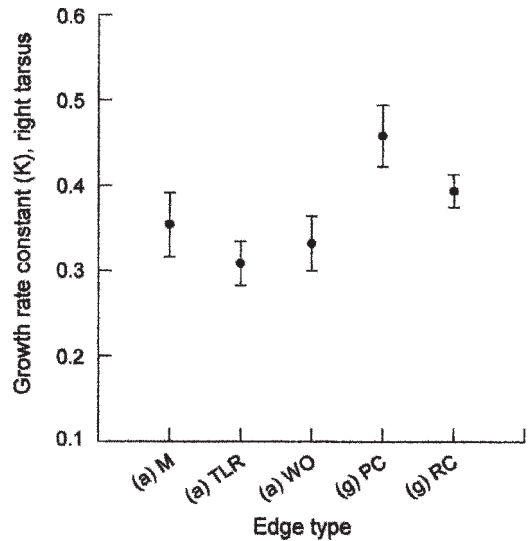


FIGURE 4. Wood Thrush nestlings in nests near gradual edge types had more rapid right tarsal growth rate constants (mean  $\pm$  SE) than those in nests near abrupt edge types in southwestern Michigan. Edge types were classified as abrupt (a; TLR = two-lane road [ $n = 14$ ], M = marsh [ $n = 5$ ], WO = wildlife opening [ $n = 6$ ]) or gradual (g; PC = powerline corridor [ $n = 5$ ], RC = recent clearcut [ $n = 16$ ]) based on whether the edge transition was stark (e.g., forest to road) and whether the transition zone containing shrub-level vegetation between the mature forest and the open land extended  $\leq 2$  m (abrupt edges) or  $> 2$  m (gradual edges).

edges, while growth rates did not differ between edge and interior for nestlings in nests located nearest to abrupt edges (two-lane road, marsh, wildlife opening). However, our comparison of growth rate constants among edge types revealed that mass growth rate constants did not differ between nestlings in nests near gradual ( $K = 0.509 \pm 0.024$ ) and abrupt edges ( $K = 0.508 \pm 0.020$ ;  $t_{48} = -0.1$ ,  $P = 0.97$ ). Thus, we

TABLE 1. The percentage of variation in the growth response variables explained by the set of predictor variables in each regression tree model ("model variance") and by each individual predictor variable within each model of the growth of nestling Wood Thrushes. Sample sizes of nests used in regression tree analyses are given in parentheses next to each growth response variable. The "+" and "-" signs indicate the direction of the effect on growth; for example, a negative effect of distance to edge in the first column indicates that the right tarsus of nestlings grew more slowly in nests farther from the forest edge.

Right tarsus (46)	%	Mass (51)	%	Right wing (51)	%
Model variance	45	Model variance	37	Model variance	35
Distance to edge (-)	37	Distance to edge (-)	18	Distance to edge (+)	35
Date of hatching (+)	8	Date of hatching (+)	18		
		Edge type (+ gradual)	1		



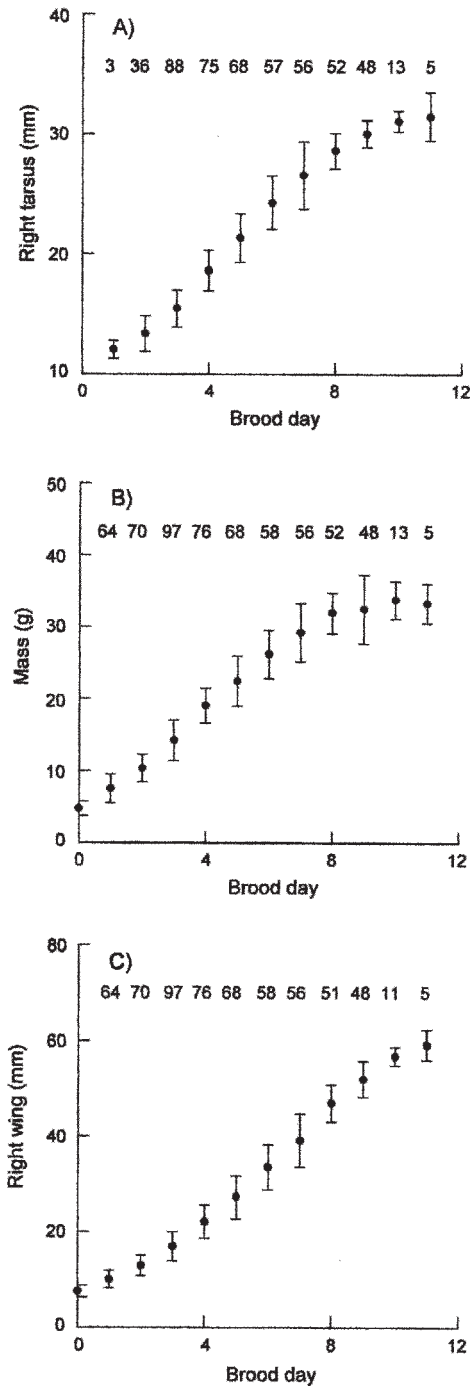


FIGURE 5. Growth curves of Wood Thrush nestlings indicating mean ( $\pm$  SD) daily measurements of all nestlings for A) right tarsus, B) mass, and C) right wing chord. Day 0 corresponds to the day the first nestling hatched. Numbers at tops of graphs indicate numbers of nestlings measured. Based on the

consider the result from the regression tree, indicating that an interaction between distance to edge and edge type influenced mass growth rate, to be lacking in support. Mean average daily mass of all nestlings was 70% of adult weight on brood day 10, based on the asymptotic value (50 g) that we used (Fig. 5).

The residual mean deviance of the regression tree for wing chord was 1.1 and distance to edge was identified as an influential predictor variable (Table 1). Nestlings in nests located farther from edges had more rapid wing chord growth rates than those in nests nearer to edges. Based on the asymptotic value (106 mm) that we used, nestling wings had reached only 56% of adult length by brood day 10 (Fig. 5).

NEST SURVIVAL

We found 175 Wood Thrush nests; 55% of 88 were successful at Allegan and 43% of 87 were successful at Barry. All nesting failures were attributed to predation, with the exception of one failure because of cowbird parasitism at Allegan. In this latter case, a female laid one egg and deserted her nest after three cowbird eggs were laid in her nest prior to incubation. Twenty-two nests were depredated during the incubation period at Allegan and 29 at Barry. Seven nests were depredated during the nestling period at Allegan and 15 at Barry. Ten nests were abandoned prior to egg-laying at Allegan, as were six nests at Barry.

DSR did not differ between nests found near abrupt or gradual edge types ( $\chi^2_1 = 1.1, P = 0.30$ ; Table 2). The risk of nest failure was significantly influenced by site ( $\beta = -0.58 \pm 0.30, \chi^2_1 = 3.8, P = 0.05$ ), but not by year ( $\beta = 0.15 \pm 0.24, \chi^2_1 = 0.4, P = 0.53$ ), distance to edge ( $\beta = -0.0007 \pm 0.0009, \chi^2_1 = 0.6, P = 0.43$ ), or edge type ( $\beta = -0.07 \pm 0.11, \chi^2_1 = 0.4, P = 0.51$ ). The hazard ratio for site was 0.56, indicating that nests at Barry were 1.8 times more likely to fail than nests at Allegan. The mean number of fledglings produced per successful nest did not differ between nests near abrupt and gradual edge types ( $t_{82} = 0.5, P = 0.62$ ; Table 2). Nests found at abrupt edges and

← asymptotic values we used, by brood day 10 tarsi had reached adult length but nestling mass was 70% of adult weight and wings were only 56% of adult length.

TABLE 2. Variation in Wood Thrush daily nest survival rates, fledglings per successful nest, and frequency of Brown-headed Cowbird parasitism in relation to nearest edge type in southwestern Michigan. Data are given as mean  $\pm$  SE (*n*).

Edge type <sup>a</sup>	Daily nest survival rate	Fledglings per successful nest	Percent of nests parasitized <sup>b</sup>
Two-lane road	0.976 $\pm$ 0.005 (57)	2.9 $\pm$ 0.2 (36)	15 (8 of 54)
Marsh	0.967 $\pm$ 0.010 (19)	2.6 $\pm$ 0.2 (9)	27 (4 of 15)
Wildlife opening	0.947 $\pm$ 0.016 (19)	2.8 $\pm$ 0.5 (8)	0 (0 of 15)
Powerline corridor	0.975 $\pm$ 0.011 (13)	2.9 $\pm$ 0.4 (8)	0 (0 of 10)
Recent clearcut	0.956 $\pm$ 0.008 (49)	2.6 $\pm$ 0.3 (23)	5 (2 of 43)
Abrupt	0.970 $\pm$ 0.005 (95)	2.8 $\pm$ 0.1 (53)	14 (12 of 84)
Gradual	0.961 $\pm$ 0.007 (62)	2.7 $\pm$ 0.2 (31)	4 (2 of 53)

<sup>a</sup> Abrupt edge types include two-lane road, marsh, and wildlife opening; gradual edge types include powerline corridor and recent clearcut.

<sup>b</sup> We only included nests observed during the incubation period in the calculation of parasitism frequency.

gradual edges were approximately evenly distributed across the nesting season, indicating that our sample sizes were not biased toward early or late season nests. This would have confounded our results because of reduced brood sizes in late season nests compared to early season nests.

Parasitism frequency was higher at Allegan (22%; 15 of 69 nests) than at Barry (2%; one of 68 nests). In Allegan, six nests  $\leq$ 100 m from edge and nine nests  $>$ 100 m from edge were parasitized. In Barry, the parasitized nest was 377 m from the nearest forest-marsh edge. Nests at abrupt edges were more likely to be parasitized than nests at gradual edges ( $G_1 = 4.2$ ,  $P = 0.04$ ; Table 2). Seven of the 15 nests parasitized at Allegan were successful and fledged at least one cowbird as well as Wood Thrush young; the nest parasitized at Barry was depredated late in the nestling period.

## DISCUSSION

### NESTLING GROWTH

We predicted that nestlings in nests near edges would have reduced growth rates compared to those in nests in the forest interior. Our prediction was based on the assumption that the forest interior would have more abundant food compared to edges (Schowalter et al. 1981, Duguay et al. 2000), leading to enhanced growth rates for nestlings in the forest interior. Contrary to our expectations, distance to the edge was negatively related to tarsal and mass growth rates for certain edge types. Nests closer to gradual edges (those formed by powerline corridors and clearcuts) had higher rates of tarsal and mass growth than nests farther from

these edges. In contrast, tarsal and mass growth rates were similar at all distances from the edge for nests adjacent to abrupt edges (formed by two-lane roads, marshes, and wildlife openings). In addition, tarsal growth rates at abrupt edges were depressed compared to rates nearest to gradual edges.

One explanation for the above patterns is that, in contrast to our assumption, gradual edges were food-abundant compared to the forest interior and abrupt edges. Powerline corridors and clearcuts contained dense shrubbery at their edges and by midseason became more structurally diverse than abrupt edges or the forest interior as ground vegetation reached maximum growth (SAK, pers. obs.). Edges are more exposed to sunlight, thus seasonal plant growth may attract herbivorous insects, which in turn could attract foraging birds (Murcia 1995). Invertebrate abundance has been found to be greater near clearcut edges than in surrounding coniferous forest in some studies (Helle and Muona 1985, Heliölä et al. 2001) and to be positively affected by habitat edges (Crist et al. 2006). Our results suggest that nestling growth rates may be related to spatial variability in food supplies. However, measurements of litter invertebrates at different edge types and different distances from the edge are necessary to definitively document these potential relationships.

The regression models explained 35%–45% of the variation in growth rates. Although distance to edge was not associated with growth rates in the direction we expected, it does explain a moderate level of variation, indicating that distance to edge is associated with aspects of

habitat quality. Variables we did not examine, for example parental care, parental age and experience, and home range quality, may also have played substantial roles in determining growth rates. In a New Jersey study, Wood Thrushes were more abundant near edges bordered by powerline corridors than narrow, unpaved roads (Rich et al. 1994), suggesting that some edge habitat may be more desirable than other edge habitat. Older and experienced breeding pairs may be better at assessing the resource quality and safety of habitat (Alatalo et al. 1986) and be more efficient at foraging and provisioning their nestlings than younger, less experienced parents. Moreover, less experienced pairs may be forced into marginal habitat for successfully raising broods if they arrive later to the breeding grounds and are less able to compete for territories and resources (Sherry and Holmes 1989, Mazerolle and Hobson 2004). Wood Thrushes forage for invertebrates, small vertebrates, and fruits on the forest floor and in the understory (Holmes and Robinson 1988). The investigation of food abundance, quality, and provisioning rates by known-age adults in the edge and interior and near different edge types, in conjunction with growth rate measurements, would aid in determining how these potential explanatory variables interact to influence growth rates.

Our second prediction, that mass and tarsal growth would be more rapid than wing chord growth, was supported by our results. Rapid growth rates of tarsi and mass may assist a nestling's begging, perching, and competitive interactions for food with its siblings (O'Connor 1977, Smith and Andersen 1982). In the first two weeks out of the nest, Wood Thrushes perch quietly in dense undergrowth near the ground with minimal short flights and will hop, rather than fly, away from pursuers (Anders et al. 1997, Vega Rivera et al. 1998). They depend on their legs for movement during the early postfledging period because wing chords do not fully develop to enable long flights until approximately 15 days postfledging (Roth et al. 1996). Hence, more rapid tarsal growth (Smith and Andersen 1982) may enhance survival of young birds.

Further, nestlings must balance their allocation of resources between growth and thermoregulation. Allocating resources to mass growth would reduce their thermoregulatory needs and

increase their chances of surviving to fledging (Dawson et al. 2005). Tree Swallows (*Tachycineta bicolor*) nesting in artificially heated nests had enhanced survival, weighed more, and had more rapid mass growth than nestlings from nests with unaltered microclimates (Dawson et al. 2005). The authors attributed this response to the greater allocation of food resources to growth because of reduced thermoregulatory costs (Dawson et al. 2005). Hence, differences in microclimates among edge types and at different distances from edges (Chen et al. 1993, Murcia 1995) could affect growth rates through trade-offs between growth and thermoregulation, in addition to changes in food supplies.

In contrast to our results for tarsal and mass growth rates, the growth rate of wing chords was positively correlated with distance to edge. We are unsure what factors may be driving this pattern. Previous work has shown that tarsus and mass, which are correlated traits (Green 2001), tend to be variable and similarly responsive to environmental conditions, in contrast to wing chords (Ashton and Armstrong 2002, Brown and Roth 2004, Charmantier et al. 2004). In this study, nestling tarsi had reached adult length by day 10 while wing chord was only 56% of adult length at fledging. Because Wood Thrush nestlings do not put as much energy into wing development, we would expect poor microclimate or food conditions or lower levels of food provisioning to manifest in slower growth of tarsi and mass. This pattern bears further investigation.

Nestlings hatching later in the season had more rapid tarsal and mass growth rates, which may have been related to an increase in the availability of food resources, although food abundance was not directly measured in this study. Females may decide when to lay their eggs based on environmental cues (Meijer et al. 1999, Brown and Roth 2002) so that their young will hatch when food is most abundant during the breeding season (van Noordwijk et al. 1995). Several studies have found positive associations between hatching date and nestling growth rates (Pravosudov and Pravosudova 1996, Boersma and Parrish 1998, McCarty and Winkler 1999), and the authors attributed these patterns to seasonal changes in food abundance and prey quality. However, it is likely that smaller brood sizes later in the season also

contributed to the more rapid growth at this time. Although the regression trees did not show brood size to be a significant predictor of tarsal or mass growth rates, brood size was correlated with hatching date, indicating that some of the hatching date effects were likely brood size effects. Nestlings from larger broods are expected to have reduced growth rates and fledging masses (Kunz and Ekman 2000) because of the inability of parents to feed each nestling at the same rate as parents of smaller broods (Naef-Daenzer and Keller 1999) and the greater amount of energy expended by nestlings in intrabrood competitions for food (Schifferli 1978). Nestling growth rates and fledging masses of Prothonotary Warblers (*Protonotaria citrea*) were lower in larger broods (Podlesak and Blem 2001). Likewise, nestling Blue Tits (*Parus caeruleus*) from experimentally enlarged broods had reduced nestling growth rates and fledging masses (Kunz and Ekman 2000).

Cowbird parasitism may affect growth and hatching and fledging success of host young of commonly parasitized species (Marvil and Cruz 1989, Dearborn et al. 1998, Burhans and Thompson 2000). We found no effect of brood parasitism on nestling growth rates, although nests near abrupt edges were more likely to be parasitized than nests near gradual edges. However, only 5% of the nests in our growth rate analyses contained cowbirds, which may have made effects difficult to detect.

Several considerations should be borne in mind when interpreting our results. First, we used data from adults nesting in the mid-Atlantic United States to determine the asymptotic values used to calculate growth rate constants. However, geographic variation in adult body size of Wood Thrushes has not been reported (Clement 2000), so we expect that data for adult Wood Thrushes from the northeastern region are comparable to measurements for adults breeding in Michigan. In addition, we used the same asymptotic values when fitting all curves so, even if differences do exist among adult masses in different areas, the relative growth rate differences remain informative even if the absolute growth rate constants were slightly biased.

Our nestling growth rate constants were calculated for the entire brood from measurements of individual nestlings that were aged separately. Wood Thrushes usually hatch within

two days of each other (Brown and Roth 2004), but those that hatched on the same day were still potentially several hours different in age. We do not know how the measurements of these "same-aged" nestlings differed over a 24 hr period. Parental care may shift in favor of first-hatched chicks, regardless of the magnitude of their age difference from later-hatched chicks, contributing to intrabrood growth variability.

A potential confounding factor affecting comparisons in growth rates among edge types is bird mobility. It is possible that a pair nesting in edge habitat flew to forage in interior habitat or foraged in more than one edge type, since seven nests of the 55 we included in analyses were within 100 m of two different edge types. It is also possible that a pair nesting near an edge preferentially foraged in a direction farther from the edge within their home range. We did not track the movements of nesting adults in this study, although we generally observed nesting males in visual or auditory contact with their mates while guarding her and their nest (SAK, pers. obs.). In addition, daily telemetry locations of nesting adults in central Georgia showed that males and females foraged less than 100 m from their nests the majority of the time (Lang et al. 2002). These results suggest that most of the food provided to nestlings comes from the vicinity of the nest.

We treated nests as independent in this study, but we observed several renesting attempts, which means that the brood growth rates of a few nests were autocorrelated. Growth has a strong genetic component (O'Connor 1975, Galbraith 1988, Rhymer 1988), which is a source of variation that needs more investigation. Cross-fostering designs have the potential to determine the extent to which variation in nestling growth is caused by genetic and environmental factors (van Noordwijk and Marks 1998, Kunz and Ekman 2000) and the heritability of specific traits (Charmantier et al. 2004).

#### NEST SURVIVAL

We found no significant edge effects on the daily survival rates of nests, the risk of nest failure, or the productivity of successful nests. While southwestern Michigan contains forested areas, such as Allegan and Barry, these landscapes are highly fragmented and surrounded by agricultural land. Regional land-cover patterns can influence the abundance and diversity

of nest predators, which could constrain the importance of effects of proximity to edge on nest predation (Thompson et al. 2002). In a study comparing the factors affecting nest success at multiple scales, Thompson et al. (2002) found that landscape context explained why some studies documented edge effects on predation patterns and others did not. Thus, high regional fragmentation levels may overwhelm potential differences in local edge effects on nest survival, although local-scale effects on nestling growth rates may still be detectable.

Brood parasitism can significantly reduce nest success of Wood Thrushes (Brittingham and Temple 1983, Donovan et al. 1995, Fauth 2001). Although our data suggest that nests near abrupt edges may be more susceptible to brood parasitism than nests near gradual edges, this increased susceptibility did not translate into reduced nest survival.

Site was the only variable identified by the Cox regression model that affected nest survival. The risk of nest failure was much greater at Barry than at Allegan when data from both years were combined. Cox proportional hazard regression may be more sensitive to differences in nest survival than comparisons of daily survival rates because constant mortality is not assumed, which is important given that twice as many nests failed during the nestling period at Barry than at Allegan. Barry contained younger forest compared to Allegan and had an understory that was less dense. Barry also had more white pine in the understory and midstory, which was used more often as a substrate for nests than at Allegan. Nests in white pine may have been more conspicuous to avian predators because needles do not conceal nests as well as deciduous leaves, and nests were usually built on the highest branch near the main stem of the tree, an easily detected location (SAK, pers. obs.)

Our analysis of nest failure did not account for partial loss of nest contents. We evaluated a nest as successful if at least one Wood Thrush fledged. Hence, a nest in which one egg was laid and one Wood Thrush fledged was considered as successful as a nest in which four eggs were laid and one Wood Thrush fledged. Cox proportional hazard regression assumes that the change in daily nest failure rate associated with a particular covariate is constant over time. However, nests that were partially depre-

dated were plausibly more likely to fail once initially found by a predator. Or, if a nestling was lost to starvation, other nestlings in that nest may have been more likely to starve than nestlings in other nests. We were unable to determine in all cases whether nests with reduced broods were the result of hatching failure, starvation, brood reduction, or partial depredation. Thus, treating all nests that fledged at least one Wood Thrush as successful regardless of partial losses could potentially conceal the influence of time-dependent covariates on nest failure rates.

In conclusion, our findings that tarsal and mass growth rate constants of nestling Wood Thrushes were more rapid near edges than in the forest interior and that tarsal growth was more rapid near gradual edge types than abrupt ones suggests that the quality of the habitat or individuals may differ with distance to edge and among edge types. Hence, nestling growth rates may be another mechanism through which the fitness of forest-interior birds is affected by forest fragmentation, although not necessarily in parallel with changes in nest predation. We did not show effects of distance to edge or edge type on nest survival, although nests near abrupt edges were more likely to be parasitized by Brown-headed Cowbirds than nests near gradual edges. Wing chord growth is likely a less useful reflection of habitat quality than tarsal or mass growth during the nestling period because wings grow more slowly to adult length.

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