



## EFFECTS OF FOREST MANAGEMENT ON POSTFLEDGING SURVIVAL OF ROSE-BREASTED GROSBEAKS (*PHEUCTICUS LUDOVICIANUS*)

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**ABSTRACT.**—Many studies have examined the effects of forest fragmentation and management on songbird nesting success, but few have quantified postfledging survival, which is a critical component of population productivity. In 2005–2006, we estimated daily postfledging survival of Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) by radiotracking 42 fledglings in forest fragments that had been managed by single-tree selection, by diameter-limit harvest, or as reference (not harvested for at least 25 years). Survival probability over the 3-week fledgling period was 0.62, and 86% of total fledgling mortality occurred during the first week out of the nest. Despite large differences in forest structure between forest management treatments, there was no effect of forest treatment on fledgling survival. Date of fledging, shrub cover, and patch size also had limited influence on fledgling survival. For all sites combined, females produced an estimated 0.23–0.37 recruiting daughters per year for the worst- and best-case scenarios of female fecundity and annual juvenile survival, which is lower than the expected annual mortality rate of breeding females (0.40–0.55). Even reference sites did not produce enough offspring to offset annual female mortality, which suggests that forest fragments in this region are population sinks. Received 23 January 2009, accepted 16 May 2009.

Key words: fledgling survival, forest fragmentation, forest management, *Pheucticus ludovicianus*, population sink, Rose-breasted Grosbeak.

### Efectos del Manejo de Bosque sobre la Supervivencia Posterior al Emplumamiento en *Pheucticus ludovicianus*

**RESUMEN.**—Muchos estudios han examinado los efectos de la fragmentación y del manejo del bosque sobre el éxito de anidación de las aves canoras, pero pocos han cuantificado la supervivencia posterior al emplumamiento, un componente crítico de la productividad poblacional. En 2005 y 2006, estimamos la supervivencia diaria posterior al emplumamiento de *Pheucticus ludovicianus* mediante el seguimiento con radio transmisores de 42 volantones en fragmentos de bosque que habían sido manejados mediante extracción selectiva de ejemplares únicos, mediante cosecha con límites de diámetro o como referencia (no cosechados por al menos 25 años). La probabilidad de supervivencia a lo largo del período de volatón de tres semanas fue de 0.62, y el 86% de la mortalidad total de los volantones ocurrió durante la primera semana fuera del nido. A pesar de las grandes diferencias en la estructura del bosque entre los tratamientos de manejo, no hubo un efecto del tratamiento del bosque en la supervivencia de los volantones. La fecha de emplumamiento, la cobertura de arbustos y el tamaño del parche también tuvieron una influencia menor en la supervivencia de los volantones. Para todos los sitios combinados, las hembras produjeron aproximadamente 0.23–0.37 hijas reclutas por año para el peor y el mejor escenario de fecundidad de las hembras y de supervivencia anual juvenil, lo cual es menor que la tasa de mortalidad anual esperada de las hembras reproductivas (0.40–0.55). Incluso los sitios de referencia no produjeron suficientes crías para compensar la mortalidad anual de las hembras, lo que sugiere que los fragmentos de bosque en esta región son sumideros poblacionales.

THE DECLINE OF forest songbird populations in many parts of the world (Newton 2004, Sauer et al. 2005) has been attributed to the widespread loss, fragmentation, and alteration of breeding habitat. It is important to consider the context in which fragmentation occurs, in particular the degree to which the landscape is fragmented (Hoover et al. 1995, Holmes et al. 2004, Jobes et al.

2004), the size of fragments (Keyser et al. 1998, Burke and Nol 2000), and the matrix in which fragments exist (Bayne and Hobson 1997a, Keyser 2002). In Australia and New Zealand, productivity of forest songbirds is often not related to fragment size and connectivity (Zanette 2000, Cooper et al. 2002, Boulton et al. 2008). In North America, nest predation and brood parasitism

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generally increase with habitat fragmentation (Donovan et al. 1995b, Robinson et al. 1995, Porneluzi and Faaborg 1999), but forests fragmented by agriculture appear to have greater increases in their predator and cowbird community than those fragmented by forestry practices (Bayne and Hobson 1997b, Duguay et al. 2001, Rodewald and Yahner 2001, Batáry and Báldi 2004).

Most research on forest songbird declines has focused on the total removal of forest cover (Rodewald and Smith 1998, Sallabanks et al. 2000). However, the quality of forest habitat may be degraded by partial harvest (e.g., uneven-aged or selection cuts, diameter-limit cuts, and “high-grades”) to a point where the habitat reduces the abundance and productivity of forest birds and becomes a population sink (Donovan et al. 1995a) despite the fact that the forest itself remains intact. Considerable research has been conducted on the effects of silviculture on forest songbirds. Forest management practices influence the density of songbirds (e.g., Chambers et al. 1999, Burke and Nol 2000, Weakland et al. 2002), food availability (Pettersson et al. 1995, Duguay et al. 2000, Smith et al. 2006), male pairing success (Burke and Nol 1998), and nesting success (Yahner 2000, Duguay et al. 2001, Rodewald and Yahner 2001, Stuart-Smith and Hayes 2003). Studies on the effects of silviculture in fragmented landscapes, as opposed to continuous managed forest, are relatively uncommon (Robinson and Robinson 1999, Keyser 2002). In areas where agricultural development has left forest cover highly fragmented, including much of the eastern deciduous forest of North America, partial harvesting is still a very common practice (Elliott 1998). It is important to know the degree to which these partially harvested, highly fragmented forests provide sustainable breeding habitat for forest songbirds.

Evaluating the effects of a particular management method and the quality of a forest fragment requires estimating the productivity of breeding songbirds (Thompson et al. 2001). Most studies monitor nesting success but do not follow the fate of nestlings after they leave the nest, even though the fledglings are vulnerable to predation and still receive care from the parents for several weeks. Fledglings are difficult to monitor visually, so radiotracking is essential for accurate estimates of survival in most species. The survival of fledgling birds can have important and unexpected effects on the population’s productivity, yet it remains understudied as a component of avian demographics. Nest success can be a poor indicator of productivity (Underwood and Roth 2002, Anders et al. 1997, King et al. 2006, Yackel Adams et al. 2006). In Hooded Warblers (*Wilsonia citrina*), for instance, only 19% of fledglings survived to independence and even large forest fragments were population sinks (Rush and Stutchbury 2008).

Forest management and fragment size may influence nesting success differently than fledgling survival because of differences in vulnerability to particular predators and shifts in habitat use during the fledgling period. In the Wood Thrush (*Hylocichla mustelina*), fledgling survivorship, but not nest success, varied in relation to annual abundance of rodents and raptors, the predators responsible for most fledgling mortality (Schmidt et al. 2008). Fragment size was associated with decreased nesting success but not fledgling survival of Hooded Warblers, perhaps because fledglings escaped predation by occupying habitat that was more

structurally complex than the nesting sites (Rush and Stutchbury 2008). Species that nest primarily in late-successional forest often shift habitat use to early-successional forest once fledglings leave the nest, possibly to find more available food resources (Anders et al. 1998, Vega Rivera et al. 1998, King et al. 2006). Thus, effects of forest management on nesting success clearly cannot be extrapolated to the fledgling period to estimate overall productivity.

We used radiotelemetry to study the influence of logging treatment and fragment characteristics on postfledging survival and movements of a migratory forest songbird, the Rose-breasted Grosbeak (*Pheucticus ludovicianus*). We chose this focal species because Rose-breasted Grosbeak abundance declined by  $-0.8\%$  year<sup>-1</sup> between 1968 and 2005, according to the North American Breeding Bird Survey (Sauer et al. 2005). This decline has been more pronounced in Canada, at  $-1.9\%$ , and larger still in Ontario, at  $-2.3\%$ . A previous study in the same study area in southwestern Ontario found that the method of timber harvest had little effect on nest success of Rose-breasted Grosbeaks (Smith et al. 2006), but there was no information on fledgling survival in this species. Our study was performed in the same region to quantify fledgling survival and to estimate productivity in forest fragments subjected to different forest management practices.

We determined fledgling survival in different forest treatments and quantified the dispersal movements and habitat of fledglings compared with random points and nest locations. At the individual level, we expected that young would be at the greatest risk of predation in the first few days after fledging (Sullivan 1989, Anders et al. 1997, Vega Rivera et al. 2000, King et al. 2006) and that survival would increase later in the season as a result of greater food abundance (Yackel Adams et al. 2006). At the territory level, shrub cover was expected to increase fledgling survival (King et al. 2006, Rush and Stutchbury 2008).

Our primary focus was on the effects of logging treatment, because harvest intensity can negatively influence nesting success of songbirds by providing suitable habitat for predators, which may also increase the likelihood of fledgling mortality. Potential predators such as squirrels and corvids have been found to increase in abundance in association with logged forests (Stuart-Smith and Hayes 2003). Heavily cut sites may, in fact, be ecological traps (Gates and Gysel 1978, Donovan and Thompson 2001, Robertson and Hutto 2007) that lure breeding birds with abundant fruit and dense understory while concealing an abundant predator community. In particular, recently harvested forest with decreased structural diversity and little regeneration should have the lowest fledgling survival. We also expected that forest fragment size would be positively correlated with fledgling survival because of reduced predation pressure in large fragments.

## METHODS

*Study site and species.*—The Rose-breasted Grosbeak is a relatively common forest songbird that breeds throughout much of eastern and central North America (Wyatt and Francis 2002). This species nests in primary and secondary deciduous and mixed forest as well as thickets, scrubland, and park areas. Eggs hatch asynchronously 12–13 days after laying, and nestlings can leave the nest 9–14 days later. Once out of the nest, the young depend on their parents for an additional 3 weeks before they disperse from

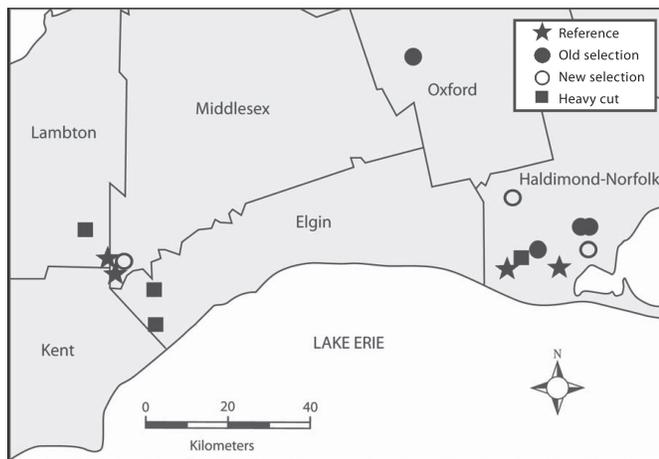


FIG. 1. Location of forest fragments in southern Ontario in which Rose-breasted Grosbeak productivity was studied in 2005–2006; symbols indicate forest management treatment (star = reference, filled circle = old selection cut, open circle = new selection cut, and filled square = heavy cut).

the natal area. For the first 2 to 5 days after leaving the nest, the fledglings are incapable of flight and move only short distances from the nest site (L. Moore pers. obs.). After the first week, they begin to forage for themselves and are capable of short flights. In southern Ontario, where our study was conducted, Rose-breasted Grosbeaks generally produce only 1 brood per season (Friesen et al. 1999).

Our study was conducted in 2005–2006 in conjunction with the Ontario Ministry of Natural Resources (OMNR) as part of their long-term research project to evaluate the effects of silvicultural and partial-harvesting practices on biodiversity (Burke et al. 2004). Forest cover averages 13% in this region (Holmes et al. 2004), and the landscape is primarily agricultural and urban.

Sixteen study sites were located in upland deciduous forest, part of the Carolinian Forest Region of southwestern Ontario (Fig. 1), near the towns of Newbury (42°41'N, 81°48'W), Ingersoll (43°02'N, 80°53'W), and Port Rowan (42°35'N, 80°15'W). Dominant tree species were Sugar Maple (*Acer saccharum*), Red Maple (*A. rubrum*), Northern Red Oak (*Quercus rubra*), White Oak (*Q. alba*), White Ash (*Fraxinus americana*), Green Ash (*F. pennsylvanica*), American Beech (*Fagus grandifolia*), and Black Cherry (*Prunus serotina*). Ownership of study sites included a mix of private, Conservation Authority, and county properties.

The 16 forest fragments (21–267 ha) were embedded in a largely agricultural landscape with 12–35% forest cover within 5 km (Table 1; Burke et al. 2004). Five reference sites had not been harvested since 1979 (>25 years prior to our study), and all harvested forests were logged between 1995 and 2004. Three selection-cut sites were harvested within 16–24 months before field work (hereafter “new selection”), and 4 sites were harvested as selection cuts between 5 and 11 years before field work (hereafter “old selection”). Four sites were cut to municipal diameter limits, more heavily than recommended by OMNR guidelines, <11 years before field work (hereafter “heavy cut”).

Selection-cut sites were harvested according to OMNR guidelines (OMNR 2000). Single trees were marked and removed to attain a site-level residual basal area of ~20 m<sup>2</sup> ha<sup>-1</sup> for all trees ≥10 cm in diameter at breast height. Prescriptions targeted the removal of poor-quality material and attempted to thin across all diameter classes. An average (± SD) of 20.2 ± 0.05% of the basal area was removed from the selection sites. By contrast, heavy-cut sites had most of the commercially marketable wood removed, particularly the largest and most valuable trees. Residual basal area after harvest was <20 m<sup>2</sup> ha<sup>-1</sup>, and an average of 38.4 ± 0.05% of the basal area was removed. Reference sites had an average basal area of 32 ± 5 m<sup>2</sup> ha<sup>-1</sup>.

*Nest and fledgling survival.*—We searched for nests from mid-May to late July each year by systematically exploring suitable habitat and observing adult behavior. We monitored nests every

TABLE 1. Forest management treatment and forest fragment characteristics where fledgling survival of Rose-breasted Grosbeaks was monitored (2005–2006).

Treatment	Site number	Treatment year	County or region	Forest area (ha)	Forest cover (%)
Reference	403	NA	Haldimand–Norfolk	262	30
	551	NA	Middlesex	97	20
	553	NA	Middlesex	107	20
	600	NA	Haldimand–Norfolk	135	26
	701	NA	Haldimand–Norfolk	146	27
Old selection	42	1998	Oxford	22	12
	77	1995	Haldimand–Norfolk	65	35
	78	1997	Haldimand–Norfolk	52	35
New selection	602	1999	Haldimand–Norfolk	196	31
	501	2002	Haldimand–Norfolk	161	21
	503	2004	Haldimand–Norfolk	169	27
Heavy cut	552	2004	Middlesex	191	20
	107	1997	Elgin	50	17
	111	1998	Haldimand–Norfolk	53	29
	121	1996	Elgin	26	15
	608	2002	Lambton	78	15

2 to 4 days until predation, abandonment, or fledging occurred. On the last visit, we evaluated evidence of fledging (i.e., presence of feces on nest rim and cup depression, adult agitation in vicinity, or adult feeding young). Only the nests whose fledglings were radiotagged were included in nest-survival analysis.

Survivorship of fledglings was assessed through radiotelemetry. On day 9 (posthatch), nestlings were removed from the nest by hand and banded with 1 aluminum and 3 color leg bands. For each individual, we recorded weight (to the nearest 0.1 g), wing length (to the nearest 0.5 mm), and fat score ranked 1–6 (Pyle 1997). Sex of fledglings was determined using plumage characteristics. Rose-breasted Grosbeak eggs hatch asynchronously, sometimes 48 h apart (Wyatt and Francis 2002). Hence, some young were too small to band or equip with a radiotransmitter when their older siblings were nearly ready to fledge. In those cases, we excluded the youngest nestling from banding or from selection for radiotracking (or both). Fledglings were included in analysis only if relocated on the same day they fledged, to ensure that they were not depredated before leaving the nest. One individual died after harness entanglement and was excluded from further analysis.

To ensure independence of observations for analysis of fledgling survival, only 1 nestling was selected quasi-randomly from each nest to receive a radiotransmitter ( $n = 18$  females,  $n = 24$  males). All transmitters were attached using cotton embroidery thread and the figure-8 backpack method described by Rappole and Tipton (1991). Transmitters (0.9 g; model BD-2B, Holohil Systems, Carp, Ontario) had a battery life span of 28–50 days. To ensure that transmitters did not weigh >5% of fledgling body mass at the time of deployment, they were not attached if the mass of the fledgling was <18 g. Fledglings were located every 2 days for 21 days after fledging or until independence from parental care (generally 18 days after fledging, or 28–30 days after hatching; Wyatt and Francis 2002). Each fledgling location was marked with flagging tape and a global positioning system (GPS; GARMIN GPSmap 76, WAAS-enabled). Field tests determined that GPS locations were reliable to within 20 m. When relocated, the condition (alive or dead), height above ground (using a Brunton clinometer), and attending parent were recorded for each fledgling. On a few occasions when a bird was too well hidden in the canopy to see, we determined its location from three different directions and recorded the canopy height for that location instead. Although opportunistic observations were

made throughout the study period, only data obtained through radiotelemetry during fixed intervals between 0 and 21 days after fledging were included in the analysis.

Forest structure, nest sites, and fledgling habitat preferences were quantified using a standardized procedure developed by the OMNR that estimates percent cover at 5 vertical strata, measures depth of duff at 5 locations, and counts shrub abundance along a 10-m transect (Smith et al. 2006). Basal area was calculated using a factor-2 metric wedge prism for timber cruising, and the dominant tree species was determined using the point-quarter method. Stem densities for all fruit-bearing plants were counted along two 10-m transects in each plot. Habitat-assessment plots were centered on circles 11.6 m in diameter. This method is similar to that used by James and Shugart (1970). Depth of duff, percent sapling cover, percent understory cover, percent regeneration (0.5–1.3 m) cover, percent canopy cover, and basal area differed significantly among forest treatment types (Table 2).

Rose-breasted Grosbeaks feed heavily on fruit late in the summer (Stutchbury et al. 2005), so we quantified fruit abundance on each site. Two randomly chosen 200-m transects were sampled in each site once each summer to quantify the abundance of fruit from late June to mid-July, shortly after the first nests fledged young and when fruit began to ripen. The number of ripe and unripe fruit and the number of stems of all species in the genera *Amelanchier*, *Lindera*, *Rubus*, and *Ribes* were recorded within 1 m of the center line. All fruit located within 1 m of the center line were counted. Fruit abundance varied significantly between forest treatment types (Table 2).

Landscape-level variables such as forest patch size, forest cover (5 km radius), and distance to edge, trail, and road were calculated using the Spatial Analyst extension in ARCGIS (ESRI, Redlands, California) from data provided by the OMNR Natural Resources Values Information System. Staff at OMNR compiled stand-history data using historical records, growth and yield plot data, and stump calculations.

For analysis of habitat variables among random locations, nests, and fledgling locations, we used a two-way analysis of variance (ANOVA) in SPSS, version 16.0 (SPSS, Chicago, Illinois) with stage (random point, nest location, and fledgling age classes 0–5 days, 5–11 days, and 12–18 days) and forest treatment as fixed factors. Variables that were not normally distributed (i.e.,

TABLE 2. Mean values ( $\pm$  SE) of vegetation variables of forest fragments that were subject to different silvicultural treatments (see text for description of forest management treatments). *P* values are given for one-way ANOVA, and superscript letters indicate a significant difference between treatments for Tukey's HSD post hoc test using  $P < 0.05$ .

Vegetation variable	Reference ( $n = 70$ )	Old selection ( $n = 39$ )	New selection ( $n = 35$ )	Heavy cut ( $n = 41$ )	<i>P</i>
Depth of duff (cm)	2.6 $\pm$ 0.2 <sup>a</sup>	3.8 $\pm$ 0.3 <sup>c</sup>	2.2 $\pm$ 0.3	1.3 $\pm$ 0.2 <sup>b</sup>	<0.0001
Percent shrub cover	14.4 $\pm$ 1.7	15.6 $\pm$ 1.9	14.9 $\pm$ 2.2	15.9 $\pm$ 2.7	0.985
Percent regeneration cover	12.1 $\pm$ 1.7	17.3 $\pm$ 2.6	19.7 $\pm$ 2.8	15.9 $\pm$ 2.2	0.075
Percent sapling cover	11.0 $\pm$ 1.6 <sup>a</sup>	19.4 $\pm$ 2.5 <sup>b</sup>	8.2 $\pm$ 1.0 <sup>a</sup>	19.4 $\pm$ 2.3 <sup>b</sup>	<0.0001
Percent understory cover	24.3 $\pm$ 2.2	26.3 $\pm$ 2.8	20.7 $\pm$ 2.7	32.4 $\pm$ 3.5	0.043
Percent canopy cover	78.7 $\pm$ 2.0	59.2 $\pm$ 4.1	57.3 $\pm$ 4.3 <sup>b</sup>	57.2 $\pm$ 4.0 <sup>a</sup>	<0.0001
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	29.0 $\pm$ 0.9 <sup>a</sup>	24.4 $\pm$ 1.1 <sup>b</sup>	23.1 $\pm$ 1.3 <sup>b</sup>	22.0 $\pm$ 1.3 <sup>b</sup>	<0.0001
Fruit abundance (number per 1 m <sup>2</sup> )	25.5 $\pm$ 12.3 <sup>a</sup>	43.4 $\pm$ 16.4	108.0 $\pm$ 50.4	151.6 $\pm$ 62.0 <sup>b</sup>	0.038

percentages) were arcsine transformed. For analysis of height we compared nest locations with fledgling locations, and for distance moved we compared the three age classes.

**Survival analysis.**—Daily nest survival and daily postfledging survival were calculated using a generalized linear model in Program MARK (White and Burnham 1999). We calculated overall nest survival on the basis of a 24-day nest cycle (average 13 incubation days and 11 nestling days for Rose-breasted Grosbeaks). Daily postfledging survival was calculated for the 21 days after fledging. A log chi-square statistic was used to compare survival rates by treatment type.

We estimated daily fledgling survival rates using the nest-survival model in MARK (White and Burnham 1999, Schmidt et al. 2008). Individual fledgling-encounter histories were coded with the date of fledging, the last day the bird was known to be alive, the last day the fledgling was searched for, the bird's fate (0 = survived, 1 = died), and seven covariates. We constructed additive models within MARK using the design matrix tools and the logit-link function. We used an information-theoretic approach to examine postfledging survival rates of Rose-breasted Grosbeaks in relation to individual, site, and landscape variables. We ranked each model using Akaike's information criterion (AIC) values corrected for small sample sizes (AIC<sub>c</sub>; Burnham and Anderson 2002) and compared models based on the difference between the best-fit model and all others ( $\Delta AIC_c$ ) as well as their Akaike weight ( $w_i$ ).

*A priori* hypotheses addressing potential sources of variation in fledgling survival included individual, territory, and fragment-level covariates. At the individual level, all models included time since fledging as a continuous variable because most studies have found that young are at high risk of predation in the first few days after fledging (Sullivan 1989, Anders et al. 1997, Vega Rivera et al. 2000, King et al. 2006). We included models with age at fledging (days posthatch) as a continuous variable because fledging was often asynchronous within broods and nestlings that fledge at a relatively young age are expected to be less mobile and, hence, more vulnerable to predation. Date of fledging was also included in models, because food resources (especially fruit) increase over the season, which may improve fledgling survival (Yackel Adams et al. 2006). Increased vegetative cover on a territory could afford young fledglings protection from predators. At the patch level, we included forest treatment type (reference, new or old selection cut, heavy cut) to assess its influence on fledgling survival. The size of the forest fragment was also included as a covariate, because it could influence predation risk via differences in predator abundance or type.

Our total model set consisted of 14 *a priori* models with the individual covariates (time, time + agefledge, time + fledgedate) run alone and in combination with the territory covariates (shrub cover) and fragment covariates (forest treatment, fragment size). We also included a model with constant daily survival rate (DSR) and a global model including all covariates. Results are presented as means  $\pm$  SE.

**RESULTS**

The DSR for nests at the egg and nestling stage ( $n = 160$ ) was 0.956 (Table 3), with an interval survival rate of 0.341 for the entire 24-day nest period (Table 3). There were no significant forest-treatment effects on DSR ( $\chi^2 = 0.998$ ,  $df = 3$ ,  $P > 0.05$ ; Table 3).

TABLE 3. Daily survival rates (DSR,  $\pm$  SE) for Rose-breasted Grosbeak nests in forest fragments that were subject to different forest management treatments (2005–2006). Interval survival rate (ISR) was calculated for a 24-day period.

Treatment	<i>n</i>	DSR	95% CI	ISR
Reference	35	0.957 $\pm$ 0.009	0.934–0.972	0.345
Old selection	31	0.952 $\pm$ 0.011	0.928–0.968	0.303
New selection	44	0.957 $\pm$ 0.008	0.939–0.970	0.347
Heavy cut	50	0.958 $\pm$ 0.008	0.941–0.971	0.361
All sites	160	0.956 $\pm$ 0.004	0.947–0.964	0.341

There was no significant difference in fledgling survival between forest-treatment types ( $\chi^2 = 0.173$ ,  $df = 3$ ,  $P = 0.98$ ; Fig 2A). Twenty-six of 42 fledglings (61.9%) survived the 3-week fledgling period, and 86% of deaths occurred during the first week after leaving the nest (Fig. 2B). Fledgling survival to independence was similar between years (2005: 9 of 15 [60%]; 2006: 17 of 27 [63%]) and between sexes (11 of 18 females [61%], 15 of 24 males [62%]).

We inferred that the causes of mortality were predation ( $n = 13$ ) and exposure or starvation ( $n = 1$ ); the cause of death of 2 individuals could not be determined. Raptors were apparently responsible for 6 predation deaths, plucked feathers having been found with the transmitters on the ground or at an elevated perch "butcher block." Five deaths were apparently caused by mammals, given that

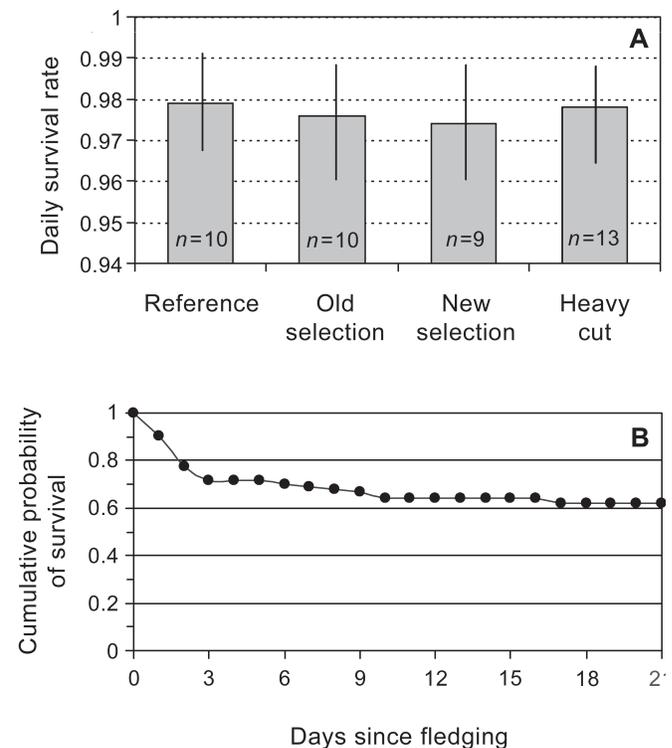


FIG. 2. (A) Daily survival rates (DSR) of fledgling Rose-breasted Grosbeaks ( $n = 42$ ) radiotracked in 4 silvicultural treatment types and (B) cumulative probabilities of fledgling survival for all sites combined.

TABLE 4. Model selection results for models with Akaike weight ( $w_i$ ) > 0.01 for factors influencing fledgling survival of Rose-breasted Grosbeaks. A total of 14 *a priori* models were considered (see text). The model with the lowest AIC score is considered to best fit the data.  $K$  is the number of parameters in each model, and  $\Delta AIC_c$  is the difference between each model and the best-fitting one. Models include the individual covariates time since fledging (time), age at fledging (agefledge), date of fledging (fledgedate), shrub cover (shrub), forest management treatment (trt), and fragment size (patchsize).

Model	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
Time + agefledge	3	120.99	0.00	0.198
Time	2	121.30	0.31	0.169
Time + agefledge + shrub	4	121.79	0.80	0.133
Time + shrub	3	121.79	0.80	0.133
Time + agefledge + patchsize	4	122.79	1.81	0.080
Time + fledgedate	3	122.80	1.81	0.080
Time + patchsize	3	122.84	1.85	0.078
Time + fledgedate + shrub	4	123.37	2.38	0.060
Time + fledgedate + patchsize	4	124.28	3.28	0.038
Time + agefledge + trt	6	126.66	5.67	0.011

the transmitters were found buried in a chipmunk burrow or with tooth marks in the plastic casing. One fledgling was observed being preyed upon by a Common Grackle (*Quiscalus quiscula*), and 1 was relocated inside a live Common Garter Snake (*Thamnophis sirtalis*).

Most fledgling mortality occurred in the first 5 days after fledging (Fig. 2A), and the model-averaged regression coefficient ( $\beta_k$ ) that describes the linear effect of time since fledging on survival was  $\beta_{\text{time}} = 1.93 \pm 0.40$  (95% confidence interval [CI]: 1.15–2.71). Seven of our models had an  $AIC_c \leq 2$  of the best-supported model, which indicates that no single model fit the data substantially better than others (Table 4). To evaluate the relative importance of variables, we summed Akaike weights for each variable and compared weightings among variables that were included the same number of times in the model set. Age-at-fledging models had a total weighting of 0.422 and fit the data 2.4 $\times$  better than models parameterized with date of fledging, which suggests little seasonal effect on fledgling survival. The best-fitting model (time + agefledge) had a similar  $AIC_c$  weight to the model parameterized with only time since fledging (Table 4), and fledgling survival did not increase with age at fledging ( $\beta = 0.36 \pm 0.25$ , 95% CI: -0.13 to 0.85).

Although forest structure differed significantly between treatment types (Table 2), fledgling survival did not vary with forest treatment (Table 4). Overall weighting of models that included forest treatment was only 0.01, compared with 0.326 for models with shrub cover and 0.118 for patch size. Although shrub cover had the strongest weighting, fledgling survival did not increase with shrub cover ( $\beta = -0.016 \pm 0.25$ , 95% CI: -0.04 to 0.01).

We examined whether fledglings were found in different habitat than nests and random points within sites (Fig. 3A, B). Canopy cover differed significantly between forest treatments (two-way ANOVA,  $F = 7.20$ ,  $df = 3$  and 4,  $P = 0$ ), and there was a significant interaction between location and forest treatment ( $F = 2.15$ ,  $df = 12$ ,  $P = 0.017$ ). Post hoc comparisons indicated that nests had less canopy cover than random points (Tukey's HSD,  $P = 0.0$ ). Older

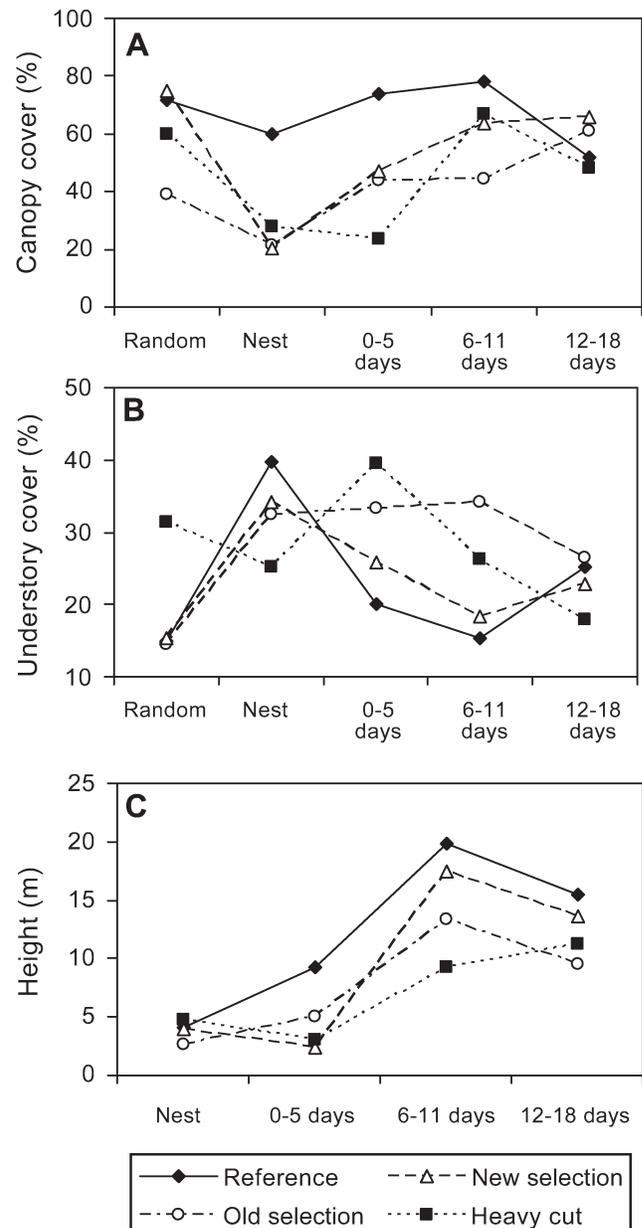


FIG. 3. (A) Canopy cover and (B) understory cover of random sites (1 per fledgling per site), nests, and fledglings (0–5 days, 6–11 days, and 12–18 days after fledging) for different forest management treatments. (C) Height above ground shown for nests and fledglings. Error bars are omitted for clarity.

fledglings occupied areas with higher canopy cover than nests (6–11 days,  $P = 0.0$ ; 12–18 days,  $P = 0.002$ ), but these locations were not significantly different from random sites ( $P = 0.99$ ,  $P = 0.95$ ). Understory cover also differed significantly between random, nest, and fledgling locations ( $F = 2.96$ ,  $df = 3$  and 4,  $P = 0.02$ ; Fig. 3B), but there was no interaction effect with treatment ( $F = 1.38$ ,  $df = 3$  and 4,  $P = 0.18$ ). Nest sites tended to have more understory cover than random locations (Tukey's HSD,  $P = 0.09$ ), but fledgling locations did not differ significantly from either nest sites or random sites

( $P > 0.17$ ). Shrub cover did not vary significantly between random, nest, and fledgling locations ( $F = 0.72$ ,  $df = 3$  and  $4$ ,  $P = 0.58$ ), and post hoc tests found no difference ( $P = 0.94$ ) between shrub cover of nests and fledglings 0–5 days old.

Fledglings became increasingly mobile as they aged and moved significantly higher into the canopy (two-way ANOVA,  $F = 22.3$ ,  $df = 3$  and  $3$ ,  $P = 0.0$ ; Fig. 3C). Young fledglings (0–5 days old) were found at heights similar to or lower than nests ( $< 5$  m), but within a week fledglings were typically found  $\geq 10$  m above ground. As expected, fledglings also moved farther away from the nest as they aged ( $F = 12.6$ ,  $df = 3$  and  $2$ ,  $P = 0.0$ ). Young fledglings (0–5 days old) were usually located  $\sim 50$  m from the nest site ( $48.5 \pm 5.6$  m,  $n = 34$ ), but older fledglings did not remain near the nest (6–11 days:  $136.3 \pm 18.8$  m; 12–18 days:  $228.1 \pm 42.3$  m). Of fledglings that survived to at least 7 days postfledging, 60.7% (17 of 28) moved to a different forest treatment than where the nest had been located. The age of dispersal out of the treatment type was  $14.2 \pm 1.02$  days (range: 7–21 days) postfledging, and little mortality was documented during this period (Fig. 2B). Six of the 17 dispersing fledglings crossed open gaps to a different forest fragment, with a median gap distance of 20 m (range: 20–50 m). Three of these fledglings were not resighted on their original fragment.

For a population to remain stable in size, a breeding female must replace itself in its lifetime, on average. In other words, the average number of female offspring produced per female that survive to become breeders must equal or exceed the average annual female mortality rate. To estimate the productivity and recruitment of Rose-breasted Grosbeaks in our study sites (Table 5), we estimated average female fecundity and multiplied that by fledgling survival and expected annual survival of independent juveniles (Donovan et al. 1995a). The mean number of female offspring per successful nest in 2005–2006 was  $1.6 \pm 0.10$ , which is similar to results of a previous study in this region (Smith et al. 2006). To

calculate average female fecundity, we used the 95% CI of number of female young per successful nest (1.39–1.80) and assumed that females that failed in their first nest attempt would reneest and succeed with similar probability (Table 3). Annual juvenile survival was estimated by multiplying fledgling survival (Fig. 3) by an estimate of the annual survival of independent juveniles based on a range of apparent annual survival rates (0.45–0.60) from other Neotropical migratory songbirds (Cilimburg et al. 2002, Sillett and Holmes 2002, Gardali et al. 2003, Stutchbury et al. 2009). We conservatively assumed that migration and wintering survival of independent juveniles are similar to that of adults. Recruitment rate (number of female offspring that survive to breed) was  $0.22 \text{ female}^{-1} \text{ season}^{-1}$  for the worst-case scenario (using the lower estimates of fecundity and survival) and 0.37 for the best scenario (Table 5).

DISCUSSION

Survival probability during the 3-week fledgling period in Rose-breasted Grosbeaks was 0.62, and daily survival probability of fledglings was strongly influenced by time since fledging. Forest management treatment (reference, selection cut, heavy cut) at the nest site did not have an effect on fledgling survival (Fig. 2A), and daily nest survival (i.e., prior to fledging) also did not differ among forest treatments (Table 3), a result similar to that of an earlier study of Rose-breasted Grosbeaks in the same study area (Smith et al. 2006). Because fledglings were radiotagged by necessity, the possibility remains that the transmitter itself affected survival in the first days out of the nest. However, our fledgling survival rates were comparable to those of other small passerines, and a recent study that documented even higher fledgling mortality radiotagged the parents rather than the young (Rush and Stutchbury 2008).

Fledgling Rose-breasted Grosbeaks had the lowest daily survival probability during the first 5 days after fledging (Fig. 2B), a pattern consistent with results of several studies of other songbirds (Sullivan 1989, Anders et al. 1997, King et al. 2006, Yackel Adams et al. 2006, Rush and Stutchbury 2008). The major cause of fledgling mortality in Rose-breasted Grosbeaks was predation by raptors and mammals. Fledglings are less vulnerable to attack as they age because they become more mobile and begging intensity decreases. In our study, newly fledged young appeared to rely largely on camouflage and parental care to avoid detection by predators. Fledglings would often remain perfectly still and could be approached to within 1 m before an attempt at flight was made (L. Moore et al. pers. obs.). Adults actively defended fledglings and were often agitated and gave alarm calls when we approached fledglings. Older fledglings typically moved vertically into denser and elevated vegetation layers (Fig. 3), which presumably limits the range of predators to which they are vulnerable.

Forest management appears to have little effect on nesting success (Smith et al. 2006; Table 3) or fledgling survival (Fig. 2A) in Rose-breasted Grosbeaks, even though forest treatments differed significantly in a suite of vegetation measures (Table 2). Logging creates gaps that increase structural heterogeneity on a site, which may be selectively utilized by fledglings to increase the probability of survival regardless of forest management treatment. King et al. (2006) found that fledgling Ovenbirds (*Seiurus*

TABLE 5. Population productivity estimates for Rose-breasted Grosbeaks breeding in forest fragments that were subject to different forest management treatments in southwestern Ontario (2005–2006). Adult and juvenile annual survival rates are unknown for this population; therefore, juvenile survival and recruitment are given as ranges based on a range of adult annual survival (0.45–0.60) in other Neotropical migratory songbirds (Cilimburg et al. 2002, Sillett and Holmes 2002, Gardali et al. 2003, Stutchbury et al. 2009).

Forest treatment	Female fecundity <sup>a</sup>	Fledgling survival probability	Juvenile annual survival <sup>b</sup>	Annual recruitment <sup>c</sup> (number of females)
Reference	0.79–1.03	0.64	0.28–0.38	0.22–0.39
Old selection	0.71–0.93	0.60	0.27–0.36	0.19–0.33
New selection	0.80–1.03	0.57	0.26–0.34	0.21–0.35
Heavy cut	0.82–1.06	0.63	0.28–0.38	0.23–0.41
Combined	0.78–1.01	0.62	0.28–0.37	0.22–0.37

<sup>a</sup>95% confidence interval of the mean number of female offspring per female per year, based on an average of  $1.6 \pm 1.0$  (SE) female nestlings per successful nest and nest success rate (Table 3), assuming one reneesting attempt for failed nests.

<sup>b</sup>Fledgling survival probability multiplied by annual survival of independent juveniles (assumed to be equal to annual adult survival).

<sup>c</sup>Female fecundity multiplied by juvenile annual survival for the worst-case scenario (lower estimate of fecundity and survival) and best-case scenario.

*aurocapilla*) selected different habitat from that used by breeding adults, preferring denser cover and protection from predators. Adult Rose-breasted Grosbeaks are known to select nest sites that are relatively low in canopy cover and high in understory cover (Smith et al. 2006). Young fledglings are most vulnerable to mortality, and we did not find that fledglings preferred areas with high shrub or understory cover compared with the nest location. Older fledglings occupied areas of higher canopy cover than nests (Fig. 3A), but fledgling locations were more similar to random points than were nest sites. Fledglings at all sites moved higher into the subcanopy and canopy within a week of fledging (Fig 3C), which may afford them greater concealment from predators and effectively eliminate the influence of vegetation structure and forest treatment on fledgling survival.

Many forest songbird species vary in productivity at the site level, such that source–sink conditions exist between populations in different forest patches (Donovan et al. 1995b, Robinson et al. 1995). For some species, conservation may require identification and protection of source habitat and management of sink habitats to improve productivity. With few exceptions, determination of source–sink forest fragments has been based on population density and nesting success, rather than estimates of fledgling survival (Anders et al. 1997). We estimated the source–sink status of forest fragments managed at different harvest intensities using nesting success and fledgling survival estimates. Annual population productivity for all sites combined was estimated at 0.22–0.37 female recruits per breeding female per year (Table 5), which is lower than the expected annual mortality rate of breeding females (0.40–0.55; Cilimburg et al. 2002, Sillett and Holmes 2002, Gardali et al. 2003, Stutchbury et al. 2009). Even reference sites did not produce enough offspring to offset annual female mortality, which suggests that forest fragments in this region are population sinks. Low regional forest cover, rather than selective logging per se, is likely contributing to population declines of Rose-breasted Grosbeaks in this region.

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