EFFECTS OF SINGLE-TREE SELECTION HARVESTING ON ROSE-BREASTED
GROSBEAKS (PHEUCTICUS LEUDOBICIANUS) IN A PREDOMINANTLY
FORESTED LANDSCAPE

by

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A thesis submitted in conformity with the requirements
for the degree of Doctor of Philosophy, Faculty of Forestry
University of Toronto

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Effects of Single-tree Selection Harvesting on Rose-breasted Grosbeaks (*Pheucticus leudovicianus*) in a Predominantly Forested Landscape

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ABSTRACT

Single-tree selection harvesting is frequently used in the tolerant hardwood forests of North America but relatively little is known about how this silvicultural system affects wildlife, including many avian species. I investigated Rose-breasted Grosbeak (*Pheucticus leudovicianus*) habitat use, survival, and nestling provisioning behaviour in twelve hardwood stands in Algonquin Provincial Park which had been harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years previously. Density, pairing success, and the number of fledglings per successful nest were all significantly lower in the > 50 years post-harvest stands than in at least one other post-harvest treatment. Density and pairing success were significantly higher in the 16-20 year post-harvest stands than in other treatments. Neither nest nor fledgling survival differed significantly among post-harvest treatments, but all stands were population sinks except those cut 16-20 years previously. Nests that were initiated earlier in the season and built in areas with higher basal area were more likely to survive, whereas fledgling survival increased with days since fledging. Nest sites had higher cover from regenerative growth, saplings, and understory, and lower basal area than random locations. During their first week out of the nest, fledglings used locations with significantly higher cover from regenerative growth, saplings, small shrubs, and raspberry and elderberry bushes than were present at
random locations. Habitat characteristics at nest and fledgling locations were
significantly different, and estimates of nest and fledgling survival were not correlated
among harvested stands. Nests attended by after-second-year (ASY) males were initiated
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contribution to nestling provisioning and nest attendance, and mean nestling weights at
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nests with SY males. This study found that single-tree selection did not have significant
negative effects on Rose-breasted Grosbeaks breeding in a predominantly forested
landscape, but like many other species of birds, experienced breeders were more
successful than less experienced breeders were.
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GENERAL INTRODUCTION

BACKGROUND

With 347.7 million hectares of forested land, Canada is home to 10% of the world’s forests and 30% of the world’s boreal forest (Natural Resources Canada 2010). Forested land in this country encompasses twelve forest regions (Rowe 1972), with the boreal forest as the most extensive, followed by the Great Lakes – St. Lawrence. The Great Lakes – St. Lawrence is a transitional forest zone located between the boreal forest to the north and the deciduous Carolinian forest to the south. It stretches from southeastern Manitoba to the Gaspé, with a gap along the northern shores of Lakes Superior (Natural Resources Canada 2010), and together with the deciduous forest region it contains the tolerant hardwood forest. Hardwood forests are common in the Acadian region of northern New England and New York, the upper Midwest, and the Maritime provinces of Canada (Seymour et al. 2002). In Ontario, tolerant hardwood forests that consist primarily of sugar maple (Acer saccharum), American beech (Fagus grandifolia), and yellow birch (Betula alleghaniensis) cover 3.6 million hectares and provide approximately 3.2% of the total provincial timber harvest (OMNR 1998). Much of this type of forest is directly affected by anthropogenic activities, such as urbanization and logging.

Forest management in North America has recently shifted away from practices designed solely to maximize timber yield towards a more ecosystem-based approach (Kohm and Franklin 1997). Within this framework the focus has been on developing and implementing economically, socially, and ecologically sustainable management practices. Efforts to achieve ecological sustainability have mainly taken the form of management
practices designed to emulate natural disturbance patterns (Perera et al. 2000, Seymour et al. 2002). In the boreal forest, even-aged silvicultural systems are most often used to emulate the large-scale disturbances characteristic of this region such as fire and wind storms (Perera et al. 2000). In contrast, in tolerant hardwood forests of North America, uneven-aged systems, such as shelterwood or selection cutting are the recommended methods of harvesting (Arboglast 1957, Franklin 1989, OMNR 2000). Disturbances in this region are typically small in scale, removing individual or small groups of trees through insect outbreaks, ice or wind storms, or natural senescence.

The selection harvesting system involves removing individual trees or small groups of trees once every 8-25 years (Hunter 1990, OMNR 2000, Seymour et al. 2002). Tree marking guidelines and targets for the residual basal area to be retained in maple dominated forests under the selection system are very similar for the Great Lakes jurisdictions (OMNR 1998), Michigan (Tubbs 1977), and Wisconsin (WDNR 2011), but they vary according to stand condition and type. In the maple and beech dominated hardwood forests of the Great Lakes region, no more than one third of the basal area for a stand is removed per entry, and a residual basal area of 16 m$^2$/ha of $>$ 24 cm dbh trees or 20 m$^2$/ha of $>$ 9 cm dbh trees is generally considered appropriate (OMNR 1998, Tubbs 1977, WDNR 2011). The removal of trees during harvesting creates many small gaps or perforations in the canopy which encourage natural regeneration by allowing more light to reach the understory layers (Robinson and Robinson 1999). In the first few years after harvesting stands typically have abundant regenerative growth, low basal area, and sparse sapling, understory, and canopy layers (Robinson and Robinson 1999, Flaspohler et al. 2002, Jobes et al. 2004). By 16-20 years after harvesting, a dense understory layer often
forms as shade-tolerant species such as sugar maple and American beech develop (Finegan 1984, Jobes et al. 2004). As the understory layer grows into the canopy, managed stands develop higher basal area, abundant cover in the seedling, regenerative growth, sapling, and canopy layers, and higher spatial complexity typical of un-harvested hardwood stands (Robinson and Robinson 1999, Kenefic and Nyland 2000, Crow et al. 2002, Flaspohler et al 2002, Jobes et al. 2004, Angers et al. 2005, Vanderwel et al. 2006).


Studies of avian demography in harvested hardwood forests are less prevalent than studies of community composition, but several studies have detected differences in
reproductive success (Yahner 2000, Barber et al. 2001, Duguay et al. 2001, Robinson and
Dellinger et al. 2007, Cooper et al. 2009, Poulin et al. 2010) and density (Rodewald and
Silvicultural practices can also affect nest predator communities (Medin and Booth 1989,
Pettersson et al. 1995, Harris and Reed 2002) and prey availability (Morse and Robinson

Although we know a little about how silviculture influences nest survival, much
less is currently known about habitat use and survival of fledglings in managed forests.
Habitat requirements of breeding adults may be different from those of family groups
during the post-fledging period (Rappole and Ballard 1987, Anders et al. 1998, Vega
Rivera et al. 1998, Cohen and Lindell 2004, King et al. 2006). For instance, dense cover
near the ground and in the sapling and understory layers may provide important cover for
the fledglings of many species regardless of the nest site characteristics selected by
adults. Since the offspring of many songbirds spend up to eight weeks on the breeding
grounds prior to migration (Anders et al. 1998), and fledgling survival strongly influences
population growth rates (Porceluzi and Faaborg 1999, Powell et al. 1999, Woodworth et
al. 1999), assessing the impact of silvicultural practices on fledglings is important.

So far, to my knowledge only one study has investigated the survival of songbird
fledglings in selection-harvested forests. This study, which was conducted in a
fragmented agricultural landscape, did not detect significant differences in juvenile
survival among harvested and un-harvested forest stands (Moore et al. 2010). No studies
have yet been done on fledgling survival in managed hardwood forests in predominantly forested landscapes, and since silviculture may affect avian populations differently in agricultural and forested landscapes (Sallabanks et al. 2000, Thompson et al. 2000), further research is necessary.

**STUDY SPECIES**

The Rose-breasted Grosbeak (Aves: Passeriformes: Cardinalidae: *Pheucticus leudovicianus*) is a Neotropical migratory songbird that breeds across much of eastern and central North America and over winters in central and south America (Wyatt and Francis 2002). Although this species is still relatively abundant, it has been declining at an annual rate of -0.8% across North America since 1966 (Sauer et al. 2008). In Ontario, Rose-breasted Grosbeaks have been declining at a rate of approximately -2.4% per year between 1966 and 2007 (Sauer et al. 2008), with an especially sharp decline of – 8.0% per year between 1985 and 2005 (Cadman et al. 2007). This species provides a good opportunity to study the effects of harvesting because, despite its declining numbers, it is still abundant enough in the landscape to allow detection of changes in relation to management practices.

Rose-breasted Grosbeaks nest in primary and secondary mixed and deciduous forests, as well as in thickets, scrublands, urban parks, gardens, and other areas which have been subject to anthropogenic disturbances (Wyatt and Francis 2002). The Rose-breasted Grosbeak is often found in regenerating forests following harvesting, and in some cases this species is more abundant in logged areas than in un-harvested ones (Holmes et al. 2004, Jobes et al. 2004, Doyon et al. 2005, Guénette and Villard 2005).
Although we know that Rose-breasted Grosbeaks tend to nest in the sapling and understory layers, one study found that they use locations with more canopy cover but lower sapling cover than random locations (Smith et al. 2007), whereas others suggest they prefer areas with relatively open canopy and sub-canopy layers (Wyatt and Francis 2002). Apart from studies in fragmented agricultural landscapes (Smith et al. 2006, 2007, Moore et al. 2010), little is known about Rose-breasted Grosbeak ecology, or how changes in forest structure resulting from silviculture influence the availability or selection of nest sites, the foraging behaviour, or the ability of this species to successfully raise its young once they leave the nest.

Rose-breasted Grosbeaks typically arrive on their breeding grounds in central Ontario during the first week of May, and nest initiation commences two weeks later. Both males and females participate in nest building, incubating, brooding, and nestling provisioning, with the males providing approximately one third of the incubation, half of the brooding, and 25-30% of the nestling provisioning (Wyatt and Francis 2002). Although bi-parental care is common in birds, in many migratory songbird species the females typically do all or most of the incubating and brooding, as well as providing much of the nestling provisioning (Stodola et al. 2010). Male Rose-breasted Grosbeak’s relatively high contribution to parental care may make this species more resilient to habitat alterations than other songbirds, because the trade-off between nest defence and foraging may be less severe. For example, if females must spend more time away from the nest foraging in altered habitats, Rose-breasted Grosbeak males can incubate and defend the nest in their absence, whereas in other species the nest may be left unattended for longer periods and be more likely to be lost to predators. However, since this species
is declining, and various forms of silviculture are implemented throughout its entire breeding range in North America, it is important to assess the effectiveness of current forest management guidelines for maintaining good quality habitat for Rose-breasted Grosbeaks.

**STUDY RATIONALE**

Changes in Rose-breasted Grosbeak abundance following harvesting have appeared in a number of silvicultural studies from across North America, with mixed results. Rose-breasted Grosbeak abundance increased following single-tree selection harvesting in the northern hardwood forests of Quebec (Doyon et al. 2005) and Ontario (Jobes et al. 2004), partial harvesting in the deciduous forest fragments of southwestern Ontario (Holmes et al. 2004), and silvicultural treatments of various intensities in New Brunswick (Guénette and Villard 2005). However, decreases in abundance were observed in response to selection harvesting and high-grading in fragmented Carolinian forests (Smith et al. 2006, Thompson et al. 2009) and to partial harvesting in boreal forests (Vanderwel et al. 2007, 2009). Other studies detected no statistical difference in abundance following harvesting (Duguay et al. 2001, Holmes and Pitt 2007). Studies of nest survival and productivity, which might provide insight into the inconsistent nature of these responses and help identify silvicultural practices that maintain or improve habitat for Rose-breasted Grosbeaks are still relatively rare.

Most research on Rose-breasted Grosbeak demography has been conducted in the highly fragmented Carolinian forest of southwestern Ontario (Smith et al. 2006, 2007, Moore et al. 2010). In the hardwood forest fragments of this agricultural landscape,
single-tree selection did not significantly affect nest survival (Smith et al. 2006, Moore et al. 2010), but density, nest success, and the ratio of after-second-year to second-year males were slightly lower in the harvested stands than in the un-logged ones (Smith et al. 2006). Fledgling survival in these stands was not significantly affected by harvesting, but it too was slightly lower in the harvested stands (Moore et al. 2010). In this landscape, both harvested and un-harvested stands were classified as population sinks (Smith et al. 2006, Moore et al. 2010). Although single-tree selection harvesting did not appear to significantly alter Rose-breasted Grosbeak survival in forest fragments, no information is available for predominantly forested landscapes. Some songbird populations are above replacement levels in predominantly forested landscapes and large forest fragments but below replacement levels in smaller fragments (Burke and Nol 2000, Falk et al. 2011), suggesting that it is important to investigate the impacts of anthropogenic activities on reproductive success in different landscape contexts. In particular, since a considerable portion of the Rose-breasted Grosbeak’s breeding range falls within managed forest landscapes, it is important to assess whether harvesting affects this species differently in predominantly forested landscapes than in fragmented agricultural ones.

To address this knowledge gap, in this thesis I investigate Rose-breasted Grosbeak habitat use in tolerant hardwood stands harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years previously in the predominantly forested landscape of Algonquin Provincial Park, Ontario, Canada. Algonquin Park was logged for white pine (Pinus strobes) in the 1800’s and for hemlock (Tsuga canadensis) and yellow birch (Betula alleghaniensis) during the 1930’s and 1940’s (Tozer and Strickland 1980). Since 1974 approximately 12% of the park has been designated as a Wilderness Zone where no
logging activity occurs. The remaining forested area of the park (57% of its area) is
managed for timber production at a rate of approximately 2% per year (Ontario Parks
1998). Stands that consist of > 60% hardwood species have been harvested using the
selection system since the 1970’s, and some have now been regenerating long enough to
allow a second harvest entry.

I used a chronosequence or space-for-time substitution approach (reviewed in
Fukami and Wardle 2005) to study succession following single-tree selection harvesting
in tolerant hardwood stands, and to look at its long-term consequences for Rose-breasted
Grosbeaks. I chose stands that were 0-5, 16-20, and 21-25 years post-harvest to
investigate three stages in the harvest rotation. The 21-25 years post-harvest stands were
chosen to provide insight into forest conditions at the stage when a second harvest is
typically carried out, to see if forest structure and reproductive output of Rose-breasted
Grosbeaks had returned to “pre-harvest” levels. There is some concern that if
regeneration times are not long enough, cumulative changes could occur. The > 50 years
post-harvest stands were chosen to approximate “un-logged” or “pre-harvest” conditions
which could be used as a reference point against which to evaluate more recently logged
stands because completely unlogged, primary growth hardwood stands were unavailable
in my study area within the park.

Chapter one examines whether Rose-breasted Grosbeak density, pairing success,
population age structure, nest initiation date, clutch size, nest survival, and productivity
differed with time since selection harvesting. Chapter two investigates important habitat
characteristics at nest sites and locations used by fledglings, tests whether these
characteristics differ among post-harvest treatments, and investigates which habitat
variables have the strongest influence on nest and fledgling survival. Chapter three tests whether nestling provisioning rates, prey load sizes, male contributions to nestling provisioning and nest attendance, and nestling weights differed with time since single-tree selection harvesting, stage of nestling development, or age of male parent. Finally, I end with a general discussion on the relevance of these findings to current forest management practices in the tolerant hardwood forests of North America.

I expected considerable changes in forest structure following single-tree selection harvesting, and that as a result of these alterations vegetation characteristics at nest sites and locations used by fledglings would significantly differ among post-harvest treatments. Stands harvested by single-tree selection 16-20 years previously typically have well developed sapling and understory layers, which appear to be preferentially selected by Rose-breasted Grosbeaks. As a result, I predicted that these stands would have higher densities, a greater proportion of after-second-year males, earlier nest initiation dates, higher pairing success, larger clutch sizes, higher nest survival rates, and greater productivity. I also expected that nestling provisioning would be more frequent and/or larger prey loads would be provided to nestlings in these stands and that nestlings would be heavier on average than in the other post-harvest treatments and the uncut stands.
CHAPTER 1: DEMOGRAPHY OF ROSE-BREASTED GROSBEAKS IN STANDS HARVESTED BY SINGLE-TREE SELECTION

ABSTRACT

Single-tree selection harvesting is frequently used in the tolerant hardwood forests of North America, but little is known about how it affects the reproductive success of migratory songbirds. Many songbirds that breed in this forest type, including the Rose-breasted Grosbeak (*Pheucticus leucopsis*) are currently experiencing population declines across their breeding ranges. I studied the demography of Rose-breasted Grosbeaks in twelve tolerant hardwood stands in the predominantly forested landscape of Algonquin Provincial Park. Nine stands had been harvested by single-tree selection 0-5, 16-20, or 21-25 years previously, and three had remained un-harvested for > 50 years. My main objectives were to test whether density, pairing success, population age structure, nest initiation date, clutch size, nest survival and productivity differed with time since single-tree selection harvesting. My secondary objective was to determine whether any of these demographic parameters varied between after-second-year (ASY) and second-year (SY) breeders. Analysis of variance indicated that density, pairing success, and the number of fledglings per successful nest were all significantly ($P < 0.05$) lower in the > 50 years post-harvest stands than in at least one other post-harvest treatment, as were clutch size, nest survival, and productivity, although not significantly so. The proportion of ASY males compared to SY males was highest in the > 50 years post-harvest stands and lowest in the 21-25 years post-harvest treatment. Density, pairing success, and productivity were all highest in the 16-20 years post-harvest treatment, and density and pairing success were significantly so. Nests attended by ASY males were
initiated significantly earlier than nests attended by SY males, and territory density and productivity were significantly higher for ASY males than SY males. Habitat characteristics did not vary significantly between nests attended by ASY and SY males. This study found that single-tree selection did not have significant negative effects on the reproductive success of Rose-breasted Grosbeaks in predominantly forested landscapes, but that all post-harvest treatments were population sinks except the 16-20 years post-harvest stands, indicating that further research into the causes of this species’ decline is necessary.
INTRODUCTION

Over half (57%) of the Neotropical migratory bird species that breed in eastern North America have been experiencing broad-scale population declines over the past forty years (Kirby et al. 2008). Habitat loss, fragmentation, and degradation are among the most frequently cited causes of declines in migratory songbirds (Donovan and Flather 2002, Sauer et al. 2007, Poulin et al. 2010). Changes in land-use, together with forest management policies intended to suppress natural disturbances such as wildfire, flooding, and insect outbreaks have also reduced the amount of habitat available for some species (Askins 1993, Brawn et al. 2001, Trani et al. 2001, Brooks 2003, DeGraaf and Yamasaki 2003). Concern over avian population declines has led to research investigating the potential effects of forest management practices on forest breeding birds (Duguay et al. 2001). In North America, uneven-aged harvesting practices, such as the shelterwood and selection systems, are becoming more prevalent in mixed and tolerant hardwood forests, because they are believed to mimic natural patterns of small-scale disturbances characteristic of these forest types (Tubbs 1977, OMNR 2000, Seymour et al. 2002). In Ontario, Canada these practices account for 13% of annual provincial harvests, and they are mostly applied in the Great Lakes – St. Lawrence forest region (Cadman et al. 2007).

Single-tree and group selection harvesting produce uneven-aged stands through the removal of individual or small groups of trees every 15-25 years (Tubbs 1977, Hunter 1990, Seymour et al. 2002). Although single-tree selection emulates natural disturbance patterns in mature hardwood forests better than some large-scale, even-aged silvicultural techniques (Hunter 1990, Seymour et al. 2002), considerable changes in forest structure occur in the years following harvesting. For example, recently logged stands typically have abundant regenerative growth, low basal area, and sparse cover in the sapling,
understory, and canopy layers (Robinson and Robinson 1999, Flaspohler et al. 2002, Jobes et al. 2004). However, increased light penetration immediately following harvesting promotes the development of shade-tolerant sugar maple and American beech seedlings, which form a dense understory layer by about 15 years after harvesting (Finegan 1984, Jobes et al. 2004). As the understory layer grows into the canopy, managed stands eventually approach pre-harvest conditions, which are characterized by high basal area, abundant cover in the seedling, regenerative growth, sapling, and canopy layers, and high spatial complexity (Robinson and Robinson 1999, Kenefic and Nyland 2000, Crow et al. 2002, Flaspohler et al. 2002, Jobes et al. 2004, Angers et al. 2005, Vanderwel et al. 2006).

experiencing lower rates of nest success in harvested forests (Robertson and Hutto 2007, Poulin et al. 2010). Differing responses to selection harvesting among avian species suggests that a more complete understanding of the link between forest management and avian population growth is important for identifying management practices that maintain good quality habitat for wildlife, and are therefore ecologically sustainable.

Since reproductive success can be reduced in areas with high densities of birds (Arcese and Smith 1988, Vickery et al. 1992), and populations can persist in areas even when reproductive rates are low (Brawn and Robinson 1996), abundance estimates alone are generally not considered sufficient indicators of habitat quality. The ideal free distribution model assumes that individuals will occupy habitats in proportion to their quality, with better habitats supporting more individuals (Fretwell and Lucas 1970, Fretwell 1972). However, recent (Schmiegelow et al. 1997) or unpredictable (Van Horne 1983) disturbances such as logging can influence avian abundances in forested habitats. Unreliable indicators of habitat quality (Remes 2003, Weldon and Haddad 2005, Nordby et al. 2009), past reproductive success (Haas 1998, Citta and Lindberg 2007), perceived predation risk (Morton 2005, Fontaine and Martin 2006), and social cues (Doliquez et al. 2004, Fletcher 2007, Seppänen et al. 2007, Ahlering et al. 2010) can also influence how birds select territories. As a result, despite recent evidence that density may be an adequate indicator of avian productivity in some hardwood forest regions (Underwood and Roth 2002, Bock and Jones 2004, Perot and Villard 2009), additional measures of demography should be included in assessments of habitat quality in managed areas (Sallabanks et al. 2000).
Age-related differences in acquisition and defence of high quality territories (Catterall et al. 1989; Donovan and Stanley 1995, Pärt 2001) may also cause a decoupling of the predicted positive relationship between density and productivity, with older, more experienced birds out-competing younger ones and monopolizing resources (Donazar and Feijoo 2002). In some species, nest initiation date, clutch size (Reynolds 1997), nest survival (Forschler and Kalko 2006), and number of fledglings per successful nest (Préault et al. 2005, Brown and Roth 2009) are influenced by the age of the breeding adults. Age-related differences in reproductive success may occur because: 1) inferior phenotypes, which have lower success, experience high mortality at young ages, 2) younger individuals postpone breeding until they can accumulate sufficient resources, 3) reproductive output increases as reproductive value decreases with age, or 4) parental skills improve with age (Forslund and Pärt 1995, Martin 1995, Espie et al. 2000, Balbontin et al. 2007). Regardless of which hypothesis is supported, if older birds are more successful at obtaining and defending territories in preferred habitats, then the ratio of older birds to younger birds could be used to assess which habitats are perceived as most desirable by breeding individuals. In addition, if older birds experience higher reproductive success than younger birds, areas with higher proportions of experienced individuals may be more productive overall. Clarifying how population age structure influences productivity is useful for better understanding the effects of anthropogenic activities.

The Rose-breasted Grosbeak (*Pheucticus leudovicianus*) is a Neotropical migrant that breeds in both harvested and un-harvested hardwood forests across North America (Wyatt and Francis 2002, Smith et al. 2006). This early-successional forest species
(Drapeau et al. 2000) uses interior and edge habitats (Freemark and Merriam 1986, Merrill et al. 1998) as well as managed forests with high tree density, extensive sapling and shrub cover, and well-developed understory layers (Webb et al. 1977, Possardt and Dodge 1978). Although Rose-breasted Grosbeaks utilize features of regenerating forests, responses to harvesting have been mixed. Estimates of abundance are typically higher in recently harvested stands than in less recently cut (Holmes et al. 2004, Jobes et al. 2004, Doyon et al. 2005) or unlogged stands (Jobes et al. 2004, Doyon et al. 2005), and Rose-breasted Grosbeaks have responded positively to silvicultural treatments of various intensities in New Brunswick (Guénette and Villard 2005). However, decreases in abundance were observed in response to selection harvesting and high-grading in fragmented Carolinian forests (Smith et al. 2006, Thompson et al. 2009) and to partial harvesting in boreal forests (Vanderwel et al. 2007, 2009), whereas other studies detected no statistical difference in abundance following harvesting (Duguay et al. 2001, Holmes and Pitt 2007). Density of territorial males and the ratio of after-second-year to second-year males were also lower in harvested stands than in un-harvested ones in the fragmented landscape (Smith et al. 2006). No information on most demographic parameters is available for Rose-breasted Grosbeaks nesting in predominantly forested landscapes, even though approximately 40% of its range falls within relatively unfragmented forests. A better understanding of how silviculture influences Rose-breasted Grosbeaks is necessary because this species is currently experiencing population declines throughout its breeding range across central and eastern North America (Smith et al. 2006, Cadman et al. 2007, Sauer et al. 2008).
Here, I examined whether changes in habitat structure resulting from single-tree selection harvesting influenced the density, population age structure, pairing success, nest initiation dates, and productivity of Rose-breasted Grosbeaks. I predicted that density and productivity would be higher in stands harvested 16-20 years previously than in more recently harvested stands or un-logged ones due to the presence of relatively well-developed sapling and understory layers that appear to be preferentially selected by grosbeaks (Wyatt and Francis 2002). I also expected that older, after-second-year males would out-compete second-year males in these stands and that the older males would experience higher reproductive success. As a result, I predicted that 16-20 years post-harvest stands would have higher densities and greater proportions of after-second-year males, and that the older, more experienced breeders would have earlier nest initiation dates, higher pairing success, larger clutch sizes, nest survival rates, and greater productivity than younger, less experienced males.

METHODS

Study Species

The Rose-breasted Grosbeak is a relatively abundant Neotropical migrant that over winters in central and South America and breeds in first- and second-growth mixed and deciduous forests throughout much of central and eastern North America (Wyatt and Francis 2002). Rose-breasted Grosbeaks typically arrive on their breeding grounds in central Ontario during the first week of May, where they begin establishing territories ranging from 0.34 – 1.3 ha (mean = 0.77 ha) (Wyatt and Francis 2004). Nesting attempts typically commence during the last two weeks of May (Smith et al. 2006). Incubation
takes 12-13 days, and fledging occurs 9-12 days after the eggs hatch (Wyatt and Francis 2002). Most pairs only raise one brood per season, but double-brooding may occasionally take place (Wyatt and Francis 2002).

**Study Area**

Nest monitoring and territory mapping of Rose-breasted Grosbeaks was carried out in twelve tolerant hardwood stands in Algonquin Provincial Park, Ontario, Canada (45° 34’N, 78°04’W; Fig. 1.1) in 2006-2008. The higher-elevation west side of this 775,000 ha park consists primarily of mixed hardwood forest, whereas the lower-elevation east side is dominated by white and red pine (Ontario Parks 1998). The tolerant hardwood stands I studied were located in the central and southern part of the park (mean nearest neighbour distance of stands = 9.3 km, range = 1.0 – 34.2 km), which has been harvested using the single-tree selection system since the early 1970’s (OMNR 1998). This type of forest management removes approximately one-third of the over-story basal area every 15-25 years, resulting in uneven-aged stands with a mix of canopy gaps, regenerative growth, and mature trees (OMNR 1998). Stands used in this study were dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), and yellow birch (*Betula alleghaniensis*) and they represented four stages in the cutting cycle: 0-5, 16-20, 21-25, and > 50 years post-harvest. Three stands (mean stand size = 34 ha) from each post-harvest treatment were studied (Table 1.1).
Figure 1.1. Map of sites used to study the effects of single-tree selection on the demography of Rose-breasted Grosbeaks in Ontario, Canada. The grey polygon indicates Algonquin Provincial Park and the numbers associated with each site indicate number of years post-harvest. Solid triangles = 0-5 years post-harvest stands, solid squares = 16-20 years post-harvest stands, solid hexagons = 21-25 years post-harvest stands, and unfilled circles = > 50 years post-harvest stands.
TABLE 1.1. Locations and characteristics of the twelve tolerant hardwood stands in Algonquin Provincial Park, Ontario, Canada that were investigated in this study.

<table>
<thead>
<tr>
<th>Site Code</th>
<th>County</th>
<th>UTM co-ordinates</th>
<th>Last harvest year</th>
<th>Post-harvest treatment (years since harvest)</th>
<th>Searched area (ha)</th>
<th>Basal area (m²/ha)</th>
<th>Percent sugar maple (Mh)¹</th>
<th>Percent American beech (Be)¹</th>
<th>Percent other tree species (Sp)¹²</th>
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<tbody>
<tr>
<td>CT</td>
<td>Nipissing</td>
<td>716200 5068315</td>
<td>2004.5</td>
<td>0-5</td>
<td>32</td>
<td>22.1</td>
<td>80.0</td>
<td>20.0</td>
<td>0.0</td>
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<td>LC</td>
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<td>41</td>
<td>19.2</td>
<td>41.7</td>
<td>20.8</td>
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<td>YO</td>
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<td>713676 5015892</td>
<td>2000.5</td>
<td>0-5</td>
<td>38</td>
<td>23.9</td>
<td>39.1</td>
<td>17.4</td>
<td>43.5</td>
</tr>
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<td>714035 5018042</td>
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<td>16-20</td>
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<td>26.7</td>
<td>50.0</td>
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<td>712007 5074748</td>
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<td>16-20</td>
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<td>26.3</td>
<td>46.1</td>
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<td>15.4</td>
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<td>21-25</td>
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<td>30.0</td>
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<td>43</td>
<td>30.5</td>
<td>37.5</td>
<td>25.0</td>
<td>37.5</td>
</tr>
</tbody>
</table>

¹Percentage of each tree species in prism sweeps at randomly located plots within each stand

²Other tree species consisted primarily of yellow birch, black cherry, striped maple, eastern hemlock, and balsam fir
Habitat Measurements

I measured habitat characteristics in 5 m radius, circular plots in 170 randomly selected locations within my 12 post-harvest stands between 2006 and 2008. In each year, the number of random plots surveyed in each stand was equal to the number of nests monitored in that stand, providing an average of 13 plots/stand and 43 plots/treatment over the three years. Survey plots were selected using a set of randomly generated UTM co-ordinates in each site, and GPS units were used to locate the coordinates on the ground. No restrictions were placed on the locations of plots, as long as they fell within the stand boundaries. Vegetation layers were measured using a modified version of the James and Shugart (1970) method. At each survey plot, percent cover by 1) forbs/grasses/ferns, 2) regenerative growth (woody growth 0.5-1.3 m tall), 3) saplings (>1.3 m tall, <2.5 cm dbh), 4) understory (≥ 2.5 cm dbh, <10.0 cm dbh), 5) sub-canopy (>10-20 m tall), and 6) canopy (>20 m tall) were visually determined, and basal area (m²/ha) was measured using a 2-factor cruising prism.

Nest Monitoring

I visited each stand once every 3-4 days to search for nests. When a nest was located, a piece of coloured flagging tape was placed within 10 m of the nest and its geographical co-ordinates were taken using a GPS unit. I then monitored nests using a mirror attached to a telescoping pole every 3-4 days to determine nest initiation date, clutch size, hatch date, number of nestlings, and number of fledglings per nest. Mean values for nest initiation date, clutch size, number of fledglings per successful nest, and number of fledglings per nest were calculated for each stand. Whenever possible, exact
dates for nest initiation, hatching, and fledging were confirmed by nest checks, but in other instances (e.g., canopy nests) published lengths for nest building (4 days), incubation (12 days), and nestling development (10 days) were used to help calculate important dates (Scott 1998). The number of eggs present in 12 of 52 (23.1%) nests could not be visually confirmed, so clutch size was estimated using the mean number of eggs per nest in the stands where these twelve nests were located. I did not include nests that were initiated on or after June 3\textsuperscript{rd} in my analysis of nest initiation dates (range = May 18\textsuperscript{th} – June 2\textsuperscript{nd}) due to uncertainty as to whether they were first attempts or not. I calculated nest survival for each stand using the Mayfield method (Mayfield 1975).

**Density and Pairing Success**

In 2007 and 2008 I estimated the density of breeding Rose-breasted Grosbeaks in each stand using a modified version of the spot mapping technique (Bibby et al. 2000). I marked the locations of all Rose-breasted Grosbeaks that were seen or heard during nine visits to all stands between May 10\textsuperscript{th} and June 2\textsuperscript{nd} using a Global Positioning System (GPS). I stopped mapping on June 2\textsuperscript{nd} due to uncertainty in determining whether individuals observed after this point had relocated after initial nest attempts in other locations (Bibby et al. 2000, Dunford and Freemark 2005). Males that were observed in the same location on three or more occasions were considered territorial. In territories where no nest was located, a male was assumed to be paired if a female was observed in his territory on at least one occasion, and unpaired if no female was observed after a total of 90 minutes of observation during one or more observation periods (Bibby et al. 2000).
The proportion of after-second-year (ASY) males relative to second-year (SY) males was also calculated in each stand by recording the age category of each singing male that was mapped over the course of the season. ASY males can be visually distinguished from SY males by their uniformly black primaries, black heads and backs, and well-defined markings (Pyle 1997). In contrast, the head and back of SY males are often streaked with brown, there is contrast between their all-brown or partially-brown primaries and their darker greater coverts, and overall their markings are much less distinct (Pyle 1997). I calculated density (no. males/ ha) and pairing success (no. paired males / total no. males) for each stand.

Population Productivity

I calculated two different measures of productivity. The first measure was used to assess the mean number of Rose-breasted Grosbeak fledglings produced per active nest in each post-harvest treatment (0-5, 16-20, 21-25, and > 50 years post-harvest).

For the second measure of productivity, I estimated whether population growth rates were above or below replacement levels in each harvest treatment. For a population to be self-sustaining, the annual female mortality rate must not exceed the average number of female offspring produced per female that survive to breed (Ricklefs 1973, Pulliam 1988, Donovan et al. 1995). In other words, the long-term change in population size ($\lambda$) must be $\geq 1$. I calculated the finite rate of increase for Rose-breasted Grosbeaks in each post-harvest treatment using a two-age-class matrix population model in the Microsoft Excel add-in program PopTools version 3.2.3 (Hood 2010). Confidence
intervals for population $\lambda$ were calculated using the bootstrapping technique with 100 iterations in the PopTools program.

The two-age-class model for calculating $\lambda$ incorporates estimates of annual adult and juvenile survival, which I did not directly measure. Following Moore et al. (2010), I used estimates of annual adult survivorship ranging from 0.40 – 0.61 obtained from literature on other Neotropical migratory songbirds. I calculated annual juvenile survivorship for each treatment as the product of fledgling survival and annual adult survival, based on the assumption that once juveniles reach independence their annual survival rate is similar to that of adults (Moore et al. 2010). To calculate annual female fecundity (number of female offspring per female per year) I assumed that Rose-breasted Grosbeak young occur in a 1:1 sex ratio, that females who initially failed to successfully nest would re-nest only once, and that the probability of nest success for the re-nesters would be similar to that experienced during first nest attempts (i.e., if 30% of nests failed during the first attempt, approximately 30% of nests in the second attempt would fail) (Smith et al. 2006, Moore et al. 2010). Following Moore et al. (2010) I used these values to calculate population growth rates under best case (high adult and juvenile survival) and worst case (low adult and juvenile survival) scenarios.

Statistical Analyses

Habitat Measurements

I tested for significant ($P < 0.05$) correlations among habitat variables using the Spearman rank correlation coefficient. When significant rank correlations were identified between independent variables, the measure I judged to be of lesser ecological
importance to Rose-breasted Grosbeak demography was omitted from further analysis (Burnham and Anderson 2002, Driscoll et al. 2005). During this process seedling cover was omitted due to significant ($P < 0.05$) correlations with regenerative growth (+), saplings (-), canopy (-) cover, and basal area (-). Percent cover in the canopy and sub-canopy layers were significantly positively correlated, so these variables were combined into one measure (hereafter referred to as canopy cover). Sapling cover was positively correlated with understory cover ($r = 0.56$, $P < 0.05$), but both variables were retained because they were judged to be of importance to Rose-breasted Grosbeak ecology.

I used redundancy analysis (RDA; ter Braak and Smilauer 1998) to test whether five habitat variables differed significantly among harvesting treatments (0-5, 16-20, 21-25, and > 50 years post-harvest) and study years (2006-2008). Habitat variables were then compared among treatments individually using two-way analysis of variance (ANOVA).

For each response variable a mean value was calculated for each stand in each year. In all tests, each stand mean was weighted according to the number of survey plots collected in that stand. I first tested the full model. Since the two-way interactions between year and post-harvest treatment were clearly not significant (i.e., $P > 0.15$) for all habitat variables tested, I removed the interaction terms and re-ran the models. Significant differences among post-harvest treatments were investigated using two-way analysis of variance followed by Tukey’s Studentized post-hoc range test ($\alpha = 0.05$). For all ANOVAs, model assumptions of homogeneity and normality were verified by examination of residuals, and no transformations were necessary. Correlations and model assumptions were tested in Statistica 7 (StatSoft Inc. 2004), redundancy analysis was
performed in CANOCO, and all other analyses were conducted in the PROC GLM module of SAS v. 8.02 (SAS Institute Inc., 1999).

**Demographic Variables**

I used redundancy analysis to investigate nine demographic variables (territory density, pairing success, proportion of ASY compared to SY males, nest initiation dates, clutch size, number of fledglings per successful nest, daily nest survival, period nest survival, and productivity) as a function of harvesting treatment (0-5, 16-20, 21-25, and > 50 years post-harvest) and study year. Demographic variables were then compared individually among harvest treatments using two-way ANOVAs.

Estimates of nest initiation date, clutch size, and survival were available for all three years (2006-2008), but all other demographic variables were only estimated for 2007 and 2008. For each response variable a mean value was calculated for each stand in each year. In all tests, each stand mean was weighted according to the number of observations collected in that stand. I first tested the full model (treatment, year, and treatment × year interaction), but re-ran the models without the interaction term since it was clearly not significant for any of the variables measured (i.e., \( P > 0.15 \)). Significant differences among post-harvest treatments were investigated using two-way analysis of variance followed by Tukey’s Studentized post-hoc range test (\( \alpha = 0.05 \)). For all ANOVAs, model assumptions of homogeneity and normality were verified by examination of residuals, and no transformations were necessary.
Relationship Between Habitat Features and Demographic Variables

I used redundancy analysis (RDA; ter Braak and Smilauer 1998) to examine the overall relationship between demographic variables and habitat characteristics in the four post-harvest treatments. Five habitat variables were retained in the analysis as well as nine demographic variables.

Male Age

I used a procedure similar to the one used for the demographic variables to compare demographic measurements and habitat characteristics at nests attended by ASY and SY males in the four post-harvest treatments. The habitat characteristics I investigated were percent cover by regenerative growth, saplings, understory, and canopy and basal area. Too few SY males were present in most sites to allow separate comparisons for each study year. I pooled measurements across study years by calculating an average for each site in each study year, then taking a weighted average of these values, with each value weighted according to the number of observations in each site. As in the above analysis, I investigated the differences in demographic variables and habitat characteristics among post-harvest treatments and between nests attended by ASY and SY males using two-way ANOVAs followed by Tukey’s Studentized post-hoc range test (α = 0.05).

RESULTS

Habitat Measurements

Redundancy analysis indicated that vegetation variables differed significantly with time since single-tree selection harvesting (F-ratio = 3.642, P = 0.002). Tukey’s
tests showed that the removal of trees resulted in significantly lower basal area and lower cover from saplings and understory in 0-5 years post-harvest stands than in other treatments (Table 1.2). As a result of the openings created by harvesting, these sites also had significantly higher cover from regenerative growth than other stands. In the 16-20 years post-harvest stands, regenerative growth had developed into a denser understory layer than was present in other post-harvest treatments. Habitat features 21-25 years after harvesting were not significantly different from those in the 16-20 years post-harvest stands in most study years, but cover from regenerative growth and saplings was significantly lower than in the > 50 years post-harvest stands. The “un-logged” stands (> 50 years post-harvest) had higher basal area and higher sapling and canopy cover than were present in the other post-harvest treatments.

**Demographic Variables**

Mean density of Rose-breasted Grosbeaks in this study was 0.212 (SE = 0.01) territories / ha, mean pairing success was 0.963 (SE = 0.01), and the mean proportion of ASY males was 0.629 (SE = 0.11), indicating that more after-second-year males successfully held territories than second-year males. Between 2006 and 2008 I monitored a total of 173 nests (20, 73, and 80 nests in the years 2006-2008 respectively), and I was able to determine exact nest initiation dates for 157 first nest attempts. Mean nest initiation date was May 26th (range = May 18th – June 2nd), with one outlying nest started on May 15th, 2006. Nest contents could be verified for 52 nests, yielding a mean clutch size of 3.81 eggs, and an average of 3.44 fledglings per successful nest. Mean daily survival rate (DSR) for Rose-breasted Grosbeak nests was 0.967 (n = 173 nests), mean
TABLE 1.2. Means of habitat variables (standard error in brackets) and results from two-way ANOVAs and Tukey’s tests comparing sites from four stages in the cutting cycle: 0-5, 16-20, 21-25, and > 50 years post-harvest (*n* = 3 per stage) and three study years (2006-2008).

<table>
<thead>
<tr>
<th>Variable</th>
<th>0-5</th>
<th>16-20</th>
<th>21-25</th>
<th>&gt;50</th>
<th><em>P</em> Treatment</th>
<th><em>P</em> Year</th>
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</thead>
<tbody>
<tr>
<td>Forb cover (%)</td>
<td>8.5 (3.5)</td>
<td>3.3 (1.4)</td>
<td>23.0 (6.1)</td>
<td>12.0 (0.1)</td>
<td>0.051</td>
<td>0.029</td>
</tr>
<tr>
<td></td>
<td>8.6 (2.2)</td>
<td>2.0 (0.6)</td>
<td>4.4 (1.6)</td>
<td>5.2 (1.6)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>6.3 (2.0)</td>
<td>2.9 (0.9)</td>
<td>7.2 (0.4)</td>
<td>6.7 (1.6)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regeneration (%)</td>
<td>14.5 (0.5)</td>
<td>4.3 (0.6)</td>
<td>4.3 (0.2)</td>
<td>12.0 (0.1)</td>
<td>&lt;0.001</td>
<td>0.061</td>
</tr>
<tr>
<td></td>
<td>17.8 (3.2)</td>
<td>7.1 (3.0)</td>
<td>4.2 (1.2)</td>
<td>11.4 (1.6)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>23.4 (4.7)</td>
<td>9.1 (2.9)</td>
<td>7.2 (3.3)</td>
<td>18.4 (5.6)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sapling cover (%)</td>
<td>6.3 (0.9)</td>
<td>16.0 (3.9)</td>
<td>9.9 (2.5)</td>
<td>25.9 (4.1)</td>
<td>&lt;0.001</td>
<td>0.108</td>
</tr>
<tr>
<td>Under-story cover (%)</td>
<td>20.8 (2.8)</td>
<td>34.5 (4.1)</td>
<td>27.1 (2.9)</td>
<td>25.3 (5.4)</td>
<td>0.066</td>
<td>0.516</td>
</tr>
<tr>
<td>Canopy cover (%)</td>
<td>81.2 (6.8)</td>
<td>90.3 (4.8)</td>
<td>89.4 (3.8)</td>
<td>93.8 (7.2)</td>
<td>0.376</td>
<td>0.060</td>
</tr>
<tr>
<td>Basal area(m²/ha)</td>
<td>22.1 (1.2)</td>
<td>27.2 (1.2)</td>
<td>27.0 (0.8)</td>
<td>28.1 (1.8)</td>
<td>0.006</td>
<td>0.954</td>
</tr>
</tbody>
</table>

*Superscript letters indicate significant differences between silvicultural treatments from Tukey’s HSD post-hoc test (α = 0.05).*
period survival rate (PSR) for the entire 24 day period was 0.559, and mean productivity was 2.02 fledglings per nest.

Density, pairing success, and the number of fledglings per successful nest were all significantly lower in the > 50 years post-harvest stands than in at least one other post-harvest treatment, and nest survival and productivity were also lowest in the > 50 years post-harvest stands (Table 1.3). The proportion of ASY males compared to SY males was highest in the > 50 years post-harvest stands and lowest in the 21-25 years post-harvest treatment, but differences were not significant ($P = 0.616$; Table 1.3). Nests were initiated significantly later in 2008 than in 2006 or 2007, and productivity estimates were significantly higher in 2008 than in 2007.

On average, female fecundity was 1.02 female fledglings per female, with Rose-breasted Grosbeak females producing 1.01 – 1.02 female fledglings / female / year (Table 1.4). Under the worst case scenario (low adult and juvenile survivorship) all post-harvest treatments were population sinks. Under the best case scenario (high adult and juvenile survival), the 16-20 years post-harvest treatment was a source, but all other treatments remained sinks.

**Relationship Between Habitat and Demographic Variables**

The first two axes of the RDA analysis explained 57% of the variance in demographic variables (41.6% and 15.4% for the first and second axes, respectively; Fig. 1.2). Sapling cover and basal area were strongly associated with the > 50 years post-harvest stands, whereas understory and forbs were weakly associated with this treatment. Regeneration and canopy cover were weakly associated with 0-5 years post-harvest
TABLE 1.3. Means of demographic variables (standard error in brackets) and results from two-way ANOVAs and Tukey’s tests comparing sites from four stages in the cutting cycle: 0-5, 16-20, 21-25, and > 50 years post-harvest (n = 3 per stage) and three study years (2006-2008). Sample sizes (n) show number of nests per treatment, but may vary slightly among demographic measures.

<table>
<thead>
<tr>
<th>Demographic Variable</th>
<th>0-5 n = 55</th>
<th>16-20 n = 34</th>
<th>21-25 n = 38</th>
<th>&gt;50 n = 29</th>
<th>P (Treatment)</th>
<th>P (Year)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density (no. territories /ha)</td>
<td>0.246 (0.02)</td>
<td>0.254 (0.03)</td>
<td>0.187 (0.02)</td>
<td>0.162 (0.01)</td>
<td>0.031</td>
<td>0.727</td>
</tr>
<tr>
<td>Pairing success (prop. males paired)</td>
<td>0.990 (0.01)</td>
<td>0.972 (0.02)</td>
<td>1.000 (0.0)</td>
<td>0.892 (0.01)</td>
<td>&lt;0.001</td>
<td>0.072</td>
</tr>
<tr>
<td>Proportion of territorial ASY males</td>
<td>0.598 (0.08)</td>
<td>0.634 (0.08)</td>
<td>0.550 (0.09)</td>
<td>0.725 (0.11)</td>
<td>0.616</td>
<td>0.473</td>
</tr>
<tr>
<td>Nest Initiation Date</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>May 27 (5.50)</td>
<td>May 26 (1.81)</td>
<td>May 24 (1.28)</td>
<td>May 24 (1.03)</td>
<td>0.430</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2007</td>
<td>May 24 (0.88)</td>
<td>May 24 (1.03)</td>
<td>May 22 (0.87)</td>
<td>May 25 (1.12)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2008</td>
<td>May 27 (0.46)</td>
<td>May 28 (0.56)</td>
<td>May 27 (0.87)</td>
<td>May 27 (0.76)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clutch size</td>
<td>4.000 (0.07)</td>
<td>3.667 (0.17)</td>
<td>3.625 (0.12)</td>
<td>3.833 (0.40)</td>
<td>0.477</td>
<td>0.283</td>
</tr>
<tr>
<td>No. fledglings / successful nest</td>
<td>3.619 (0.13)</td>
<td>3.333 (0.24)</td>
<td>3.500 (0.16)</td>
<td>2.833 (0.48)</td>
<td>0.012</td>
<td>0.060</td>
</tr>
<tr>
<td>Mayfield period nest survival rate</td>
<td>0.524 (0.09)</td>
<td>0.598 (0.09)</td>
<td>0.654 (0.12)</td>
<td>0.437 (0.09)</td>
<td>0.350</td>
<td>0.308</td>
</tr>
<tr>
<td>Productivity (no. fledglings / nest)</td>
<td>2.305 (0.35)</td>
<td>1.603 (0.28)</td>
<td>2.282 (0.47)</td>
<td>1.383 (0.62)</td>
<td>0.593</td>
<td>0.113</td>
</tr>
</tbody>
</table>

Superscript letters indicate significant differences between silvicultural treatments from Tukey’s HSD post-hoc test (α = 0.05).
TABLE 1.4. Population growth rates for Rose-breasted Grosbeaks breeding in 12 tolerant hardwood stands in Algonquin Provincial Park harvested by single-tree selection. Stands represent four stages in the cutting cycle: 0-5, 16-20, 21-25, and > 50 years post-harvest. Models show intrinsic (λ) and exponential (r) population growth rates under best case (high adult and juvenile survival) and worst case (low adult and juvenile survival) scenarios. Treatments are designated as sources if λ is ≥ 1 and a sink if λ is < 1.

<table>
<thead>
<tr>
<th>Time since harvest (years)</th>
<th>Adult survival probability a</th>
<th>Annual juvenile survival b</th>
<th>Female fecundity c</th>
<th>λ</th>
<th>Upper and lower 95% CI</th>
<th>Population status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Best Case Scenario</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-5</td>
<td>0.61</td>
<td>0.337</td>
<td>1.019</td>
<td>0.966</td>
<td>0.864 - 1.070</td>
<td>Sink</td>
</tr>
<tr>
<td>16-20</td>
<td>0.61</td>
<td>0.417</td>
<td>1.012</td>
<td>1.025</td>
<td>0.922 - 1.128</td>
<td>source</td>
</tr>
<tr>
<td>21-25</td>
<td>0.61</td>
<td>0.249</td>
<td>1.022</td>
<td>0.893</td>
<td>0.790 - 0.996</td>
<td>Sink</td>
</tr>
<tr>
<td>&gt; 50</td>
<td>0.61</td>
<td>0.198</td>
<td>1.012</td>
<td>0.848</td>
<td>0.745 - 0.951</td>
<td>Sink</td>
</tr>
<tr>
<td>Worst Case Scenario</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-5</td>
<td>0.40</td>
<td>0.221</td>
<td>1.019</td>
<td>0.713</td>
<td>0.610 - 0.816</td>
<td>Sink</td>
</tr>
<tr>
<td>16-20</td>
<td>0.40</td>
<td>0.274</td>
<td>1.012</td>
<td>0.760</td>
<td>0.657 - 0.863</td>
<td>Sink</td>
</tr>
<tr>
<td>21-25</td>
<td>0.40</td>
<td>0.163</td>
<td>1.022</td>
<td>0.649</td>
<td>0.546 - 0.752</td>
<td>Sink</td>
</tr>
<tr>
<td>&gt; 50</td>
<td>0.40</td>
<td>0.130</td>
<td>1.012</td>
<td>0.614</td>
<td>0.511 - 0.717</td>
<td>Sink</td>
</tr>
</tbody>
</table>

a Estimates obtained from literature on other Neotropical migratory songbirds
b Fledgling survival probability multiplied by annual juvenile survival rate, assumed to be equal to adult survival probability
c Mean no. of female offspring / successful nest / year, assuming one attempt at re-nesting following nest failure
stands. All demographic variables were weakly associated with harvested stands, except for nest initiation date, the proportion of territorial ASY males compared to SY males, and clutch size, which were not clearly associated with any treatment.

**Age of Male Parent**

Nests attended by ASY males were initiated significantly earlier than nests attended by SY males ($F_{1,3} = 19.97, P = 0.0002$) (Table 1.5). Territory density was significantly higher for ASY males than SY males in all post-harvest treatments ($F_{1,3} = 10.15, P = 0.005$), and productivity (no. fledglings produced per active nest) was also significantly higher for ASY males than for SY males ($F_{1,3} = 3.94, P = 0.050$). Differences between nests attended by ASY males and those attended by SY males were not significant for clutch size ($F_{1,3} = 0.02, P = 0.892$), mean number of fledglings produced per successful nest ($F_{1,3} = 0.66, P = 0.429$), daily survival rate ($F_{1,3} = 1.56, P = 0.226$), or period survival rate ($F_{1,22} = 1.32, P = 0.174$), but all of these measures were slightly higher at nests attended by ASY males than those attended by SY males.

Multivariate analysis of variance indicated that there were no significant differences in percent cover by regenerative growth, saplings, understory, and canopy cover or in basal area at nests attended by ASY and SY males ($F_{5,14} = 0.42, P = 0.827$). The interaction between post-harvest treatment and male age (ASY or SY) was also not significant ($F_{15,39.05} = 0.78, P = 0.691$).
Figure 1.2. Relationship between seven demographic variables for Rose-breasted Grosbeaks and six habitat features in four post-harvest treatments in Algonquin Provincial Park. Demographic variables are mean clutch size, territory density, number of fledglings per successful nest, pairing success, productivity, proportion of territorial ASY males, and nest survival. Habitat features are percent cover by forbs, regenerative growth, saplings, understory, and canopy and basal area. Filled triangles = 0-5 years post-harvest stands, filled squares = 16-20 years post-harvest stands, filled octagons = 21-25 years post-harvest stands, empty circles = > 50 years post-harvest stands. Inter-sample scaling was used, and the species scores were centered and standardized (RDA on a correlation matrix between demographic variables). The first axis explained 41.6% of the variance in demographic variables and the second axis explained 15.4%.
TABLE 1.5. Means of demographic variables (standard error in brackets) and results from two-way ANOVAs and Tukey's tests comparing sites from four stages in the cutting cycle: 0-5, 16-20, 21-25, and > 50 years post-harvest (n = 3 per stage) and three study years (2006-2008). Results are shown for after-second-year (ASY) and second-year (SY) males. Bold values indicate significant differences between SY and ASY males.

<table>
<thead>
<tr>
<th>Demographic Variable</th>
<th>Time Since Harvest (years)(^1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male Age</td>
</tr>
<tr>
<td>Density (no. territories /ha)</td>
<td>ASY</td>
</tr>
<tr>
<td></td>
<td>SY</td>
</tr>
<tr>
<td>Nest initiation date</td>
<td>ASY</td>
</tr>
<tr>
<td></td>
<td>SY</td>
</tr>
<tr>
<td>Clutch size</td>
<td>ASY</td>
</tr>
<tr>
<td></td>
<td>SY</td>
</tr>
<tr>
<td>No. fledglings / successful nest</td>
<td>ASY</td>
</tr>
<tr>
<td></td>
<td>SY</td>
</tr>
<tr>
<td>Daily nest survival</td>
<td>ASY</td>
</tr>
<tr>
<td></td>
<td>SY</td>
</tr>
<tr>
<td>Period nest survival</td>
<td>ASY</td>
</tr>
<tr>
<td></td>
<td>SY</td>
</tr>
<tr>
<td>Productivity (no. fledglings / pair)</td>
<td>ASY</td>
</tr>
<tr>
<td></td>
<td>SY</td>
</tr>
</tbody>
</table>

\(^1\)Superscript letters indicate significant differences between silvicultural treatments from Tukey’s HSD post-hoc test (α = 0.05).
**DISCUSSION**

Habitat characteristics differed significantly among stands harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years previously. As in other studies, the most recently harvested stands had significantly higher cover from regenerative growth, lower basal area, and lower sapling, understory, and canopy cover than other post-harvest treatments (Robinson and Robinson 1999, Flaspohler et al. 2002, Jobes et al. 2004, Moore et al. 2010). Increased light penetration in newly logged stands typically promotes the establishment of shade-tolerant sugar maple and American beech seedlings (Finegan 1984, Jobes et al. 2004), and in this study resulted in significantly higher understory cover by 16-20 years post-harvest. As previously demonstrated, the >50 years post-harvest stands had higher basal area and higher sapling cover than other stands (Robinson and Robinson 1999, Flaspohler et al. 2002, Jobes et al. 2004).

Single-tree selection harvesting did not appear to have a significant negative effect on any of the demographic measures included in this study, and density, pairing success, and the number of fledglings produced per successful nest were all significantly lower in the > 50 years post-harvest treatment than in the harvested stands. However, Rose-breasted Grosbeaks were below replacement levels in all stands except the 16-20 years post-harvest treatment, even using the most optimistic measures of adult and juvenile survival.

**Demographic Measures**

In the predominantly forested landscape of Algonquin Provincial Park Rose-breasted Grosbeak density ranged from 0.16-0.24 male territories per hectare, which is
similar to the range of densities (0.20-0.24) reported for forest fragments in south-western Ontario (Smith et al. 2006). However, whereas density was lower in the uncut stands than in the harvested ones in the predominantly forested landscape, the opposite was true in forest fragments in the agricultural landscape, where Rose-breasted Grosbeaks appeared to be attracted to the higher shrub cover, particularly in heavily cut stands (Smith et al. 2006). Nest predation and brood parasitism by Brown-headed Cowbirds (*Molothus ater*) are often higher (Paton 1994, Hoover et al. 1995, Rodewald et al. 2002, Phillips et al. 2005, Falk et al. 2011), and pairing success is lower (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998) in fragmented agricultural landscapes than in continuously forested regions. As a result, openings in the understory and canopy created by silviculture, which potentially expose songbird nests to visual predators and brood parasites, could have a greater impact in fragmented landscapes than in predominantly forested regions (Andrén 1995, Hanski et al. 1996).

Higher rates of nest predation and brood parasitism following harvesting could result in lower recruitment of individuals into selection harvested stands, and therefore lower densities relative to un-harvested fragments. Rose-breasted Grosbeak nests are parasitized in fragmented agricultural landscapes (Smith et al. 2006, 2007), but were not in my predominantly forested landscape, and estimates of nest survival were considerably lower for the fragmented landscape (0.341-0.390; Smith et al. 2006, 2007, Moore et al. 2010) than in my study area (0.559). These results suggest that the effects of timber harvesting to some extent depend on landscape context, and that adverse effects may be fewer in forested regions than in fragmented landscapes.
Rose-breasted Grosbeak productivity, represented by the number of fledglings produced per successful nest, was highest in the 0-5 years post-harvest stands and lowest in the > 50 years post-harvest treatments. The number of fledglings produced per successful nest ranged from 2.8-3.6, which is comparable to, but slightly higher than estimates from southwestern Ontario, which ranged from 2.4 (Smith et al. 2006) to 3.2 (Moore et al. 2010). While more young were fledged on average from successful nests in uncut stands (2.8) than in harvested ones (2.4) in the fragmented landscape (Smith et al. 2006), in the predominantly forested landscape significantly more young were fledged per successful nest in 0-5 years post-harvest stands (3.6) than in uncut sites (2.8). Estimates of the number of fledglings produced per active nest, which incorporate nest survival rates, were also lower in the > 50 years post-harvest stands than in the more recently harvested treatments in my study landscape, but not significantly so. Together these results suggest that single-tree selection harvesting may have less of a negative impact on Rose-breasted Grosbeak productivity in forested regions than in more fragmented landscapes.

As predicted, density was highest in the 16-20 year post-harvest stands and the population growth model indicated that these stands were at or closer to replacement levels than the other post-harvest treatments. The 16-20 years post-harvest treatment appeared to attract Rose-breasted Grosbeaks and to have high productivity, but in general, most demographic measures were higher in more recently cut stands than in the un-logged ones. Previously harvested stands were associated with higher regenerative growth and understory cover, both of which are features previously identified as important to Rose-breasted Grosbeak demography (Smith et al. 2006, 2007). Other
studies have found greater abundances of early-successional species in regenerating forests as well (Annand and Thompson 1997, Simon et al. 2000, Gram et al. 2003, Holmes et al. 2004, Jobes et al. 2004, Holmes and Pitt 2007, Robertson and Hutto 2007, Atwell et al. 2008), suggesting that forest management may provide additional nesting habitat and/or food resources for disturbance-dependent songbirds. In my study Rose-breasted Grosbeaks built their nests at a wide range of heights (1.5 – 22 m), and they were observed foraging in vegetation ranging from ground level to the upper layers of the canopy. This species’ ability to demonstrate plasticity in nest site selection and foraging substrate use may help explain why all demographic measures were not clearly higher in one post-harvest treatment than the others.

**Population Productivity**

Population growth estimates indicated that even under the best case scenario, Rose-breasted Grosbeaks in my study area were not replacing themselves except in the 16-20 years post-harvest treatments. Although population growth estimates have not previously been determined for Rose-breasted Grosbeaks in predominantly forested landscapes, this species is frequently found in regenerating forests 15 years after harvesting (Pelletier and Dauphin 1996), and often increases in abundance following logging (i.e., Jobes et al. 2004, Doyon et al. 2005). This study indicates that the dense understory and sapling layers characteristic of hardwood stands 16-20 years post-harvest are important for Rose-breasted Grosbeaks, and that access to regenerating forests may provide some benefits for this species in forested areas.
Population growth models are highly sensitive to small changes in estimates of annual survival rates for adults and juveniles (Porneluzi and Faaborg 1999, Powell et al. 1999, Woodworth 1999), which despite technological advancements in radio tracking are still difficult to accurately obtain (Greenwood and Harvey 1982, Payne 1991, Paradis et al. 1998, Anders and Marshall 2005). Common responses to this problem are to estimate juvenile survival by dividing adult mortality by the average number of offspring fledged (Ricklefs 1973), to assume juveniles are half as likely to survive as adults (Greenberg 1980), or to adopt 0.31 as an estimate of juvenile survival (Temple and Carey 1988). Empirical estimates of juvenile survival from fledging to fall migration range from 0.28 to 0.75 for Juncos (Junco phaenotus), Wood Thrush (Hylocichla mustelina), and Lark Buntins (Calamospiza melanocorys) (Sullivan 1989, Anders et al. 1997, Powell et al. 2000, Yackel Adams et al. 2001). Annual adult survival is often assumed to be 0.62 (Anders and Marshall 2005), and empirical estimates of annual survival for breeding songbird females range from 0.40-0.55 (Cilimburg et al. 2002, Sillett and Holmes 2002, Gardali et al. 2003, Stutchbury et al. 2009). I incorporated a range of values for adult and juvenile survival by calculating growth rates under a worst case scenario (adult survival = 0.40, and low juvenile survival) and a best case scenario (adult survival = 0.61, and high juvenile survival), as well as using stand specific values for female fecundity, nest success, and fledgling survival to improve accuracy (Anders and Marshall 2005).

Although these results should be accepted with caution, this study suggests that harvested hardwood stands in predominantly forested landscapes may be population sources for Rose-breasted Grosbeaks by 16-20 years post-harvest.
Population Age Structure

The proportion of territorial ASY males compared to territorial SY males was investigated to determine whether older, more experienced males were out-competing younger, less-experienced ones for “high quality” habitats. Although breeding pairs with ASY males began nest building significantly earlier than pairs with SY males, my prediction that the 16-20 years post-harvest treatment would have the highest proportion of ASY males was not supported. The proportion of territories held by experienced males was highest in the un-harvested stands, although among-treatment differences were not significant. According to the ideal-free distribution theory, a higher proportion of older, more experienced males in the > 50 years post-harvest stands indicates that these stands may provide better quality habitat for Rose-breasted Grosbeaks. However, since overall density, pairing success, and productivity were lowest in this treatment, this interpretation seems unlikely. Instead, I propose that ASY males may have been out-competing SY males in this treatment for a more limited number of available territories than were offered in harvested stands. Older males were less productive in the > 50 years post-harvest stands than in other treatments, but even in these stands their productivity was higher than that of younger males in most other treatments. The opposing patterns in density, nest initiation dates, productivity, and proportion of older, more experienced males among the post-harvest treatments indicates that the factors which influence reproductive success and habitat quality are complicated, and as a result, assessments of the effects of harvesting or other disturbances should be based on more than one demographic measure whenever possible.
Rose-breasted Grosbeak nests attended by after-second-year males were started significantly earlier, and had significantly higher productivity than nests attended by second-year males, suggesting that more experienced breeders had a reproductive advantage over less experienced birds. First-time breeders of other species have shown lower nest survival than older individuals (Pärt 2001, Forschler and Kalko 2006) and they sometimes occupy poorer quality habitats (Greenwood and Harvey 1982, Møller 1991, Holmes et al. 1996). In some cases, second-year birds may have limited access to high-quality territories as a result of later arrival on the breeding grounds, incomplete knowledge of where to find good territories, and despotic distribution of more experienced breeders (Sherry and Holmes 1989, Holmes et al. 1996, Bayne and Hobson 2001, Part 2001a). However, in my study habitat characteristics at nests attended by SY males did not significantly differ from those at nests with ASY males, suggesting that differences in territory quality were likely not the main cause of differences in reproductive success. Lack of experience or differences in timing may be more likely explanations for the lower reproductive success of first-time Rose-breasted Grosbeak breeders.

Single-tree selection harvesting did not have a significantly negative effect on any of the demographic measures investigated in this study. However, since fewer birds were present in the > 50 years post-harvest stands, sample sizes for most demographic measures were smaller in this treatment than in the others. In addition, nests in the 21-25 and > 50 years post-harvest stands tended to be higher up, making precise estimates of nest initiation dates, brood sizes, and nest outcomes more difficult to obtain. Weighted analyses were used in an effort to address these potential differences in sample size, but it
is possible they still had an effect on among-treatment comparisons. Finally, a small proportion of territorial males (3-5%) could not be accurately aged, and although the proportion was consistent among treatments, this source of uncertainty may have affected the among-treatment comparisons. Increasing the number of stands studied might be one way for future studies to increase the power of the tests and confirm that no significantly negative effects are occurring as a result of single-tree selection cutting.

Conclusions

Density, pairing success, and productivity were higher in the more recently harvested stands than in the > 50 years post-harvest treatment, suggesting that in tolerant hardwood stands in predominantly forested landscapes, single-tree selection harvesting does not appear to have negative effects on Rose-breasted Grosbeaks. However, the proportion of older, more experienced males was highest in the > 50 years post-harvest stands, indicating that these may have been perceived as providing higher quality habitat by Rose-breasted Grosbeaks than more recently harvested stands. In addition, population growth rates calculated from a wide range of realistic estimates of juvenile and adult survival were below replacement levels in my study landscape, except in the 16-20 years post-harvest stands, suggesting that further research is needed to help identify the underlying causes of the decline in this species’ numbers. Selection harvesting influenced Rose-breasted Grosbeaks differently in the predominantly forested region than in the fragmented landscape, underscoring the importance of considering landscape and regional contexts when designing silvicultural prescriptions (Thompson et al. 1995).
CHAPTER 2: SURVIVAL AND HABITAT USE BY ADULT AND FLEDGLING ROSE-BREASTED GROSBEAKS (*PHEUCTICUS LEUDOVICIANUS*) IN A FORESTED LANDSCAPE HARVESTED BY SINGLE-TREE SELECTION

**ABSTRACT**

Many songbirds that nest in the managed hardwood forests of North America are currently declining, but although fledgling survival can have a considerable influence on population growth, few studies have investigated how silvicultural practices influence fledglings. I studied nest and fledgling survival and habitat use of Rose-breasted Grosbeaks (*Pheucticus leudovicianus*) in twelve hardwood stands in a predominantly forested landscape that had been harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years previously. Mean nest and fledgling survival in each treatment were estimated using the Mayfield method, and I used an information theoretic approach to assess relative support for models explaining nest and fledgling survival as a function of habitat characteristics. Nest sites had higher cover from regenerative growth, saplings, and understory, and lower basal area than random locations. During their first week out of the nest, fledglings used locations with significantly higher cover from regenerative growth, saplings, small shrubs, and raspberry and elderberry bushes than were present at random locations. Mayfield daily survival for Rose-breasted Grosbeak nests (*n* = 173) was 0.967 and period survival rate was 0.559. Daily fledgling survival (*n* = 46) was 0.920 and period survival over the 21 day observation period was 0.551. Neither nest nor fledgling survival differed significantly among post-harvest treatments (*P* > 0.05). The best model for explaining nest survival included basal area, nest initiation date, and sampling year, and suggested that nests initiated earlier in the season and built in locations with higher basal area had a better chance of survival. The best model for explaining fledgling survival included the number of days since fledging, indicating that as...
fledglings age their probability of surviving increases. Habitat characteristics at nest and fledgling locations were significantly different, and estimates of nest and fledgling survival were not correlated among harvested stands, suggesting that assessments of habitat quality for songbirds should not be limited to the nest stage. The lack of significant difference in survival among post-harvest treatments suggests that single-tree selection harvesting is likely not contributing to the observed declines in Rose-breasted Grosbeak populations.
INTRODUCTION

During the past decade there has been a shift in North America toward developing and implementing forest management practices that mimic natural disturbance patterns (Seymour et al. 2002). Under these guidelines, single-tree selection has been implemented in much of the tolerant hardwood forests in northeastern North America (Tubbs 1977, OMNR 1998, Seymour et al. 2002). Although this low-intensity method of harvesting should have minimal long-term impacts on wildlife (OMNR 2000), many migratory songbirds that breed in this forest type are currently experiencing population declines (Newton et al. 2004, Blancher et al. 2009). For some passerines nest survival rates remain stable before and after single-tree selection harvesting (Bourque and Villard 2001, Duguay et al. 2001, Gram et al. 2003, Smith et al. 2006, Dellinger et al. 2007, Cooper et al. 2009, Moore et al. 2010), whereas others experience lower rates of nest success in harvested forests (Barber et al. 2001, Robinson and Robinson 2001, Robertson and Hutto 2007, Poulin et al. 2010). Nest survival and habitat requirements have been well described for many North American birds (Akresh et al. 2009), but far fewer studies have investigated fledgling survival and habitat requirements once the young leave the nest (Anders and Marshall 2005, King et al. 2006, Yackel Adams et al. 2006, Poulin et al. 2010). Since evaluating the long-term impacts of forest management and other factors on declining songbird populations requires accurate population models (Stutchbury et al. 2009) that are highly sensitive to estimates of juvenile survival (Porceluzi and Faaborg 1999, Powell et al. 1999, Woodworth et al. 1999), studies of fledgling survivorship are necessary.

The fledglings of many songbirds that nest in managed hardwood forests across North America spend up to eight weeks on the breeding grounds prior to migration (Anders et al. 1998). Mortality during this period is typically high, especially during the first week out of
the nest when the young are unable to fly very well (Anders et al. 1997, 1998, Vega Rivera et al. 1998, Monró et al. 2002, Kershner et al. 2004, Yackel Adams 2006, Rush and Stutchbury 2008). Recent studies have shown that the habitat requirements of breeding adults may be different from those of family groups during the post-fledging period (Rappole and Ballard 1987, Anders et al. 1998, Vega Rivera et al. 1998, Cohen and Lindell 2004, King et al. 2006; but see Berkeley et al. 2007, Ciudad et al. 2009). For example, the amount and structure of understory cover is often important during the first week post-fledging (King et al. 2006, Mitchell et al. 2010), and the young of several species move out of the open, mature forest used by adults for nest building into edge or early- to mid-successional forests (Anders et al. 1998, Vega Rivera et al. 1998, Pagen et al. 2000, Vitz and Rodewald 2006). These differences suggest that conclusions based solely on studies of nest success may be insufficient to assess the long-term impacts of forest management on songbird populations.

Recent studies have found correlations between fledgling survival and the amount of coarse woody debris (Mitchell et al. 2010), the amount and structure of understory cover (Mitchell et al. 2010), shrub cover (Moore et al. 2010), fledging date (Monros et al. 2002, Yackel Adams et al. 2006, Moore et al. 2010), and weather (Yackel Adams et al. 2006). A number of studies found that fledglings use areas with dense cover (Anders et al. 1998, Vega Rivera et al. 1998), locations with greater than average vertical structure 0-3 m above ground (King et al. 2006), and regenerating clear-cuts (Pagen et al. 2000, Vitz and Rodewald 2006). One hypothesis to explain these patterns of resource use is the predator avoidance hypothesis, which suggests that young birds seek habitats with more cover because they provide protection from potential predators, especially during pre-migration molting (Anders et al. 1998, Vega Rivera et al. 1998). Alternatively, the optimal foraging hypothesis suggests that juveniles’ movements are primarily determined by the need to find food (Vega Rivera et al.
1998). We are beginning to identify some of the habitat types and features that are important for songbird fledglings, but we do not yet have a good understanding of the primary factors driving resource use during the post-fledging period.

Studies of fledgling survival and habitat requirements have recently become more prevalent, but to my knowledge only two studies have investigated fledgling survival in managed forests (Lang et al. 2002, Moore et al. 2010). Thinning and burning in a > 30 year old loblolly pine (*Pinus taeda*) forest had no effect on habitat use prior to parental independence or on dispersal distances of Wood Thrush fledglings (*Hylocichla mustelina*) (Lang et al. 2002). Similarly, the survival of Rose-breasted Grosbeak (*Pheucticus leudovicianus*) fledglings in deciduous forest fragments in an agricultural landscape was not significantly affected by single-tree or diameter-limit harvesting (Moore et al. 2010). Single-tree selection cutting results in stands which are characterized by abundant regenerative growth, low basal area, and sparse cover in the sapling, understory, and canopy layers a few years after harvesting (Robinson and Robinson 1999, Flaspohler et al. 2002, Jobes et al. 2004). By 16-20 years post-harvest a dense understory layer typically forms (Finegan 1984, Jobes et al. 2004), and eventually stands re-develop higher basal area, abundant cover in the seedling, regenerative growth, sapling, and canopy layers, and high spatial complexity (Robinson and Robinson 1999, Kenefic and Nyland 2000, Crow et al. 2002, Flaspohler et al. 2002, Jobes et al. 2004, Angers et al. 2005, Vanderwel et al. 2006). Since fledglings appear to benefit from increased cover near the ground, it is reasonable to expect that single-tree selection would not have a significant negative impact on their survival in a predominantly forested landscape.

Here I investigated the influence of single-tree selection on survival probability and habitat use of adult and fledgling Rose-breasted Grosbeaks (*Pheucticus leudovicianus*) in a
predominantly forested landscape. This species has been declining at an annual rate of approximately -2.4% on its breeding grounds in Ontario between 1966 and 2007 (Sauer et al. 2008), with especially sharp declines (-8% per year) between 1985 and 2005 (Cadman et al. 2007). The Rose-breasted Grosbeak is a Neotropical migrant that nests in deciduous and mixed forests throughout central and eastern North America (Wyatt and Francis 2002), primarily in the sapling and understory layers in sites with relatively open canopy and sub-canopy layers compared to random locations (Wyatt and Francis 2002). In the highly fragmented deciduous forests of southwestern Ontario, neither nest survival (Smith et al. 2006) nor fledgling survival (Moore et al. 2010) were affected by timber harvesting, but both harvested and un-harvested sites were population sinks (Smith et al. 2006, Moore et al. 2010). Although Rose-breasted Grosbeaks are declining, to my knowledge no studies have investigated the demography of this species in managed stands in predominantly forested landscapes, or investigated whether populations are self-sustaining in these areas.

I took a chronosequence approach to investigate the response of Rose-breasted Grosbeaks to the structural changes that follow single-tree selection. Specifically, my main objectives were to 1) identify important habitat characteristics at nest sites and locations used by fledglings, and determine whether these differed among post-harvest treatments, 2) estimate rates of nest and fledgling survival, and test whether these differed among post-harvest treatments, and 3) determine which habitat features had the strongest influence on nest success and fledgling survival in harvested stands. I expected habitat features to differ among post-harvest treatments due to forest growth and development, and that as a result vegetation characteristics at nest sites and fledgling locations would also differ among post-harvest treatments. I predicted that nest survival would initially decrease following harvesting, due to a reduction in regenerative growth and cover in the understory and canopy
layers, but that it would increase again by 16-20 years post-harvest with the development of a dense understory layer. In contrast, I expected that fledgling survival would increase shortly after harvesting due to an increase in cover near the ground from slash, raspberry bushes, and saplings, but that it would decrease by 16-20 years post-harvest as the forest floor became more open with the development of the understory and canopy layers.

METHODS

Study Species

Rose-breasted Grosbeaks typically arrive on their breeding grounds in central Ontario during the first week of May. In the highly fragmented deciduous forests of southwestern Ontario, Rose-breasted Grosbeaks nest in locations with more canopy cover but lower sapling cover and basal area than are available at random sites (Smith et al. 2007). In these fragmented forests nest survival is negatively associated with nest concealment, but positively associated with canopy cover, sapling cover, and nest height (Smith et al. 2007). Both males and females incubate and care for the young, which usually fledge 9-12 days after hatching (Scott 1998). Little is known about the post-fledging period, but young are unable to fly at the time of fledging and remain dependent on the adults for approximately three weeks after leaving the nest (Wyatt and Francis 2002).

Study Area

The study was conducted in twelve tolerant hardwood stands in Algonquin Provincial Park, Ontario, Canada (45° 34’N, 78°04´W) between 2006 and 2008 (Fig. 1.1). The west side of this 775, 000 ha park is dominated by mixed hardwood forest, whereas the east side consists primarily of white and red pine (Ontario Parks 1998). The stands I studied were
located in the central and southern part of the park (mean nearest neighbour distance among stands = 9.3 km, range = 1.0 – 34.2 km). Tolerant hardwood stands in this part of the park have been harvested using the single-tree selection system since the early 1970’s (OMNR 1998). This silvicultural system removes approximately one-third of the over-story basal area every 20-25 years, resulting in uneven-aged stands with a mix of canopy gaps, regenerative growth, and mature trees (OMNR 1998). Dominant tree species in the stands I studied included sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), and yellow birch (*Betula alleghaniensis*).

In this study, three temporal stages in the cutting cycle were studied: 0-5, 16-20, and 21-25 years post-harvest. Stands that had not been logged for > 50 years were studied to represent “un-logged” control conditions. Three sites from each temporal stage in the cutting cycle were studied (mean stand size = 34 ha) (Table 1.1).

**Nest Searching and Monitoring**

Nest searching and monitoring were undertaken from May to August, 2006-2008. Nests were monitored every 3-4 days using a mirror attached to a telescoping pole to determine clutch size, hatching date, number of nestlings and fledglings, nest outcome, and age of nestlings at the time of fledging. For nests that were too high to visually confirm hatching dates, nestling age was estimated using the observed nest initiation date and clutch size, published lengths for nest building (4 days) and incubation (12 days) (Scott 1998), and the assumption that one egg was laid per day.
Radio Attachment and Tracking

For lower nests (≤ 2 m), all nestlings were removed from the nest nine days after hatching (1-2 days prior to fledging) and given a uniquely-numbered aluminium US Fish and Wildlife Service leg band and a unique combination of three coloured leg bands. All nestlings were weighed using a SC-HT-S-232 digital scale with an accuracy of 0.01 g, and a Holohil Systems (Carp, Ontario) BD-2 radio-transmitter was attached to the nestling with the greatest mass. The transmitters weighed 0.6 g, (approximately 2.4% of a fledgling’s body weight on day nine post-hatching) which is less than the 5% recommended by Caccamise and Hedin (1985). Leg harnesses made from thin cotton thread were used to attach the transmitters following the method developed by Rappole and Tipton (1991). Once all the nestlings had been weighed, banded, and a transmitter had been attached they were returned to the nest. For nests that were located too high to reach, fledglings were located and captured on the ground immediately below their nest at the time of fledging, and bands and a radio-transmitter were attached. For these nests, transmitters were attached to the heaviest fledgling captured. Nestlings in lower nests, which were tagged prior to fledging, did not leave their nests at a earlier age than young that were tagged post-fledging (mean age at fledging = 10.1 and 10.3 days respectively), suggesting that radio-tag attachment likely did not cause early fledging.

Once out of the nest, radio-tagged juveniles were located every second day for a period of three weeks (11 possible observations per individual, mean = 7.5 observations per individual) using programmable receivers and three-element Yagi antennas. Juveniles were tracked on the ground, and the exact location of each radio-tagged individual was determined visually, unless the bird was hidden by canopy foliage. The place where the bird was first sighted was marked using a GPS unit and flagging tape, and the height and level of
concealment of the bird were recorded. In some instances determining the exact location of a bird took several minutes, but this usually only happened when birds were located in the canopy and not visible from below. I did not observe any instances when the tracker’s movements caused the fledgling to change locations. In cases where the fledgling was first seen flying from one location to another, the spot it was leaving from was marked. Juveniles were considered dead if mortality was visually confirmed (i.e. a whole or partial carcass was found) or were considered to have an unknown fate if their harness was located intact without signs of predation, or if the signal was lost.

**Habitat Measurements**

Habitat characteristics were measured at nest sites, fledgling locations, and at a corresponding number of random points. Random plots used for comparison with nests were selected using a random number generator to produce a set of UTM co-ordinates located within each stand, and a GPS unit was used to locate those co-ordinates on the ground. Random surveys were not done in predominantly coniferous patches or swampy areas, but otherwise there were no restrictions on the location of random plots as long as they fell within the study stands.

For each fledgling that was tracked, habitat characteristics were surveyed at three locations, one that was occupied during the first 7 days post-fledging, one that was occupied between days 8 and 14, and one that was occupied between days 15 and 21. For each fledgling, the location to be surveyed from each week-long period was randomly chosen from amongst their known locations. Random points used for comparison with fledgling locations were chosen to represent the type of habitat that would have been encountered if the fledgling had moved the same linear distance since it was last observed, but in a different
direction. To determine the locations of random plots, I calculated the linear distance between the fledgling location of interest (i.e., day 9 post-fledging) and its location when last observed (i.e., day 7 post-fledging). I then walked this distance in a straight line from the fledgling’s location when last seen (i.e. day 7 post-fledging) in a direction randomly chosen by blindly spinning my compass. This random point was paired with the fledgling location of interest (i.e. day 9 post-fledging). Due to fledgling mortality, sample sizes were smaller for habitats surveyed during the second and third weeks post-fledging than during the first week.

At fledgling locations, nests, and corresponding random points vegetation layers were measured in 5 m radius circular plots using a modified version of the James and Shugart (1970) method. Percent cover by: 1) forbs/grasses/ferns, 2) regenerative growth (woody growth 0.5-1.3 m tall), 3) saplings (>1.3 m tall, <2.5 cm dbh), 4) understory (>2.5 cm dbh, <10.0 cm dbh), 5) sub-canopy (>10 m tall), and 6) canopy (>20 m tall) were visually estimated, and basal area (m$^2$/ha) was measured using a 2-factor cruising prism. At nest sites, percent concealment and nest height were visually estimated, and fledgling concealment and height were also visually estimated. At fledgling locations and corresponding plots percent cover by small shrubs (< 2.5 cm dbh), large shrubs (2.6-8 cm dbh), wild red raspberries (*Rubus spp*), and red elderberry (*Sambucus spp*) plants were also assessed. These variables were selected for measurement because they have been shown to be correlated with the nest and fledgling locations of songbirds elsewhere (Wyatt and Francis 2002, Smith et al. 2006, Moore et al. 2010).
Statistical Analyses

Habitat Measurements

I used the Spearman rank correlation coefficient to test for significant ($P < 0.05$) correlations among seven habitat measures, and a suite of relatively uncorrelated variables that were judged to be of ecological importance to Rose-breasted Grosbeaks was retained for further analysis (Burnham and Anderson 2002, Driscoll et al. 2005). Seedling cover was significantly correlated with basal area (-), percent cover by regenerative growth (+), and understory cover (-), and so was omitted from the analysis. Percent cover by forbs was omitted due to significant correlations with regenerative growth (-), and understory (-), whereas sub-canopy and canopy cover were combined into a single measure (hereafter referred to as canopy cover) due to a significant positive correlation. Understory cover was positively correlated with regenerative growth ($r = 0.60$), but both variables were retained because they were judged to be of importance to Rose-breasted Grosbeaks.

Do habitat features differ between used and un-used plots?

With the exception of canopy cover, vegetation characteristics at nest sites and random plots differed significantly among post-harvest treatments ($F_{12,135.22} = 2.42, P = 0.007$), but not among study years ($F_{8,102} = 0.87, P = 0.542$), and interactions between post-harvest treatment and year were not significant ($F_{30,202} = 0.54, P = 0.975$). Canopy cover differed significantly among study years ($F_{1,3} = 9.58, P = 0.010$), so each year was analyzed separately. All other habitat characteristics at nest sites and random plots were pooled across study years by calculating average values for each site in each year, and then taking a weighted average of those values. When data on vegetation characteristics at locations occupied by fledglings was broken down by year and treatment, sample sizes were too small
(n < 3 in some cases) to allow meaningful analysis of habitat use. As a result, habitat use data for fledglings were also pooled across study years, by calculating average values for each site in each year, and then taking a weighted average of those two values.

I used weighted MANOVA to test for overall differences in habitat characteristics among post-harvest treatments and between nest and random locations. Habitat variables were then tested individually using split-plot analysis of variance (ANOVA). The residuals for each habitat variable were examined, and as a result I square root transformed canopy cover and log-transformed regenerative growth (log_{10} + 0.05). Tukey’s Studentized post-hoc range test was performed on the results of split-plot ANOVAs that identified significant among treatment differences.

I used a similar procedure to test for differences between habitat characteristics at points used by fledglings and random locations, but separate comparisons were made for habitat use during the first, second, and third weeks post-fledging. To obtain normality and homoscedasticity I log-transformed regenerative growth (log_{10} + 0.05), and square-root transformed sapling, understory, and canopy cover.

**Do habitat features differ between nest and fledgling plots?**

I used weighted MANOVA to test for overall differences in habitat characteristics at nest sites and locations used by fledglings. Habitat variables were then tested individually using split-plot ANOVAs, and Tukey’s Studentized post-hoc range tests were performed on variables that significantly differed among treatments.
Nest and Fledgling Survival

Nest and fledgling survival were determined for each post-harvest treatment using the Mayfield estimator (Mayfield 1961, 1975). Daily survival rate (DSR) for nests was calculated as 1 – no. of failed nests / no. of exposure days, where exposure days were equal to the number of days the nest was under observation. Period survival rate (PSR) was calculated as $(DSR)^d$, where $d$ represented the number of days between the onset of incubation and fledging (24 days for Rose-breasted Grosbeaks). DSR estimates the probability that a nest will survive one day, and PSR estimates the probability that a nest will survive until the young fledge. Similar estimates were calculated for fledglings, but for DSR the number of fledglings that died was substituted for the number of failed nests, and for PSR, $d$ represented the 21 day observation period for the fledglings.

Are estimates of nest and fledgling survival correlated among harvest treatments?

To test whether single-tree selection harvesting had a similar influence on nest and fledgling survival over the course of the harvesting rotation, I calculated a Spearman rank correlation coefficient for nest and fledgling survival.

How do habitat characteristics influence nest and fledgling survival?

I constructed a set of 42 models containing 1-3 variables to explain nest survival and a set of 75 models containing 1-4 variables to explain fledgling survival (Appendix 2.1). Each model represented a hypothesis to explain nest and fledgling survival based on literature reviews, significant differences in vegetation between points occupied by nests or fledglings and random locations, and my own observation of the study species. The
following variables were included in the set of candidate models explaining nest and fledgling survival:

1) **REGENERATIVE GROWTH** – In this study, percent cover from regenerative growth at Rose-breasted Grosbeak nest locations was significantly higher than at random locations. Minimum nest height was 1.5 m, suggesting that regenerating vegetation (0.5 – 1.3 m tall) may help conceal nests from potential predators on the ground. Similarly, this vegetation layer can provide cover for fledglings, especially during their first week out of the nest when they are learning to fly (King et al. 2006). Percent cover from regenerative growth was included in models for both nest and fledgling survival.

2) **SAPLING COVER** – In forest fragments percent cover by saplings was positively associated with Rose-breasted Grosbeak nest survival, even though nests were placed in areas with fewer saplings than were present at random locations (Smith et al. 2007). In my study, Rose-breasted Grosbeaks used nest sites with significantly higher sapling cover than was present at random locations, suggesting this variable may be important to survival. I expected saplings to provide cover for fledglings during the first and second weeks out of the nest when movement is limited and mortality is high (i.e., Yackel Adams et al. 2006, Moore et al. 2010). Percent cover by saplings was included in models explaining both nest and fledgling survival.

3) **UNDERSTORY COVER** – Understory cover was significantly higher at Rose-breasted Grosbeak nest locations than at random points in my study suggesting that the understory layer was important for nest placement and camouflage. Structure and amount of understory vegetation have also been related to fledgling survival (King et
al. 2006, Mitchell et al. 2010). I included percent cover by understory in models of nest and fledgling survival.

4) CANOPY COVER – In forest fragments Rose-breasted Grosbeaks selected nest sites with lower canopy cover than was present at random locations, even though this variable was positively associated with nest survival (Smith et al. 2007). In my study, mean nest height for Rose-breasted Grosbeaks was 9.6 m, suggesting that the sub-canopy and canopy layers would be important for nest placement, concealment, and survival. Although canopy cover has not been directly related to fledgling survival to my knowledge, juveniles were frequently observed feeding in the canopy once they could fly, so I expected this variable to be important for fledgling survival as well, and included it in models explaining both nest and fledgling survival.

5) BASAL AREA – Basal area was lower around Rose-breasted Grosbeak nests than at random locations in forest fragments (Smith et al. 2007) and in my study. Although the connection between fledgling survival and basal area has not been previously established to my knowledge, basal area was included in models of both nest and fledgling survival to determine whether habitat requirements differ before and after fledging.

6) POST-HARVEST TREATMENT – Neither nest survival (Smith et al. 2006) nor fledgling survival (Moore et al. 2010) of Rose-breasted Grosbeaks were significantly influenced by selection harvesting in forest fragments. Harvest treatment was included in the models for both nest and fledgling survival to test whether Rose-breasted Grosbeaks responded similarly to selection cutting in a predominantly forested landscape. Models including each variable, treatment, and an interaction term were also tested for both nest and fledgling survival.
7) CONCEALMENT – For some species, nests that are more camouflaged from potential nest predators may be more likely to succeed (Martin and Roper 1988, Filliater et al. 1994, Colombelli-Négrel and Kleindorfer 2009). In forest fragments Rose-breasted Grosbeak nest survival was positively associated with nest concealment, even though nests were placed in areas with less than average cover (Smith et al. 2007). Fledglings of several species use areas with greater concealment from dense vegetation (Anders et al. 1998, Vega Rivera et al. 1998, Marshall et al. 2003), likely to avoid predation. Percent concealment was included in models of nest and fledgling survival.

8) HEIGHT – For Rose-breasted Grosbeaks in forest fragments in southern Ontario nest height is positively associated with nest survival (Smith et al. 2007), and these two variables are correlated in several other species as well (Burhans et al. 2002, Prokop 2004, Colombelli-Negrel and Kleindorfer 2009). Although I am unaware of any studies linking fledgling height to survival, I expected that as fledglings learned to fly and moved up into the canopy their chances of survival would increase. Height was included in models explaining nest and fledgling survival.

9) AGE OF MALE PARENT – First time breeders of some birds have lower nest survival than older individuals (Pärt 2001, Forschler and Kalko 2006), as well has producing smaller clutch sizes (Reynolds 1997) and fewer fledglings (Préault et al. 2005, Brown and Roth 2009). Age of male parent (second-year or after-second-year) was included in models of nest survival, but since only two of the fledglings I tracked came from nests with second-year males it was not included in models explaining fledgling survival.
10) DATE – Nests initiated earlier in the breeding season can have higher survival rates than nests initiated later on (i.e., Spanhove et al. 2009), so nest initiation date was included in models for nest survival. Date of hatching (Monró et al. 2002) and date of fledging (Yackel Adams et al. 2006, Middleton and Green 2008, Moore et al. 2010) can be correlated with fledgling survival, so date of fledging was included in models explaining fledgling survival.

11) DAYS SINCE FLEDGING – For many songbird species, fledgling mortality is highest during the first 1-7 days out of the nest, when fledglings are not yet competent fliers (Sullivan 1989, Anders et al. 1997, Naef-Daenzer et al. 2001, Cohen and Lindell 2004, Kershner et al. 2004, King et al. 2006, Yackel Adams et al. 2006, Moore et al. 2010). Time since fledging was included in models for fledgling survival.

12) YEAR – There is often yearly variation in survival estimates, so year was included in models for both nest and fledgling survival.

13) TIME SINCE HATCHING – The time between hatching and fledging ranges from 9-12 days for Rose-breasted Grosbeaks (Wyatt and Francis 2002). If older nestlings are larger and more fully developed at the time of fledging than younger ones, they could be expected to have higher post-fledging survival, especially if their feathers and wing muscles are more fully developed. Time since hatching was included in models of fledgling survival.

14) WEIGHT AT FLEDGING – The body condition of nestlings at the time of fledging can influence their ability to find suitable habitats for foraging and predator avoidance, and nestlings that are in poorer condition may have lower chances of survival (Magrath 1991, Naef-Daenzer et al. 2001, Vitz and Rodewald 2010).
Nestling weight at the time of fledging was included as a measure of body condition in models explaining fledgling survival.

15) RASPBERRY COVER – Although raspberry bushes did not produce ripe fruit during the three week period when fledglings were tracked, dense patches of raspberries could have provided camouflage and protection for fledglings before they were proficient fliers. Percent cover by raspberries was included in models explaining fledgling survival.

16) ELDERBERRY COVER – Rose-breasted Grosbeaks have been observed feeding red elderberries (*Sambucus racemosa*) to their fledglings (Stutchbury et al. 2005), and elderberries appeared to be an important food source for fledglings in my study. Percent cover by elderberry plants was included as a rough estimate of elderberry abundance in models explaining fledgling survival.

17) SHRUB COVER – Survival of Ovenbird (*Seiurus aurocapilla*) (King et al. 2006), Hooded Warbler (*Wilsonia citrina*) (Rush and Stutchbury 2008), and Rose-breasted Grosbeak (Moore et al. 2010) fledglings was positively associated with the amount of shrub cover, likely because small shrubs provide shelter from potential predators. Percent cover by small (< 2.5 cm dbh) shrubs was included as an explanatory variable in models of fledgling survival.

Shaffer’s logistic-exposure method (2004) was used to compare the set of models containing variables explaining nest survival. I considered each variable separately (11 models), together with sampling year (10 models), and combined with sampling year and date of nest initiation (9 models). I also included a set of models containing each variable separately, post-harvest treatment, and their interaction term (10 models). A null model
(containing the intercept only) and a global model (containing all the variables under consideration) were also included in my set of 42 candidate models containing 1-3 variables explaining nest survival. Shaffer’s logistic-exposure method uses Akaike’s Information Criteria (corrected for small sample sizes: AICc) (Burnham and Anderson 2002) to compare the relative strength of competing models and was implemented in the PROC GENMOD module of SAS (v. 8.02).

Fledgling survival was analyzed using the nest survival model in Program MARK (v. 6.0) (White and Burnham 1999, Schmidt et al. 2008). For each fledgling only one record was included, which corresponded to the last time that individual had been observed alive or dead. This approach to modeling survival assumes that habitat quality determines survival, and reduces bias resulting from decreasing sample sizes with time. Individual records were coded with the date of fledging, the last day the bird was known to be alive, the last day the fledgling was tracked, the fledgling’s fate (0 = survived, 1 = died), and 16 explanatory variables. I considered each variable separately (16 models), together with sampling year (15 models), combined with sampling year and time since fledging (14 models), and in models containing sampling year, date of fledging, and time since fledging (13 models). I also included models containing each variable separately, post-harvest treatment, and their interaction term (15 models), as well as a null model and global model in the set of 75 candidate models containing 1-4 variables explaining fledgling survival.

RESULTS

Do habitat features differ between used and un-used plots?

Nest Sites. – Habitat characteristics were measured at 94 Rose-breasted Grosbeak nests and at 94 corresponding random plots. Multivariate analysis of variance showed
significant differences in vegetation characteristics among post-harvest treatments ($F_{15, 149.47} = 4.54, P < 0.0001$) and between nest and random plots ($F_{5, 54} = 7.56, P < 0.0001$) but the interaction between treatment and plot type was not significant ($F_{15, 149.47} = 0.83, P = 0.642$).

Regenerative growth was significantly higher at Rose-breasted Grosbeak nest sites ($18.7 ± 2.8\%$) than at random locations ($12.8 ± 1\%$; $F_{1, 3} = 6.37, P = 0.014$; Fig. 2.1a). Sapling cover was higher at nest sites ($17.7 ± 1.5\%$) than at random locations ($12.8 ± 1.8\%$), except in the > 50 years post-harvest stands, but differences were not significant ($F_{1, 3} = 2.71, P = 0.105$; Fig. 2.1b). Understory cover was also significantly higher at nest sites ($41.7 ± 2.9\%$) than at random locations ($26.7 ± 2.0\%$; $F_{1, 3} = 18.60, P < 0.0001$; Fig. 2.1c). In contrast, Rose-breasted Grosbeaks used nest sites with significantly lower basal area ($21.7 ± 0.6 \text{ m}^2 / \text{ha}$) than was available ($25.6 ± 0.7 \text{ m}^2 / \text{ha}$; $F_{1, 3} = 21.21, P < 0.0001$; Fig. 2.1d). Canopy cover was higher at random locations ($90.9 ± 5.0\%$) than at nest sites ($70.0 ± 10.2\%$) in 2006 ($F_{1, 3} = 9.92, P = 0.010$), but differences were not significant in 2007 ($F_{1, 3} = 0.35, P = 0.565$) or 2008 ($F_{1, 3} = 1.62, P = 0.221$).

Nest height was higher on average in the > 50 years post-harvest treatment (mean = 11.08 m) than in the other stands (0-5: 8.60 m, 16-20: 9.19 m, 21-25: 9.89 m), but differences were not significant ($F_{1, 3} = 1.31, P = 0.27$). Low (0-4 m) nests accounted for 21.1% of the nests in my sample, and the highest number of these nests (16) was found in the 0-5 years post-harvest treatment (Table 2.1). Nests of medium height (4.5-9 m) comprised 33.3% of the nests I located, and occurred in approximately equal proportions in all post-harvest treatments except the > 50 years post-harvest stands, which had a lower proportion (18.8%). Nests in the sub-canopy (10-20 m) and canopy (> 20 m) layers accounted for 45.5% of the nests I monitored. High nests occurred in approximately equal proportions in all treatments except the 0-5 years post-harvest treatment which had fewer (35.1%).
harvest treatment had the highest proportion of very high nests (9.4%). In general, in the 0-5
years post-harvest stands 63.1% of the nests were located below 9 m, whereas in the 16-20,
21-25, and > 50 years post-harvest treatments the proportions were 56.8, 46.8, and 46.9%
respectively (Table 2.1).

Plots in the 0-5 years post-harvest stands had significantly lower sapling \((F_{1,3} = 5.39,
P = 0.002)\) and understory \((F_{1,3} = 4.48, P = 0.007)\) cover and lower basal area \((F_{1,3} = 8.57, P < 0.001)\) than plots in the other post-harvest treatments (Fig. 2.1b-d). In contrast, canopy
openings created by the removal of trees resulted in significantly higher cover from
regenerative growth \((F_{1,3} = 8.60, P < 0.001)\) in the 0-5 post-harvest stands than in the other
post-harvest treatments (Fig. 2.1a). By 16-20 years after harvesting, regenerative growth had
developed into a dense understory layer, giving these stands significantly lower regenerative
growth \((F_{1,3} = 8.60, P < 0.001)\) and higher understory \((F_{1,3} = 4.48, P = 0.007)\) cover than the
other post-harvest treatments (Fig. 2.1a, c). Habitat features 21-25 years after harvesting
were not significantly different from those in the 16-20 and > 50 years post-harvest stands.

Nest and random plots in the > 50 years post-harvest stands had significantly higher basal
area \((F_{1,3} = 8.57, P < 0.001)\) than those in the 16-20 and 21-25 years post-harvest stands, and
regenerative growth \((F_{1,3} = 8.60, P < 0.001)\) and sapling cover \((F_{1,3} = 5.39, P = 0.002)\) were
also high (Fig. 2.1a,b,d).

Fledgling Locations. – Habitat characteristics were measured at 85 fledgling plots and
85 random locations \((n = 44, 22, \text{ and } 19 \text{ in weeks 1, 2, and 3 post-fledging respectively})\).
Weighted multivariate analysis of variance showed significant differences in vegetation
characteristics among post-harvest treatments in week one post-fledging (Week 1: \(F_{18,201.3} =
2.95, P = 0.0001\); Week 2: \(F_{18,88.17} = 1.60, P = 0.070\); Week 3: \(F_{15,61.1} = 1.40, P = 0.175\) and
between fledgling and random plots in week one post-fledging (Week 1: \(F_{6,71} = 2.09, P =
\)
0.050; Week 2: $F_{5, 31} = 0.490, P = 0.808$; Week 3: $F_{5, 22} = 1.57, P = 0.209$). Interactions between treatment and plot type were not significant in any week post-fledging (Week 1: $F_{18, 201.3} = 0.43, P = 0.981$; Week 2: $F_{18, 88.167} = 1.38, P = 0.160$; Week 3: $F_{15, 61.13} = 0.59, P = 0.872$).

During the first week post-fledging, regenerative growth was significantly higher at locations used by Rose-breasted Grosbeak fledglings ($17.4 \pm 2.9\%$) than at random plots ($9.2 \pm 2.8\%$; $F_{1, 3} = 4.78, P = 0.032$; Fig. 2.2a). Percent cover by saplings was also significantly higher at fledgling locations ($17.4 \pm 2.8\%$) than at random plots ($10.7 \pm 1.6\%; F_{1, 3} = 4.17, P = 0.045$; Fig. 2.2b). During their first week out of the nest, fledglings used locations with more abundant small shrubs ($11.3 \pm 3.8\%$) than were available at random locations ($3.8 \pm 0.9\%; F_{1, 3} = 4.88, P = 0.030$; Fig. 2.2d). Raspberry and elderberry cover were also more abundant at fledgling locations ($8.1 \pm 3.7\%$ and $1.3 \pm 0.6\%$ respectively) than at random points ($0.8 \pm 0.4\%$ and $0.1 \pm 0.08\%$ respectively) during the first week post-fledging (raspberry: $F_{1, 3} = 4.13, P = 0.045$; elderberry: $F_{1, 3} = 4.11, P = 0.042$; Fig. 2.2e,f).

During the second and third weeks out of the nest, habitat use by fledglings was highly variable and most vegetation measurements did not significantly differ between used and un-used plots. However, during both the second and third weeks out of the nest fledglings used locations with significantly lower basal area ($22.5 \pm 1.6 \text{ m}^2/\text{ha}$ and $21.2 \pm 1.6 \text{ m}^2/\text{ha}$ respectively) than was present at random locations ($23.9 \pm 1.3 \text{ m}^2/\text{ha}$ and $26.2 \pm 1.7 \text{ m}^2/\text{ha}$ respectively; $F_{1, 3} = 2.86, P = 0.020$ and $F_{1, 3} = 3.65, P = 0.014$ respectively).

Fledgling and random plots in the 0-5 years post-harvest stands had significantly lower sapling cover ($F_{1, 3} = 3.84, P = 0.013$) and basal area ($F_{1, 3} = 8.47, P < 0.0001$) than other post-harvest treatments, and significantly higher cover from small shrubs ($F_{1, 3} = 4.65, P = 0.005$) and raspberry bushes ($F_{1, 3} = 6.38, P = 0.0007$) than were present in all other stands.
Figure 2.1. (A) Regeneration cover, (B) sapling cover, (C) understory cover, (D) basal area at nest and random plots in 12 hardwood stands in Algonquin Provincial Park harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years previously. Means and standard errors are shown.
TABLE 2.1. Number of Rose-breasted Grosbeak nests located in four height categories (low, medium, high, and very high) in 12 stands harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years prior to sampling. Number of nests in each category is shown with row percentages in brackets. Row totals represent the number of nests in each post-harvest treatment and column totals represent the number of nests in each height category.

<table>
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<th>Time since harvest</th>
<th>Low (0-4.0 m)</th>
<th>Medium (4.5 – 9 m)</th>
<th>High (10-20 m)</th>
<th>Very High (&gt; 20 m)</th>
<th>Row Total</th>
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<td>0-5</td>
<td>16 (28.1)</td>
<td>20 (35.1)</td>
<td>20 (35.1)</td>
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<td>19 (43.2)</td>
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<td>21-25</td>
<td>8 (17.0)</td>
<td>14 (29.8)</td>
<td>23 (48.9)</td>
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<td>47 (100.0)</td>
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<td>&gt; 50</td>
<td>9 (28.1)</td>
<td>6 (18.8)</td>
<td>14 (43.8)</td>
<td>3 (9.4)</td>
<td>32 (100.0)</td>
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<tr>
<td><strong>Column Total</strong></td>
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<td><strong>60 (33.3)</strong></td>
<td><strong>76 (42.2)</strong></td>
<td><strong>6 (3.3)</strong></td>
<td><strong>180 (100.0)</strong></td>
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</table>
Figure 2.2. (A) Regenerative cover, (B) sapling cover, (C) basal area, (D) small shrub (< 2.5 cm dbh), (E) raspberry cover, and (F) elderberry cover at locations occupied by fledglings and random plots in 12 hardwood stands in Algonquin Provincial Park harvested by single-tree selection 0-5, 16-20, 21-25 and > 50 years previously. Means and standard errors are shown.
Habitat characteristics in the 16-20 and 21-25 years post-harvest stands were generally intermediate between the 0-5 and > 50 years post-harvest stands, but sapling cover was significantly higher ($F_{1,3} = 3.84, P = 0.013$) in the 16-20 years post-harvest stands than in the 0-5 years post-harvest treatment (Fig. 2.2b). The > 50 years post-harvest treatment had higher sapling ($F_{1,3} = 3.84, P = 0.013$) and understory cover ($F_{1,3} = 3.18, P = 0.029$) and higher basal area ($F_{1,3} = 8.47, P < 0.0001$) than other stands.

**Do habitat features differ between nest and fledgling plots?**

Weighted multivariate analysis of variance indicated that habitat characteristics at nest sites and fledgling locations differed significantly among post-harvest treatments ($F_{15, 367.56} = 1.91, P < 0.021$), and between nest and fledgling plots ($F_{15, 367.56} = 3.06, P = 0.0001$). Interactions between treatment and plot type were not significant ($F_{45,598.04} = 1.02, P = 0.445$).

Individual split-plot ANOVAs indicated that nest plots had significantly higher percent cover from understory than was present at locations used by fledglings during their first ($F_{3,3} = 4.89, P = 0.003$) and second ($F_{3,3} = 3.89, P = 0.005$) weeks out of the nest (Fig. 2.3b). Nest plots also had significantly lower basal area than was present at locations used by fledglings during their first week out of the nest ($F_{3,3} = 9.18, P < 0.0001$) (Fig. 2.3c).

Nest and fledgling plots in 0-5 years post-harvest stands had significantly higher percent cover from regenerative growth than similar plots in the 16-20 and 21-25 years post-harvest stands ($F_{3,3} = 4.90, P = 0.003$) (Fig. 2.3a). Nest and fledgling plots in 0-5 years post-harvest stands also had significantly lower basal area than similar plots in 21-25 and > 50 years post-harvest stands ($F_{3,3} = 9.18, P < 0.0001$) (Fig. 2.3c).
FIGURE 2.3. (A) Regeneration cover, (B) understory cover, and (C) basal area at nest sites and locations occupied by fledglings 1-7, 8-14, and 15-21 days post-fledging in 12 hardwood stands harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years previously. Means and standard errors are shown.
Nest Success and Fledgling Survival

Nest Success. – A total of 173 Rose-breasted Grosbeak nests were monitored over three years (20, 73, and 80 nests respectively in the years 2006-2008), 97 (56.0%) of which were successful. Of the 73 nests that failed, 32 (43.8%) failed during the nestling stage, 22 (30.1%) failed during the egg stage, and 19 (26%) failed either very late in the egg stage or very early in the nestling stage. I also observed 25 nest building attempts that were abandoned before eggs were laid. During both the egg and nestling stages, the primary cause of nest failure was predation (68 of the 73 nests), presumably by small mammals or avian nest predators. The secondary cause of nest failure was nest abandonment during the egg stage (5 of the 73 nests), for unknown reasons.

Fledgling Survival. – Over three years 46 fledglings were radio-tagged of which 18 (38%) survived the three week-tracking period, 17 (40%) were confirmed dead, and 11 (23%) were lost during the tracking period, presumably due to malfunctioning radio-tags (n = 10) or harness failure (n = 1). The 10 cases where radio-tag failure was assumed all occurred during a two week period in 2008 when signals were lost for ten individuals that were 3-6 days post-fledging and would not have been capable of flying large distances. In all years, fledgling mortality was highest during the first week (1-7 days) post-fledging, with 12 confirmed deaths (67%) occurring during this interval. Fledgling survival to independence was similar between 2006 (67%; n = 3, 1 confirmed death) and 2007 (65%; n = 23, 8 confirmed deaths total). Unfortunately, in 2008 only 2 fledglings were tracked for the entire 21 day period (10 were lost as a result of malfunctioning radio-tags, 9 were confirmed dead).

The primary causes of fledgling mortality appeared to be predation by hawks and mammals. Four transmitters were recovered amid piles of feathers on top of elevated
perches, presumably having been left by raptors (Moore et al. 2010). One transmitter was found on the ground directly below an active Red-tailed Hawk’s (*Buteo jamaicensis*) nest, and the transmitter from another fledgling ended up in a Broad-winged Hawk’s (*Buteo platypterus*) nest. One transmitter was found in the scat of a mammal, and the remains of 5 fledglings were found buried approximately 6 cm below the leaf litter, having been partially consumed presumably by a mammal. The five remaining transmitters showed signs of predation (partial remains of fledglings, or heavily chewed transmitter harnesses), but predator identity was unclear.

**Are estimates of nest and fledgling survival correlated among post-harvest treatments?**

Mean Mayfield daily survival rate (DSR) for Rose-breasted Grosbeak nests during the egg and nestling stages was 0.967 (*n* = 173 nests) and the mean period survival rate (PSR) for the entire 24 day nesting period was 0.559. The model containing post-harvest treatment did not have any support as an explanatory variable for nest survival (AICc weight = 0.00), indicating that single-tree selection does not strongly influence nest success. When nest survival estimates for each post-harvest treatment were combined across study years, nest survival was highest in the 21-25 years post-harvest stands and lowest in the > 50 years post-harvest treatment (Fig. 2.4).

Mean daily survival rate for Rose-breasted Grosbeak fledglings was 0.920 (*n* = 47), and the probability of a fledgling surviving the entire 21 day tracking period was 0.510. The model containing post-harvest treatment had little support as an explanatory variable for fledgling survival (AICc weight = 0.01), suggesting that fledgling survival is not strongly influenced by single-tree selection harvesting. Like nest survival, fledgling survival was
FIGURE 2.4. Mayfield estimates of the probability of Rose-breasted Grosbeak nests surviving to fledge young and fledglings surviving their first three weeks out of the nest in 12 stands in Algonquin Provincial Park harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years previously. Treatment means calculated from weighted site means and standard error are shown. Samples sizes (n) are shown for the number of nests and fledglings respectively that were monitored in each treatment during 2007 and 2008.
lowest in the > 50 years post-harvest stands, but it was highest in the 16-20 years post-harvest treatment (Fig. 2.4).

The Spearman rank correlation coefficient indicated that nest and fledgling survival were not significantly correlated in harvested stands ($r = 0.28, P > 0.05; n = 12$).

**How do habitat characteristics influence nest and fledgling survival?**

*Nest Survival.* – The model with the best support for explaining variation in daily nest survival included nest initiation date, sampling year, and basal area (Table 2.2). The top nine of forty-two models tested included nest initiation date and sampling year, with weights ranging from 0.313-0.001. The model averaged estimate (regression coefficient averaged across models in the candidate set) for basal area was positive, indicating that nests were more likely to survive in areas with greater basal area (Table 2.2). Nest initiation date was negatively associated with nest survival, indicating that earlier nests had a higher probability of survival.

*Fledgling Survival.* – The model with the strongest support for explaining variation in fledgling survival included number of days since fledging (Table 2.3). The model containing days since fledging and year also had some support, and these two variables appeared in the top nineteen of seventy-five models, with weights ranging from 0.280-0.020. The model averaged estimate for days since fledging was positive, suggesting that older fledglings had a higher probability of continued survival.
TABLE 2.2. Support for models predicting daily nest survival rates of Rose-breasted Grosbeaks in Algonquin Provincial Park (2006-2008) as a function of percent cover of regenerative growth, saplings, and understory, basal area (m$^2$/ha), time-since harvest (0-5, 16-20, 21-25, or >50 years), nest concealment (%), nest height (m) and nest initiation date. Shown are model averaged parameter estimates, unconditional standard error, number of model parameters (k), deviance, Akaike’s Information Criteria corrected for small sample sizes (AICc), $\Delta_i$ (AICc model $i$ – AICc model minimum), and Akaike model weights for models that fall within 2 AICc units of the best fit model. Statistics for the global model (including all variables) and the null model (intercept only) are also shown.

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<th>Model</th>
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<th>Model Averaged Estimate</th>
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<th>K</th>
<th>Deviance</th>
<th>AICc</th>
<th>$\Delta_i$</th>
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## Table 2.3. Support for models predicting daily survival rates of Rose-breasted Grosbeak fledglings in Algonquin Provincial Park 1-21 days after fledging (2006-2008). Predictor variables include percent cover of regenerative growth, saplings, understory, canopy, small shrubs, raspberries, and elderberries, basal area (m²/ha), time since harvest, concealment (%), height (m), weight (g), fledging date, and days since fledging, days since hatching, and sampling year. Shown are model averaged parameter estimates, unconditional standard error, number of model parameters (k), deviance, Akaike’s Information Criteria corrected for small sample sizes (AICc), Δᵢ (AICc modelᵢ – AICc model minimum) and Akaike model weights for models that fall within 2 AICc units of the best fit model. Statistics for the global model (including all variables), the null model (intercept only), and the model with the most support containing post-harvesting treatment are also shown.

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<th>Model</th>
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</table>
Habitat characteristics at Rose-breasted Grosbeak nest sites and locations used by fledglings differed significantly among stands harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years post-harvest. As expected, nest and fledgling plots in the most recently harvested stands had lower basal area, lower sapling, understory and canopy cover, and more shrubs, raspberry, and elderberry bushes than plots in other post-harvest treatments. In general, nest and fledgling locations in the 16-20 and 21-25 years post-harvest treatments had lower cover from regenerative growth and higher understory cover than plots in other treatments. In the > 50 years post-harvest treatment basal area was higher than in other stands, and cover from regenerative growth, saplings, and canopy were also high. Despite these differences, which are generally consistent with structural changes reported in other long-term studies of single-tree selection (Crow et al. 2002, Kenefic and Nyland 2000), neither nest success nor fledgling survival significantly differed among post-harvest treatments. Rose-breasted Grosbeaks also exhibited plasticity in nest site selection without showing differences in survival rates in managed forest fragments in southern Ontario (Smith et al. 2007), suggesting that single-tree selection harvesting likely does not have a significant negative effect on this species.

Previous research has suggested that single-tree selection may provide suitable habitat for many forest songbirds, and may have only limited effects on their reproductive success (Barber et al. 2001, Duguay et al. 2001, Lang et al. 2002, Smith et al. 2006, Poulin et al. 2010). This appears true for Rose-breasted Grosbeaks as well, who showed no significant differences in nest success (Smith et al. 2006, 2007, Moore et al. 2010) or fledgling survival (Moore et al. 2010) in managed stands in the highly fragmented agricultural landscape of
southern Ontario. Although single-tree selection harvesting does not appear to negatively influence Rose-breasted Grosbeak survival in either fragmented or predominantly forested landscapes, there were differences in survival rates among the two landscape types. Estimates of nest survival, which ranged from 0.341 (Moore et al. 2010) to 0.390 (Smith et al. 2006, 2007) in the fragmented landscape, were considerably lower than my estimate (0.559) in the predominantly forested landscape. In contrast, fledgling survival was slightly higher (0.620) in the fragmented landscape (Moore et al. 2010) than in the predominantly forested one (0.510). The net effect of these measures suggests that overall survival is lower in the fragmented landscape, likely due to higher levels of nest predation. The contrasting patterns of nest and fledgling survival indicate either that Rose-breasted Grosbeaks respond differently to selective pressures during the nest and fledgling stages, or that nest and fledgling survival are most strongly influenced by different variables.

Estimates of nest and fledgling survival in my study were not significantly correlated among post-harvest treatments, supporting the idea that Rose-breasted Grosbeak responses to environmental factors differ between reproductive phases. Seventy percent of the fledgling deaths I observed were attributed to predation by hawks and small mammals, and 67% of these deaths occurred in the 21-25 and > 50 years post-harvest sites. Raptors and chipmunks have previously been identified as common predators of Wood Thrush (Schmidt et al. 2008) and Rose-breasted Grosbeak fledglings (Moore et al. 2010). One study found that partial harvesting in hardwood stands had relatively little impact on the density of eastern chipmunks (Holloway and Malcolm 2006), but this species is positively associated with many features present in un-logged stands, such as the number of declining trees, the density of understory cover, and the amount of downed woody debris (Bennet et al. 1994, Mahan and
Yahner 1996, Zollner and Crane 2003, Holloway and Malcolm 2006). Mature forest may also provide more open or better quality habitat for forest-breeding birds of prey such as Broad-winged Hawks, which nest in tall, large diameter trees and typically remain below a well developed canopy layer when hunting for insects, amphibians, small mammals, and birds (Goodrich et al. 1996). Higher predation by raptors and chipmunks on fledglings, but not necessarily nests, in less recently harvested stands may help explain differences in nest and fledgling survival rates among post-harvest treatments.

Significant differences also existed between the habitat characteristics present at nest sites and fledgling locations, which may help explain differences in survival patterns. Specifically, nest plots had significantly lower basal area and higher percent cover from understory than were present at locations used by fledglings during their first and second weeks out of the nest. There was substantial variation associated with the habitat measurements at locations occupied by fledglings, likely because they moved around in search of food and shelter. The high degree of movement and variation in habitat use made it difficult to identify important habitat features for fledglings during their second and third weeks out of the nest. The fledglings of some species move into habitat types that contrast significantly with those used by nesting adults (Lang et al. 2002, White et al. 2005), whereas in other species habitat use during the nesting and post-fledging periods is similar (Berkeley et al. 2007, Ciudad et al. 2009). Rose-breasted Grosbeak fledglings appeared to use similar habitats to nesting adults with only a few significant differences, but this could partially be the result of the relative similarity of habitat types available in the predominantly forested study landscape.
Rose-breasted Grosbeaks tended to use nest sites with lower basal area and higher cover from regenerative growth, saplings, and understory than was available at random locations in all post-harvest treatments. In the fragmented woodlots of southern Ontario Rose-breasted Grosbeaks also used nest sites with lower basal area and higher sapling cover than was available at random points (Smith et al. 2007). Although grosbeaks consistently build nests in locations with lower basal area, nest survival was positively associated with this habitat feature in my study. Previous research has shown that although Rose-breasted Grosbeak nest survival was positively associated with canopy cover, adults used nest sites with lower canopy cover than was present at random locations (Smith et al. 2007). Together these studies suggest that Rose-breasted Grosbeaks do not necessarily select nest sites with habitat features that maximize reproductive success. Although there is no obvious explanation for this, Smith et al. (2007) have suggested this species may be experiencing an ecological trap. Locations with lower basal area and canopy cover may appear attractive because they are typically associated with other desirable features, such as denser understory and sapling layers, which may not be present in managed forests during all stages in the harvest rotation.

The best models for explaining nest success included basal area, nest initiation date, and sampling year. Nests that were started earlier in the season and built in locations with higher basal area were more likely to be successful. Higher survival rates for nests initiated earlier in the season have been reported for several other avian species (e.g. Middleton and Green 2008, Spanhove et al. 2009). Older, more experienced birds often begin breeding earlier than less experienced adults, and higher rates of nest and juvenile survival earlier in the season are often attributed to age related differences in the timing of nest initiation.
(Hatchwell 1991, Middleton and Green 2008). Older birds may have higher reproductive success because they are more skillful than younger birds at selecting high quality nest sites, foraging, defending their offspring, and working together in pairs (Forslund and Part 1995, Martin 1995, Espie et al. 2000, Balbontin et al. 2007). In the fragmented forests of southern Ontario Rose-breasted Grosbeak nest survival was best explained by a negative association with nest concealment, and positive relationships with nest height and canopy and sapling cover (Smith et al. 2007). Differences in the composition and foraging tactics of predator communities in the two landscapes may account for the importance of different habitat features in explaining nest survival in the two landscapes.

Nest survival was also positively associated with basal area, which was significantly higher in the > 50 years post-harvest treatment than in the more recently harvested stands. However, despite the positive association between nest survival and basal area, mean nest success was slightly lower in the > 50 years post-harvest stands than in the other post-harvest treatments, suggesting that additional factors or more complex relationships among habitat measures may influence nest survival. For example, in the 16-20 and 21-25 years post-harvest treatments, which had the highest mean nest survival rates, nest sites had relatively high understory cover as well as high basal area. In comparison, the > 50 years post-harvest treatment had the highest basal area but relatively low understory cover, suggesting understory cover may have been important as well. Although the model containing understory cover did not fall within 2 units of the best fit model explaining nest survival, it was ranked third and had an AICc weight of 0.11. Alternatively, higher basal area may be beneficial up to a certain point, after which nest survival begins to decrease. Although the exact nature of the relationship between basal area and nest survival may still be uncertain,
my study suggests that if basal area is further reduced in hardwood stands following a second selection harvest, the chances of nest survival may also decrease.

In contrast to nesting adults, during their first week out of the nest, fledgling Rose-breasted Grosbeaks used locations with higher cover from regenerative growth, saplings, small shrubs, raspberry and elderberry bushes. A similar pattern of habitat use was observed in Wood Thrush (*Hylocichla mustelina*) fledglings, which moved into areas with more dense forest cover relative to the open, mature forest used by adults for nest building (Anders et al. 1998, Vega Rivera et al. 1998). Ovenbird fledglings (*Seiurus aurocapilla*) also occupied locations with greater vertical structure 0-3 m above ground than was present at nest or random plots (King et al. 2006). Due to fledgling movement the habitat characteristics observed at Rose-breasted Grosbeak fledgling locations were highly variable, but this study suggests that in predominantly forested landscapes Rose-breasted Grosbeak fledglings use areas with higher than average cover.

The fledglings of many mature-forest bird species have been observed in regenerating clear-cuts during the post-fledging period (Pagen et al. 2000, Vitz and Rodewald 2006), possibly because these areas provide increased cover for thermoregulation, protection from predators (Weathers and Sullivan 1989, Morton et al. 1991), and abundant food sources (Anders et al. 1998, Vega Rivera et al. 1998, Vitz and Rodewald 2007). In this study, during the first week after leaving their nests Rose-breasted Grosbeak fledglings used sites with higher cover from raspberry bushes than was present at random locations, and although differences were not significant, fledglings also selected areas with higher than average cover from elderberry bushes during all three weeks post-fledging. Rose-breasted Grosbeaks have been videotaped feeding on red elderberries in the wild (Stutchbury et al. 2005), and both
adults and fledglings were frequently observed feeding extensively on both elderberries and raspberries in my study area. Availability of food resources has been identified as an important determinant of fledgling movement patterns during the post-fledging period for several forest-breeding songbird species (Stutchbury et al. 2005, Vitz and Rodewald 2007, Ciudad et al. 2009). Movement patterns of Rose-breasted Grosbeak families during the post-breeding season may be partially determined by the availability of berry bushes, and since recently harvested stands had higher cover from raspberries, this treatment may represent preferred habitat during this period.

The best model to explain fledgling survival included the number of days since fledging, indicating that the probability of survival increased with fledgling age. In forest fragments, Rose-breasted Grosbeak fledgling survival was best explained by positive associations with date of fledging, patch size, and percent shrub cover (Moore et al. 2010). Many studies of forest songbirds have reported higher fledgling mortality during the first 1-7 days out of the nest (Sullivan 1989, Anders et al. 1997, Naef-Daenzer et al. 2001, Cohen and Lindell 2004, Kershner et al. 2004, King et al. 2006, Yackel Adams et al. 2006, Moore et al. 2010) when fledglings are unable to fly and capable of only limited movement. Other factors which have been commonly associated with fledgling survival prior to independence include habitat type (Krementz et al. 1989, Anders et al. 1997, Vega Rivera et al. 1998), amount of coarse woody debris, amount and structure of understory cover (Mitchell et al. 2010), age of parents (Rush and Stutchbury 2008), hatching date and fledgling mass (Monróes et al. 2002), date of fledging, and weather (Yackel Adams 2006). Although age at fledging is variable for Rose-breasted Grosbeaks (9-12 days post-hatching), and the model containing days since hatching was ranked as the third best-fit model explaining fledgling survival, the model
containing days since fledging had more support. The results of my study are consistent with
the growing body of evidence that indicates that fledgling survival increases considerably
with age, and it indicates that for Rose-breasted Grosbeaks the relationship between survival
and age may be more strongly influenced by days since fledging than the length of time spent
in the nest.

Overall, single-tree selection harvesting did not appear to have a significant negative
effect on Rose-breasted Grosbeak nest or fledgling survival. However, since fewer nests and
fledglings were monitored in the > 50 years post-harvest stands, sample sizes were smaller in
this treatment than in the others. Differences in samples sizes were addressed using weighted
analyses, but it is possible they influenced among-treatment comparisons. Incorporating a
larger number of unharvested stands into future studies so as to increase sample sizes in this
treatment may help provide insight into the relationship between basal area and nest survival.
In addition, a relatively large set of candidate models was ranked to explain the survival rates
of a relatively small number of fledglings. Increasing the number of fledglings tracked might
be one way for future studies to increase the power of the tests and confirm that single-tree
selection harvesting does not negatively influence nest or fledgling survival.

Conclusions

Despite significant differences in habitat features at nest sites and fledgling locations
in stands harvested 0-5, 16-20, 21-25, and > 50 years previously, single-tree selection did not
appear to negatively influence Rose-breasted Grosbeak nest or fledgling survival.
Differences in habitat characteristics between nest sites and locations used by fledglings
indicate that creating a mosaic of forest stands in different stages of the harvest rotation
might provide Rose-breasted Grosbeaks with access to better quality habitats during all stages in the breeding cycle. Un-even aged silvicultural techniques applied over relatively small areas likely provide higher quality habitat overall for Rose-breasted Grosbeaks than even-aged practices applied over larger areas, because they provide easier access to habitats in different stages of regeneration. Differences in nest and fledgling survival among post-harvest treatments also suggest that future studies attempting to assess the impact of forest management techniques or other habitat alterations on avian populations should consider both nest and fledgling requirements.
APPENDIX 2.1. List of candidate models used to explain Rose-breasted Grosbeak nest and fledgling survival in twelve tolerant hardwood stands in Algonquin Provincial Park harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years previously.

<table>
<thead>
<tr>
<th>Model no.</th>
<th>Predictor variables included</th>
<th>Plots for which model was used</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Regenerative growth</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>2</td>
<td>Sapling cover</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>3</td>
<td>Understory cover</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>4</td>
<td>Canopy cover</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>5</td>
<td>Basal area</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>6</td>
<td>Post-harvest treatment</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>7</td>
<td>Concealment</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>8</td>
<td>Height (nest, fledgling)</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>9</td>
<td>Date (nest initiation, fledging)</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>10</td>
<td>Year</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>11</td>
<td>Age of male parent</td>
<td>Nest</td>
</tr>
<tr>
<td>12</td>
<td>Small shrub cover</td>
<td>Fledgling</td>
</tr>
<tr>
<td>13</td>
<td>Raspberry cover</td>
<td>Fledgling</td>
</tr>
<tr>
<td>14</td>
<td>Elderberry cover</td>
<td>Fledgling</td>
</tr>
<tr>
<td>15</td>
<td>Days since fledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>16</td>
<td>Fledgling weight</td>
<td>Fledgling</td>
</tr>
<tr>
<td>17</td>
<td>Time since hatching</td>
<td>Fledgling</td>
</tr>
</tbody>
</table>

Models with two variables

| 18        | Regenerative growth + year                                 | Nest and fledgling             |
| 19        | Sapling cover + year                                       | Nest and fledgling             |
| 20        | Understory cover + year                                    | Nest and fledgling             |
| 21        | Canopy cover + year                                        | Nest and fledgling             |
| 22        | Basal area + year                                          | Nest and fledgling             |
| 23        | Post-harvest treatment + year                              | Nest and fledgling             |
| 24        | Concealment + year                                         | Nest and fledgling             |
| 25        | Height + year                                              | Nest and fledgling             |
| 26        | Date + year                                                | Nest and fledgling             |
| 27        | Age of male parent + year                                  | Nest                           |
| 28        | Small shrub cover + year                                   | Fledgling                      |
| 29        | Raspberry cover + year                                     | Fledgling                      |
| 30        | Elderberry cover + year                                    | Fledgling                      |
| 31        | Days since fledging + year                                 | Fledgling                      |
| 32        | Fledgling weight + year                                    | Fledgling                      |
| 33        | Age at fledging + year                                     | Fledgling                      |

Models with three variables

| 34        | Regenerative growth + year + date                          | Nest and fledgling             |
| 35        | Sapling cover year + year + date                           | Nest and fledgling             |
| 36        | Understory cover year + year + date                        | Nest and fledgling             |
| 37        | Canopy cover year + year + date                            | Nest and fledgling             |
| 38        | Basal area year + date                                     | Nest and fledgling             |
| 39        | Post-harvest treatment year + date                          | Nest and fledgling             |
## APPENDIX 2.1 Cont’d

<table>
<thead>
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<th>Model no.</th>
<th>Predictor variables included</th>
<th>Plots for which model was used</th>
</tr>
</thead>
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<tr>
<td>40</td>
<td>Concealment + year + date</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>41</td>
<td>Height + year + date</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>42</td>
<td>Age of male parent + year + date</td>
<td>Nest</td>
</tr>
<tr>
<td>43</td>
<td>Small shrub cover + year</td>
<td>Fledgling</td>
</tr>
<tr>
<td>44</td>
<td>Raspberry cover + year + date</td>
<td>Fledgling</td>
</tr>
<tr>
<td>45</td>
<td>Elderberry cover + year + date</td>
<td>Fledgling</td>
</tr>
<tr>
<td>46</td>
<td>Days since fledging + year + date</td>
<td>Fledgling</td>
</tr>
<tr>
<td>47</td>
<td>Fledgling weight + year + date</td>
<td>Fledgling</td>
</tr>
<tr>
<td>48</td>
<td>Age at fledging + year + date</td>
<td>Fledgling</td>
</tr>
</tbody>
</table>

**Models with four variables**

<table>
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<th>Predictor variables included</th>
<th>Plots for which model was used</th>
</tr>
</thead>
<tbody>
<tr>
<td>49</td>
<td>Regenerative growth + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>50</td>
<td>Sapling cover year + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>51</td>
<td>Understory cover + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>52</td>
<td>Canopy cover + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>53</td>
<td>Basal area + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>54</td>
<td>Post-harvest treatment + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>55</td>
<td>Concealment + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>56</td>
<td>Height + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>57</td>
<td>Small shrub cover + year + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>58</td>
<td>Raspberry cover + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>59</td>
<td>Elderberry cover + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>60</td>
<td>Fledgling weight + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>61</td>
<td>Age at fledging + year + date + dsfledging</td>
<td>Fledgling</td>
</tr>
</tbody>
</table>

**Models with an interaction term**

<table>
<thead>
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<th>Model no.</th>
<th>Predictor variables included</th>
<th>Plots for which model was used</th>
</tr>
</thead>
<tbody>
<tr>
<td>62</td>
<td>Regenerative growth, treatment, treatment * regen</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>63</td>
<td>Sapling cover, treatment, treatment * saplings</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>64</td>
<td>Understory cover, treatment, treatment * understory</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>65</td>
<td>Canopy cover, treatment, treatment * canopy</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>66</td>
<td>Basal area, treatment, treatment * basal area</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>67</td>
<td>Concealment, treatment, treatment * concealment</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>68</td>
<td>Height, treatment, treatment * height</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>69</td>
<td>Date, treatment, treatment * date</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>70</td>
<td>Year, treatment, treatment * year</td>
<td>Nest and fledgling</td>
</tr>
<tr>
<td>71</td>
<td>Age of male, treatment, treatment * age of male parent</td>
<td>Nest</td>
</tr>
<tr>
<td>72</td>
<td>Small shrubs, treatment, treatment * small shrubs</td>
<td>Fledgling</td>
</tr>
<tr>
<td>73</td>
<td>Raspberry cover, treatment, treatment * raspberries</td>
<td>Fledgling</td>
</tr>
<tr>
<td>74</td>
<td>Elderberry cover, treatment, treatment * elderberries</td>
<td>Fledgling</td>
</tr>
<tr>
<td>75</td>
<td>Days since fledging, treatment, treatment * dsfledging</td>
<td>Fledgling</td>
</tr>
<tr>
<td>76</td>
<td>Fledgling weight, treatment, treatment * fledgling weight</td>
<td>Fledgling</td>
</tr>
<tr>
<td>77</td>
<td>Age at fledging, treatment, treatment * age</td>
<td>Fledgling</td>
</tr>
</tbody>
</table>
Prey availability in hardwood forests influences many aspects of songbird reproduction, but few studies have investigated how timber harvesting in these forests influences the ability of breeding birds to provide food for their offspring. I conducted one hour feeding watches at Rose-breasted Grosbeak (Pheucticus leucopsis) nests in twelve hardwood stands in Algonquin Provincial Park which had been harvested using single-tree selection 0-5, 16-20, 21-25, and > 50 years previously. My main objectives were to test whether nestling provisioning rates (# trips/nestling/hr), male contribution to nestling provisioning, nest attendance, male contribution to nest attendance, prey load sizes, and nestling weights at the time of fledging differed with time since harvest, stage of nestling development (< 5 or > 5 days old), or age of male parent (SY or ASY). None of the response variables differed significantly among harvesting treatments in either study year (P > 0.08), but they differed with stage of nestling development in 2007 (P = 0.006), and with age of male parent in both years (P < 0.04). Specifically, in 2007 provisioning was less frequent (P < 0.01) for < 5 day old nestlings than for > 5 day old nestlings. Nest attendance was higher (P < 0.01) for < 5 day old nestlings than for > 5 day old nestlings, except in the > 50 years post-harvest treatment. In 2008, nestling provisioning was higher at nests attended by ASY males than at those attended by SY males (P = 0.002), and ASY males contributed more to nestling provisioning (P = 0.02) and to nest attendance (P < 0.01) than SY males did. Mean nestling weight was higher at nests attended by ASY males than SY males in both study years, with the difference
significant \((P = 0.04)\) in 2008, suggesting that younger breeders could not compensate for lower provisioning rates with larger prey load sizes. This study suggests that the age of the male parent is more important in determining nestling provisioning rates than time since single-tree selection harvesting.
INTRODUCTION

During the nesting season, most songbirds can be classified as ‘central place foragers’ because they carry prey back to centrally located nests (Orians and Pearson 1979). According to this model, adults forage close to their nests until available resources become depleted and then exploit food sources further away (Naef-Daenzer 2000). To maximize nestling provisioning, there should be a positive correlation between the distance travelled while foraging and the prey load size delivered to the nestlings (Grieco 2002). Predator avoidance (e.g., Newman and Caraco 1988) and conspecific competition (Giraldeau et al. 1994) can influence the relationship between time spent foraging and prey load size (Sejberg et al. 2000). Assessments of the relationship between foraging rate and prey load size can be used to test whether changes in forest structure resulting from silvicultural practices influence invertebrate abundance, prey availability, or the foraging patterns of breeding songbirds.

Previous studies in hardwood forests have shown that selection harvesting alters invertebrate communities, with some taxa increasing in abundance and others decreasing relative to un-harvested stands (Werner and Raffa 2000, Latty et al. 2006, Nol et al. 2006, Shields et al. 2008). Changes in the abundance of understory plants (Heliolä et al. 2001, Heyborne et al. 2003, Latty et al. 2006), quantity of coarse woody debris (Martikainen et al. 2000, Latty et al. 2006), availability of large diameter woody material (Hammond et al. 2004), snag volume, and gap area (Latty et al. 2006) have been linked to changes in arthropod abundance following harvesting. For insectivorous songbirds, prey abundance can influence the timing of nest initiation (Marshall et al. 2002), clutch size (Zanette et al. 2006, Robertson 2009), brood size (Preston and Rotenbury 2006), number of broods per season (Rodenhhouse and Holmes 1992, Nagy and Holmes 2005), population density

Prey availability depends on prey abundance (Holmes and Schultz 1988), prey characteristics (Cooper and Whitmore 1990, Holmes and Schultz 1988), a bird’s morphology and foraging strategies (Hutto 1990, Holmes and Robinson 1988, Holmes and Schultz 1988), and vegetation structure (Robinson and Holmes 1982, Holmes and Schultz 1988). Foraging behaviour of songbirds is strongly associated with certain aspects of forest structure, including volume and height of trees, amount of dead wood, tree species composition (Naka 2003), and canopy characteristics (Bohm and Kalko 2009). Large diameter trees with highly structured bark, large canopy volume, and large amounts of dead wood typically sustain more insects than small diameter trees, smaller volume canopies, and lesser amounts of dead wood (Mariani and Manuwal 1990). As a result, changes in forest structure and composition resulting from silvicultural practices such as single-tree selection could influence insectivorous passerines.

and American beech (*Fagus grandifolia*) (Poulson and Platt 1989, Kelty et al. 2003), whereas shade-intolerant species such as yellow birch (*Betula alleghaniensis*) and black cherry (*Prunus serotina*) are out-competed (Solomon and Grove 1999, Crow et al. 2002, Webster and Lorimer 2002). If prey becomes less abundant or more difficult to detect as a result of these changes, adults may spend more time searching for food, leave their nests undefended for longer periods of time (Arcese and Smith 1988, Wolf et al. 1990, Martin 1992), and potentially obtain less food for themselves and their nestlings. In addition, younger, less experienced birds may not be able to respond to these structural changes as efficiently as older birds (Ratcliffe et al. 1998).

The Rose-breasted Grosbeak (*Pheucticus leudovicianus*) is a Neotropical migrant that frequently breeds in both harvested and un-harvested hardwood forests across North America (Wyatt and Francis 2002, Smith et al. 2006). Although it is still relatively abundant, this species is now of conservation concern in Ontario (Smith et al. 2006) due to annual population declines of -2.4% in Ontario between 1966 and 2007 (Sauer et al. 2008) and an especially sharp decline (-8% per year) between 1985 and 2005 (Cadman et al. 2007). Rose-breasted Grosbeaks respond inconsistently to harvesting, reacting negatively to selection harvesting in the Carolinian forest (Smith et al. 2006, Thompson et al. 2009) and partial harvesting in the boreal (Vanderwel et al. 2007, 2009), positively to various silvicultural treatments in New Brunswick (Guénette and Villard 2005), but showing no difference in abundance following selection harvesting (Holmes and Pitt 2007) and clear cutting (Duguay et al. 2001) in other regions. Although we know that Rose-breasted Grosbeaks feed primarily on invertebrate prey during the nesting season
(Wyatt and Francis 2002), little information is available on how selection harvesting influences the feeding ecology of this declining species.

Here, I tested whether changes in habitat structure resulting from single-tree selection harvesting influence nestling provisioning rates in Rose-breasted Grosbeaks. My main objectives were to test whether nestling provisioning rates, male contribution to nestling provisioning and nest attendance, prey load sizes, and nestling weights differed as a function of 1) time since single-tree selection harvesting, 2) stage in the nestling’s development, and 3) age of the male parent. I predicted that nestling provisioning rates would be highest, and prey load sizes would be largest by 16-20 years post-harvest, because these stands have the well-developed sapling and understory layers (Finegan 1984, Jobes et al. 2004) preferred by this species (Wyatt and Francis 2002). Even in unaltered habitats, the energy costs of nestling care are high for adult songbirds (Thompson et al. 1998, Reid et al. 2002), and although both male and female Rose-breasted Grosbeaks provision their nestlings, females of many species provide most of the parental care (Stodola et al. 2010). If food items are easier to find and locate in the 16-20 year post-harvest stands, I would expect male contribution to nestling provisioning and nest attendance to be lower in this treatment than in the others. I also expected that nestling provisioning rates and prey load sizes would increase with nestling age (Norment 2003, Mitrus et al. 2010), and that nestlings cared for by older, more experienced males would be provisioned more frequently and receive larger prey load sizes than nestlings attended by younger males (Wunderle 1991, Limmer and Becker 2009). Finally, I predicted that if selection harvesting negatively affected the feeding ecology of Rose-
breasted Grosbeaks, nestling mass at the time of fledging would be higher in the 16-20 years post-harvest stands than in the other treatments.

**METHODS**

**Study Species**

During 2006 – 2008 Rose-breasted Grosbeaks arrived on their breeding grounds during the first week of May, began nest building by the last week of May, and cared for their nestlings throughout June and July. During the nestling provisioning period, Rose-breasted Grosbeak diets consist primarily of insects, including Coleoptera (McAtee 1908) and Lepidoptera larvae (Robinson and Holmes 1982, Holmes and Schultz 1988). Much of the time, this songbird perches and gleans invertebrate prey from the periphery of foliage and branches throughout the canopy, but it also collects invertebrates from branches and tree trunks while hovering (Holmes and Schultz 1988) and occasionally hawks for insects or forages at ground level (Wyatt and Francis 2002). When Rose-breasted Grosbeaks forage in the canopy, invertebrates are obtained from the underside of leaves during more than 65% of feeding attempts, making them lower-leaf specialists (Holmes and Schultz 1988). Both male and female Rose-breasted Grosbeaks incubate and provision their young, which typically fledge 9-12 days after hatching (Scott 1998).

**Study Area**

Fieldwork was carried out during May-August in 2007 and 2008 in twelve tolerant hardwood forest stands in Algonquin Provincial Park, Ontario, Canada (45°34’N, 78°04’W). The higher-elevation west side of this 775,000 ha park consists
primarily of mixed hardwood forest, whereas the lower-elevation east side is dominated by white and red pine (Ontario Parks 1998). The tolerant hardwood stands I studied were located in the central and southern part of this park (mean nearest neighbour distance among stands = 9.3 km, range = 1.0 – 34.2 km) (Fig. 1.1).

The hardwood forest stands were dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), and yellow birch (*Betula alleghaniensis*), and had been harvested using single-tree selection since the early 1970’s (OMNR 1998). This uneven-aged silvicultural system removes approximately one-third of the over-story basal area every 21-25 years (OMNR 1998). I studied four temporal stages in the single-tree selection cutting cycle: 0-5, 16-20, and 21-25 years post-harvest and stands that had not been logged for >50 years. Three sites (mean stand size = 34 ha) from each temporal stage were studied.

**Nest Monitoring**

Nests were monitored every 3-4 days using a mirror attached to a telescoping pole to determine date of nest initiation, clutch size, hatching date, number of nestlings, and fledging success.

**Nestling Provisioning**

Provisioning data were collected when the nestlings were 1-4 days old (*n* = 54; hereafter Stage 1 nestlings) and again when they were 6-9 days old (*n* = 33; hereafter Stage 2 nestlings). Altricial passerine nestlings can be aged based on whether their eyes are open or closed, they can vocalize or not, and the developmental stage of their pin
feathers (Jongsomjit et al. 2007). By day 5-6 after hatching Rose-breasted Grosbeak
nestlings open their eyes and are capable of making audible noises (Wyatt and Francis
2002). Nestlings were confirmed to be less than five days old if they were blind and
inaudible, and more than five days old if they could see and make sounds. To avoid
ambiguous estimates of nestling age I did not observe nestlings when they were thought
to be exactly 5 days old.

Nests were observed for 1 h periods between 06:00 and 12:00 h when nestlings
were 1-4 days old ($n = 54$, mean age = 2.2 d) and 6-9 days old ($n = 33$, mean age = 6.5 d).
Thirty-four nests were observed only during the first developmental stage, thirteen nests
were only observed when nestlings were 6-9 days old, and twenty nests were observed
during both developmental stages. Since feeding rate can vary with weather (Keller and
van Noordwijk 1994) and time of day (Cowie and Hinsley 1988), no observations were
collected if it was windy or raining, and I ensured that the proportion of observations
taken in the early (06:00-08:00), mid (08:00-10:00), and late (10:00-12:00) morning were
approximately equal among post-harvest treatments.

Observations were made using binoculars or a 20X telescope from concealed
locations at distances of approximately 15-30 m from the nest. I recorded the sex of the
bird bringing the food, the age if the bird was male (after-second-year or second-year),
the time of each feeding event, and the size of the prey delivered relative to the size of the
adult’s beak. After-second-year (hereafter ASY) males can be distinguished from
second-year (hereafter SY) males by visible differences in their plumage (Pyle 1997).
While ASY males have uniformly black primaries, black heads and backs, and well-
defined markings, SY males have less defined markings and often have brown streaking
on their heads, backs, and primary feathers (Pyle 1997). At the end of each 1 h observation period nest contents were checked using a telescoping pole with a mirror attached to the end to count the number of nestlings present. Standardized feeding rates were then calculated as the number of provisioning trips/nestling/hour.

**Prey Load Sizes**

Prey load sizes were visually assessed and categorized as small (barely visible in the adult’s beak), medium (visible in less than one-half the length of the adult’s beak), or large (filling more than one-half the adult’s beak) (Schaefer et al. 2004). When possible, I visually identified prey types into broad taxonomic groups (e.g., insect order).

**Nest Attendance**

During the one-hour nest observations, I recorded the total amount of time that an adult was present at the nest (either brooding the nestlings or sitting within c. 30 cm of the nest) and the sex of the adult in attendance. I calculated the proportion of time the nest was attended, and the proportion of the total nest attendance that was contributed by the male.

**Nestling Weights**

I weighed nestlings at the time of fledging to the nearest 0.01g using a SC-HT-S-232 digital scale. Whenever possible, multiple fledglings from each nest were weighed and an average weight for the brood was calculated. For some higher nests (22.6%; 12 of 53 nests) only one weight measurement was obtained because I was unable to capture
more than one fledgling once they had left the nest. These nests were distributed
approximately equally among the 0-5 (3.8%), 16-20 (5.7%), and 21-25 (5.6%) years post-
harvest stands, whereas the > 50 years post-harvest treatment had a slightly higher
proportion (7.5%).

Statistical Analyses

I used split-split plot analysis of variance to investigate four response variables as
a function of harvesting treatment (0-5, 16-20, 21-25, and > 50 years post-harvest), stage
of nestling development (< 5 or > 5 d old), and adult male age (SY or ASY). Harvesting
treatment was the whole-plot factor and the latter two were split-plot factors (Littell et al.
1996). Response variables were 1) nestling provisioning rate (number of
trips/nestling/h), 2) male contribution to nestling provisioning, 3) nest attendance, and 4) male contribution to nest attendance. I first used multivariate analysis of variance to test
for significant relationships between the three predictor variables and each of the
response variables, and then I used univariate split-split plot analyses of variance to
investigate each response variable separately.

For each response variable a mean value was calculated for each stand from the
data collected during the 1 h nest observation periods. In all tests, each stand mean was
weighted according to the number of observations collected in that stand. Separate
analyses were conducted for 2007 and 2008 due to significant (P < 0.002) among year
differences in nestling provisioning rates, and model assumptions of homogeneity and
normality were verified by examination of residuals. I obtained homogeneity of variance
for nestling provisioning rates using a log transformation (log(x + 1)). All statistical
analyses were conducted in the PROC GLM module of SAS (v. 8.02). I first tested the full model. If the 3-way interaction was clearly not significant (i.e., \( P > 0.15 \)) it was removed from the analysis and the model rerun. Similarly, any 2-way interactions that were clearly not significant in the second run were excluded from the final run.

I used contingency table analysis to investigate prey load size (small, medium, or large) as a function of harvesting treatment (0-5, 16-20, 21-25, and > 50 years post-harvest), stage of nestling development (< 5 or > 5 d old), and adult male age (SY or ASY). Model significance was determined using the Mantel-Haenszel Chi-square test statistic that is appropriate when 50% or more of the expected cell frequencies are less than 5 (SAS 2001). Analyses were conducted in the PROC FREQ module of SAS (v. 8.02).

I could not use split-split plot analyses of variance to investigate nestling weight at the time of fledging as a function of harvesting treatment (0-5, 16-20, 21-25, and > 50 years post-harvest) and male age (SY or ASY) due to insufficient sample size (\( n = 63 \)). Since harvesting treatment did not have a significant effect on any of the other response variables tested, I collapsed harvesting treatment into just two levels: harvested (i.e., 0-25 years post-harvest) and unharvested (> 50 years post-harvest) for inclusion into the analyses of nestling weights. Split-plot analysis of variance was conducted in SAS using the procedure described above to investigate nestling weight as a function of harvest treatment and male age.
RESULTS

Multivariate analysis of variance indicated that the response variables differed significantly among study years ($F_{23.4, 48.75} = 8.89, P = 0.002$), so separate analyses were performed for 2007 and 2008. Multivariate analysis of variance indicated that there were no significant differences in nestling provisioning rates, male contribution to nestling provisioning, nest attendance, or male contribution to nest attendance among post-harvest treatments in either study year (2007: $F_{12, 26.75} = 1.48, P = 0.192$; 2008: $F_{12, 39.98} = 1.83, P = 0.076$). In 2007, response variables differed significantly with stage of nestling development ($F_{4,10} = 6.87, P = 0.006$) but there was a significant interaction between stage of nestling development and harvesting treatment ($F_{12, 26.75} = 3.95, P = 0.002$) for nest attendance and male contribution to nest attendance. In 2008, response variables did not differ significantly between stages of nestling development ($F_{4,15} = 1.27, P = 0.327$). Response variables differed significantly with age of male parent during both study years (2007: $F_{4,10} = 3.64, P = 0.044$; 2008: $F_{4,15} = 6.44, P = 0.003$) but there was a significant interaction between harvest treatment and male age in 2007 ($F_{12, 26.75} = 2.89, P = 0.011$) for nest attendance, and an almost significant interaction between harvest treatment and male age in 2008 ($F_{12, 39.98} = 1.92, P = 0.061$) for nestling provisioning rates.

Nestling Provisioning Rates

In total I completed 1 h nest watches at 130 nests (90 in 2007 and 40 in 2008). Nestlings were provisioned on average at a rate of 0.67 trips/nestling/h (SE = 0.07, range = 0-4.33 trips/nestling/h, $n = 130$). Nestling provisioning rates did not differ significantly among harvest treatments in either year (2007: $F_{1,3} = 0.21, P = 0.887$; 2008: $F_{1,3} = 2.77, P$
= 0.078), although provisioning rates were lowest in the > 50 years post-harvest stands in both study years (Table 3.1). Provisioning was less frequent for Stage 1 nestlings (< 5 days old) than for Stage 2 nestlings (> 5 days old) in all post-harvest treatments in 2007 ($F_{1,3} = 9.79, P = 0.005$), but in 2008 differences were not significant ($F_{1,3} = 1.72, P = 0.209$), and the mean provisioning rate in the 0-5 years post-harvest stands was higher for Stage 1 nestlings than for Stage 2 nestlings (interaction: $F_{1,3} = 3.67, P = 0.036$). Nestling provisioning was more frequent at nests attended by ASY males than at those attended by SY males in all post-harvest treatments in 2007, although not significantly so ($F_{1,3} = 3.47, P = 0.078$). Mean provisioning rates were significantly higher at nests attended by ASY males in all stands in 2008 ($F_{1,3} = 13.45, P = 0.002$) as well, except the 21-25 years post-harvest treatment (interaction: $F_{1,3} = 3.67, P = 0.063$) (Table 3.1).

**Male Contribution to Nestling Provisioning**

On average, males contributed 35.2 (± 3.2 SE) % of the feeding events. Male contribution to nestling provisioning did not differ significantly among post-harvest treatments in either year (2007: $F_{1,3} = 1.54, P = 0.243$; 2008: $F_{1,3} = 1.27, P = 0.31$), and among-treatment differences were not consistent between years (Table 3.2). Male contribution to nestling provisioning did not differ significantly with nestling age in either year (2007: $F_{1,3} = 1.50, P = 0.238$; 2008: $F_{1,3} = 0.01, P = 0.952$), but in both years it tended to be lower for Stage 1 than Stage 2 nestlings in all stands except the > 50 years post-harvest stands. In 2007, contributions from ASY and SY males did not consistently differ among post-harvested treatments ($F_{1,3} = 1.52, P = 0.236$), but in 2008 ASY males
contributed significantly more ($F_{1,3} = 6.68, P = 0.017$) than SY males in all post-harvest treatments except the 16-20 years post-harvest stands.

Nest Attendance

Nests were attended by adults 66.7 ($\pm$ 3.2) % of the time, with male attendance accounting for only 18.8 ($\pm$ 1.9) % of that time. Nest attendance did not significantly differ among harvest treatments in either year (2007: $F_{1,3} = 2.32, P = 0.123$; 2008: $F_{1,3} = 0.47, P = 0.709$), and trends were not consistent among study years (Table 3.3). In 2007, nest attendance was higher when nestlings were < 5 days old than when nestlings were > 5 days old ($F_{1,3} = 8.18, P = 0.013$), except in the > 50 years post-harvest treatment (interaction: $F_{1,3} = 4.35, P = 0.025$). In 2008, nest attendance was also generally higher for < 5 day old nestlings, but not significantly so ($F_{1,3} = 1.23, P = 0.281$). In 2007, ASY males attended their nests less than SY males ($F_{1,3} = 0.19, P = 0.673$) except in the > 50 years post-harvest treatment (interaction: $F_{1,3} = 3.95, P = 0.033$). In 2008, nest attendance by ASY and SY males did not differ significantly among harvest treatments ($F_{1,3} = 1.23, P = 0.281$).

Male Contribution to Nest Attendance

Nest attendance was observed at 102 nests with ASY males and 28 nests with SY males. The proportion of time males spent at the nest relative to females differed significantly with time since harvest in both study years (2007: $F_{1,3} = 3.80, P = 0.031$; 2008: $F_{1,3} = 4.53, P = 0.013$). In 2007, male contribution was significantly lower in the 16-20 year post-harvest treatment than in the other treatments, but in 2008 male
TABLE 3.1. Mean nestling provisioning rates at Rose-breasted Grosbeak nests in 12 hardwood stands in Algonquin Provincial Park harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years prior to study (standard errors and sample sizes are in parentheses). Mean nestling provisioning rates (no. trips/ nestling/ h) are presented for nests attended by second-year (SY) and after-second-year (ASY) males, and for nests with Stage 1 (< 5 days old) and Stage 2 (> 5 days old) nestlings.

<table>
<thead>
<tr>
<th>Time since harvest (years)</th>
<th>0-5</th>
<th>16-20</th>
<th>21-25</th>
<th>&gt;50</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2007</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overall treatment mean</td>
<td>0.676 (0.175, 34)</td>
<td>0.667 (0.191, 14)</td>
<td>0.520 (0.142, 26)</td>
<td>0.459 (0.177, 16)</td>
</tr>
<tr>
<td>Nestling development</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage 1</td>
<td>0.391 (0.081, 22)</td>
<td>0.002 (0.001, 6)</td>
<td>0.314 (0.082, 16)</td>
<td>0.250 (0.164, 8)</td>
</tr>
<tr>
<td>Stage 2</td>
<td>1.193 (0.447, 12)</td>
<td>1.167 (0.189, 8)</td>
<td>0.850 (0.330, 10)</td>
<td>0.667 (0.309, 8)</td>
</tr>
<tr>
<td>Male Age</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>ASY</td>
<td>0.766 (0.193, 30)</td>
<td>0.800 (0.249, 10)</td>
<td>0.507 (0.154, 23)</td>
<td>0.612 (0.220, 12)</td>
</tr>
<tr>
<td>SY</td>
<td>0.002 (0.001, 4)</td>
<td>0.335 (0.193, 4)</td>
<td>0.670 (0.001, 3)</td>
<td>0.001 (0.001, 4)</td>
</tr>
<tr>
<td><strong>2008</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overall treatment mean</td>
<td>0.767 (0.290, 10)</td>
<td>0.765 (0.178, 10)</td>
<td>1.137 (0.252, 11)</td>
<td>0.667 (0.190, 9)</td>
</tr>
<tr>
<td>Nestling development</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Stage 1</td>
<td>1.083 (0.293, 6)</td>
<td>0.570 (0.115, 7)</td>
<td>0.811 (0.220, 7)</td>
<td>0.667 (0.202, 7)</td>
</tr>
<tr>
<td>Stage 2</td>
<td>0.436 (0.172, 4)</td>
<td>1.220 (0.485, 3)</td>
<td>1.707 (0.493, 4)</td>
<td>0.665 (0.665, 2)</td>
</tr>
<tr>
<td>Male Age</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>ASY</td>
<td>1.767 (0.290, 8)</td>
<td>0.582 (0.145, 4)</td>
<td>1.585 (0.338, 6)</td>
<td>1.000 (0.001, 6)</td>
</tr>
<tr>
<td>SY</td>
<td>0.500 (0.001, 2)</td>
<td>0.887 (0.281, 6)</td>
<td>0.600 (0.214, 5)</td>
<td>0.141 (0.001, 3)</td>
</tr>
</tbody>
</table>
TABLE 3.2. Mean proportion of feeding events contributed by male Rose-breasted Grosbeaks in 12 hardwood stands in Algonquin Provincial Park harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years prior to study (stand errors and sample sizes are in parentheses). Mean proportion of feeding events are presented for second-year (SY) and after-second-year (ASY) males, and for nests with Stage 1 (< 5 days old) and Stage 2 (> 5 days old) nestlings.

<table>
<thead>
<tr>
<th>Time since harvest (years)</th>
<th>0-5</th>
<th>16-20</th>
<th>21-25</th>
<th>&gt;50</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall treatment mean</td>
<td>0.466 (0.068, 34)</td>
<td>0.338 (0.081, 14)</td>
<td>0.286 (0.101, 26)</td>
<td>0.125 (0.060, 16)</td>
</tr>
<tr>
<td>Nestling development</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Stage 1</td>
<td>0.405 (0.082, 22)</td>
<td>0.154 (0.067, 6)</td>
<td>0.222 (0.088, 16)</td>
<td>0.167 (0.110, 8)</td>
</tr>
<tr>
<td>Stage 2</td>
<td>0.580 (0.118, 12)</td>
<td>0.522 (0.131, 8)</td>
<td>0.400 (0.245, 10)</td>
<td>0.082 (0.054, 8)</td>
</tr>
<tr>
<td>Male Age</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ASY</td>
<td>0.496 (0.069, 30)</td>
<td>0.309 (0.082, 10)</td>
<td>0.250 (0.115, 23)</td>
<td>0.167 (0.077, 12)</td>
</tr>
<tr>
<td>SY</td>
<td>0.001 (0.000, 4)</td>
<td>0.500 (0.289, 4)</td>
<td>0.500 (0.001, 3)</td>
<td>0.001 (0.000, 4)</td>
</tr>
<tr>
<td>Nestling development</td>
<td></td>
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</tr>
<tr>
<td>Stage 1</td>
<td>0.274 (0.107, 6)</td>
<td>0.357 (0.148, 7)</td>
<td>0.486 (0.110, 7)</td>
<td>0.500 (0.159, 7)</td>
</tr>
<tr>
<td>Stage 2</td>
<td>0.300 (0.200, 4)</td>
<td>0.167 (0.167, 3)</td>
<td>0.518 (0.017, 4)</td>
<td>0.375 (0.375, 2)</td>
</tr>
<tr>
<td>Male Age</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ASY</td>
<td>0.342 (0.110, 8)</td>
<td>0.292 (0.172, 4)</td>
<td>0.578 (0.087, 6)</td>
<td>0.708 (0.109, 6)</td>
</tr>
<tr>
<td>SY</td>
<td>0.001 (0.000, 2)</td>
<td>0.305 (0.163, 6)</td>
<td>0.400 (0.100, 5)</td>
<td>0.001 (0.000, 3)</td>
</tr>
</tbody>
</table>
TABLE 3.3. Mean nest attendance at Rose-breasted Grosbeak nests in 12 hardwood stands in Algonquin Provincial Park harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years prior to study (standard errors and sample sizes are in parentheses). Mean nest attendance is presented for nests attended by second-year (SY) and after-second-year (ASY) males, and for nests with Stage 1 (< 5 days old) and Stage 2 (> 5 days old) nestlings.

<table>
<thead>
<tr>
<th>Time since harvest (years)</th>
<th>0-5</th>
<th>16-20</th>
<th>21-25</th>
<th>&gt;50</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall treatment mean</td>
<td>0.694 (0.053, 34)</td>
<td>0.581 (0.084, 14)</td>
<td>0.713 (0.081, 26)</td>
<td>0.595 (0.120, 16)</td>
</tr>
<tr>
<td>Nestling development</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage 1</td>
<td>0.719 (0.059, 22)</td>
<td>0.793 (0.065, 6)</td>
<td>0.998 (0.002, 16)</td>
<td>0.500 (0.189, 8)</td>
</tr>
<tr>
<td>Stage 2</td>
<td>0.645 (0.108, 12)</td>
<td>0.422 (0.110, 8)</td>
<td>0.257 (0.101, 10)</td>
<td>0.690 (0.152, 8)</td>
</tr>
<tr>
<td>Male Age</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ASY</td>
<td>0.673 (0.055, 30)</td>
<td>0.464 (0.091, 10)</td>
<td>0.689 (0.086, 23)</td>
<td>0.793 (0.108, 12)</td>
</tr>
<tr>
<td>SY</td>
<td>1.000 (0.001, 4)</td>
<td>0.875 (0.072, 4)</td>
<td>1.000 (0.001, 3)</td>
<td>0.002 (0.001, 4)</td>
</tr>
<tr>
<td>Nestling development</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage 1</td>
<td>0.675 (0.099, 10)</td>
<td>0.827 (0.102, 10)</td>
<td>0.663 (0.092, 11)</td>
<td>0.576 (0.152, 9)</td>
</tr>
<tr>
<td>Stage 2</td>
<td>0.647 (0.131, 6)</td>
<td>0.860 (0.578, 7)</td>
<td>0.721 (0.115, 7)</td>
<td>0.593 (0.167, 7)</td>
</tr>
<tr>
<td>Male Age</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ASY</td>
<td>0.658 (0.110, 8)</td>
<td>0.820 (0.149, 4)</td>
<td>0.705 (0.090, 6)</td>
<td>0.385 (0.182, 6)</td>
</tr>
<tr>
<td>SY</td>
<td>1.000 (0.001, 2)</td>
<td>0.665 (0.143, 6)</td>
<td>0.612 (0.183, 5)</td>
<td>0.957 (0.043, 3)</td>
</tr>
</tbody>
</table>
contribution was significantly higher in this treatment than in the others (Table 3.4). In 2007, males contributed significantly more to nest attendance when nestlings were < 5 days old than when they were > 5 days old ($F_{1,3} = 8.54, P = 0.010$) except in the > 50 years post-harvest treatment (interaction: $F_{1,3} = 5.33, P = 0.010$). In 2008 nest attendance by males was also higher when nestling were < 5 days old, but not significantly so ($F_{1,3} = 3.36, P = 0.081$). ASY males contributed significantly more to nest attendance than SY males in both study years (2007: $F_{1,3} = 13.45, P = 0.002$; 2008: $F_{1,3} = 17.31, P < 0.001$).

**Prey Load Sizes**

During 37 of 73 (51%) feeding events it was possible for observers to accurately identify the type of food item being delivered to the nestlings. Insect matter which could not be identified to family was delivered to nestlings during 16 feeding events (22%), adult Lepidoptera were brought during 11 visits (15%), and larval Lepidoptera were brought during 8 feeding events (11%). Rose-breasted Grosbeak adults were also observed feeding dragonflies (1%) and leaf buds (1%) to their nestlings.

Small prey loads were the most frequently delivered in all post-harvest treatments except the 16-20 years post-harvest stands, where large loads were the most frequently provided, although differences were not significant ($X^2 = 3.098, df = 1, P = 0.078$) (Table 3.5).

The age of the male parent was not significantly associated with the prey load sizes delivered ($X^2 = 1.576, df = 1, P = 0.209$). Small prey loads were most frequently delivered at nests attended by ASY males, followed by large and then medium loads. At nests attended
TABLE 3.4. Mean nest attendance contributed by male Rose-breasted Grosbeaks in 12 hardwood stands in Algonquin Provincial Park harvested by single-tree selection 0-5, 16-20, 21-25, and > 50 years prior to study (standard errors and sample sizes are in parentheses). Mean nest attendance is presented for second-year (SY) and after-second-year (ASY) males, and for nests with Stage 1 (< 5 days old) and Stage 2 (> 5 days old) nestlings.

<table>
<thead>
<tr>
<th>Time since harvest (years)</th>
<th>0-5</th>
<th>16-20</th>
<th>21-25</th>
<th>&gt;50</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2007</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overall treatment mean</td>
<td>0.282 (0.045, 34)</td>
<td>0.056 (0.182, 14)</td>
<td>0.220 (0.037, 26)</td>
<td>0.162 (0.045, 16)</td>
</tr>
<tr>
<td>Nestling development</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage 1</td>
<td>0.388 (0.053, 22)</td>
<td>0.280 (0.103, 6)</td>
<td>0.298 (0.025, 16)</td>
<td>0.132 (0.053, 8)</td>
</tr>
<tr>
<td>Stage 2</td>
<td>0.082 (0.040, 12)</td>
<td>0.085 (0.033, 8)</td>
<td>0.080 (0.049, 10)</td>
<td>0.192 (0.075, 8)</td>
</tr>
<tr>
<td>Male Age</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ASY</td>
<td>0.301 (0.046, 30)</td>
<td>0.211 (0.065, 10)</td>
<td>0.215 (0.043, 23)</td>
<td>0.217 (0.051, 12)</td>
</tr>
<tr>
<td>SY</td>
<td>0.001 (0.000, 4)</td>
<td>0.025 (0.014, 4)</td>
<td>0.250 (0.000, 3)</td>
<td>0.001 (0.000, 4)</td>
</tr>
<tr>
<td><strong>2008</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overall treatment mean</td>
<td>0.094 (0.043, 10)</td>
<td>0.820 (0.053, 10)</td>
<td>0.125 (0.043, 11)</td>
<td>0.070 (0.042, 9)</td>
</tr>
<tr>
<td>Nestling development</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage 1</td>
<td>0.137 (0.068, 6)</td>
<td>0.204 (0.070, 7)</td>
<td>0.160 (0.062, 7)</td>
<td>0.900 (0.052, 7)</td>
</tr>
<tr>
<td>Stage 2</td>
<td>0.034 (0.034, 4)</td>
<td>0.130 (0.098, 3)</td>
<td>0.065 (0.009, 4)</td>
<td>0.001 (0.000, 2)</td>
</tr>
<tr>
<td>Male Age</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ASY</td>
<td>0.113 (0.050, 8)</td>
<td>0.360 (0.037, 4)</td>
<td>0.138 (0.045, 6)</td>
<td>0.105 (0.059, 6)</td>
</tr>
<tr>
<td>SY</td>
<td>0.001 (0.000, 2)</td>
<td>0.063 (0.031, 6)</td>
<td>0.110 (0.079, 5)</td>
<td>0.001 (0.000, 3)</td>
</tr>
</tbody>
</table>
TABLE 3.5. Observed frequencies for prey load sizes delivered to Rose-breasted Grosbeak nests in 12 hardwood stands in Algonquin Provincial Park harvested by single-tree selection (row percents are in parentheses). Mean prey load sizes are presented for harvest treatment (0-5, 16-20, 21-25, and > 50 years post-harvest), for nests with < 5 or > 5 days old nestlings, and for nests attended by after-second-year (ASY) and second-year (SY) male parents.

<table>
<thead>
<tr>
<th>Prey Load Size</th>
<th>Small</th>
<th>Medium</th>
<th>Large</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Years Since Harvest</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0-5</td>
<td>35 (51.5)</td>
<td>19 (27.9)</td>
</tr>
<tr>
<td></td>
<td>16 – 20</td>
<td>13 (35.1)</td>
<td>9 (24.3)</td>
</tr>
<tr>
<td></td>
<td>21 – 25</td>
<td>29 (46.8)</td>
<td>17 (27.4)</td>
</tr>
<tr>
<td></td>
<td>&gt; 50</td>
<td>14 (63.6)</td>
<td>2 (9.1)</td>
</tr>
<tr>
<td></td>
<td>Nestling Age</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>&lt; 5 days</td>
<td>45 (60.0)</td>
<td>23 (30.7)</td>
</tr>
<tr>
<td></td>
<td>&gt; 5 days</td>
<td>45 (39.8)</td>
<td>24 (21.2)</td>
</tr>
<tr>
<td></td>
<td>Male Age</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>ASY</td>
<td>81 (50.0)</td>
<td>38 (23.4)</td>
</tr>
<tr>
<td></td>
<td>SY</td>
<td>14 (48.3)</td>
<td>9 (31.0)</td>
</tr>
</tbody>
</table>
by SY males small prey loads were also most frequently delivered, followed by medium and then large loads.

**Nestling Weights at Fledging**

Mean nestling weight at the time of fledging was 31.1 g (± 0.4 g) (range = 22.5 – 37.5 g, n = 63). Mean nestling weight did not significantly differ with harvest treatment in 2007 (harvested: 30.6g; unharvested: 30.3g; $F_{1,1} = 0.19, P = 0.665$) or in 2008 (harvested: 31.5g; unharvested 32.3g; $F_{1,1} = 0.19, P = 0.672$). Mean nestling weight was higher at nests attended by ASY males than SY males in both 2007 (ASY: 30.8g; SY: 29.6g) and 2008 (ASY: 32.0g; SY: 30.3g) but only significantly so in 2008 (2007: $F_{1,1} = 1.87, P = 0.180$; 2008: $F_{1,1} = 4.80, P = 0.043$).

**DISCUSSION**

**Single-tree Selection Harvesting**

Nestling provisioning rates, nest attendance, the size of prey loads being delivered to nestlings, and nestling weights did not significantly differ among post-harvest treatments in either study year. Previous research has found that harvesting can alter prey availability for insectivorous songbirds (Pettersson et al. 1995, Duguay et al. 2000), but most studies have focused on the effects of clear-cutting on ground-dwelling arthropods (Niemelä et al. 1993, Greenberg and McGrane 1996, Marra and Edmonds 1998, Heliölä et al. 2001, Koivula et al. 2002). Studies of invertebrate responses to less-intensive silvicultural methods are less frequent (Koivula 2002, Moore et al. 2002, Siira-Pietikainen et al. 2003, Pihlaja et al. 2006),
and most focus on changes in diversity and species richness (i.e., Werner and Raffa 2000, Ulyshen et al. 2004, Latty et al. 2006, Shields et al. 2008), making potential changes in prey availability for songbirds difficult to assess (Halaj et al. 2008). Two studies concluded that there was no difference in overall abundance of ground invertebrates following selection harvesting (Atlegrim and Sjoberg 1996, Moore et al. 2002), but one study found that in the first fifteen years after single-tree selection harvesting there was an increase in the abundance of generalist and open habitat ground beetles, but similar species richness compared to unharvested hardwood stands (Vance and Nol 2003). I am unaware of any studies which have investigated the consequences of single-tree selection for nestling provisioning rates or nestling condition at the time of fledging.

Nestling growth rates have been linked to variations in food abundance resulting from natural causes (Price 1985, Dias and Blondel 1996, Holmes et al. 1996) and from clear-cut harvesting (Duguay et al. 2000). My study suggests that if there were any changes in arthropod abundance or prey availability resulting from single-tree selection harvesting they did not appear to have a significantly negative influence on the Rose-breasted Grosbeak’s ability to find food during the nestling phase.

Studies investigating changes in arthropod diversity and species richness following selection harvesting show that responses are largely taxon specific, with groups that favour more open habitat increasing whereas mature forest groups decrease in abundance (Werner and Raffa 2000, Latty et al. 2006, Shields et al. 2008). In particular, spiders (Arachnida) decreased following harvesting (Moore et al. 2002), millipedes (Polydesmida), snails (Stylommatophora) (Strayer et al. 1986, Moore et al. 2002), hoverflies (Diptera), bees
(Hymenoptera), and click beetles (Coleoptera) (Nol et al. 2006) were more abundant, and there was no difference in the abundance of Carabid beetles (Coleoptera) (Moore et al. 2002) and crickets (Orthoptera) (Moore et al. 2002) before and after harvesting. In addition, wood-boring insects (Ulyshen et al. 2004, Shields et al. 2008), grasshoppers (Orthoperta) and wolf-spiders (Araneae) (Shields et al. 2008) were more abundant in canopy gaps than in surrounding areas with higher canopy cover, but weevils (Coleoptera) (Shields et al. 2007) and rove beetles (Coleoptera) (Yu et al. 2006) were less abundant in these areas. If any taxon-specific changes in invertebrate abundance occurred after single-tree selection, Rose-breasted Grosbeaks were able to compensate sufficiently to maintain nestling provisioning rates and nestling masses at the time of fledging.

The absence of significant differences in nestling provisioning rates, nest attendance, and nestling weights among post-harvest treatments could be the result of minimal changes in arthropod abundance or prey availability following single-tree selection harvesting (Atlegrim and Sjoberg 1996, Moore et al. 2002). Alternatively, while there is evidence to suggest that food is limiting for songbirds during the breeding season (Martin 1986), it is possible that Rose-breasted Grosbeaks were able to compensate for any changes in food availability by altering their foraging behaviour. For example, Coquerel’s Coua (Coua coquereli) were able to maintain their rate of prey capture despite structural changes following logging by adjusting their feeding activities (Chouteau 2009). Feeding rate can also vary with weather (Keller and van Noordwijk 1994), time of day (Cowie and Hinsley 1988), and intensity of nestling begging (Ottosson et al. 1997, Burford et al. 1998, Greico 2001), and although I do not think it is likely given the relatively large sample sizes here,
variations in feeding rates caused by these factors may have obscured differences among post-harvest treatments.

A lack of significant differences in the proportion of time Rose-breasted Grosbeaks allocated to nest attendance, or in the proportion of nest attendance provided by males in the varying post-harvest treatments also supports the conclusion that single-tree selection had minimal impacts on Rose-breasted Grosbeak feeding ecology. Fedy and Martin (2009) demonstrated that time spent foraging was negatively correlated with time spent brooding by females of Red-faced Warblers (*Cardellina rubrifrons*) and Gray-headed Juncos (*Junco hyemalis caniceps*). When males were not in attendance females spent more time being vigilant, their foraging efficiency decreased, and they spent less time on the nest (Fedy and Martin 2009). In my study nest attendance and nestling provisioning rates were both slightly higher in more recently harvested stands than in un-harvested ones, which suggests that prey were more abundant or more easily located and captured after selection cutting. Since male contribution to nest attendance was also slightly higher in more recently harvested stands, an alternative hypothesis is that predation pressure, and the need for nest defence, were also higher following selection harvesting. However, no aspect of Rose-breasted Grosbeak feeding ecology that I studied showed consistently significant differences among post-harvest treatments.

**Nestling Development**

Nestling provisioning was less frequent and nest attendance was higher for < 5 day old nestlings than for > 5 day old nestlings, but differences were only significant in 2007,
possibly as a result of larger sample sizes during that year. Larger nestlings have greater energy requirements, and in many species both males and females increase the frequency of feeding as nestlings mature (e.g. Haggerty 1992, Norment 2003; Mitrus et al. 2010). In addition, parents adjust their provisioning rates and the amount of food they bring according to the frequency and intensity of nestling begging, and older nestlings are capable of more vigorous and sustained demands (Haggerty 1992). Also as expected, Rose-breasted Grosbeak nest attendance was higher when nestlings were <5 days old than when nestlings were >5 days old during both study years. In many passerines the amount of time spent brooding decreases with the age of the nestlings, partially because more time is spent foraging and thermoregulatory requirements of nestlings are lower (Moreno 1987, Sanz and Moreno 1995, Sanz and Tinbergen 1999, Chastel and Kersten 2002).

In both study years male Rose-breasted Grosbeaks contributed less to nestling provisioning and nest attendance than females did during both stages of nestling development. According to Evolutionary Stable Strategy (ESS) models, males and females of monogamous species with biparental care should make approximately equal contributions to parental care (Maynard-Smith 1977, Winkler 1987). However, in situations where paternity is uncertain or the opportunity for additional fertilizations is high, males may provide less parental care than females (Maynard-Smith 1977, Breitwisch et al. 1986, Smith et al. 1988, Westneat 1988). Males contribute slightly less to nestling provisioning than females in Northern Mockingbirds (Mimus polyglottos) (Breitwisch et al. 1986), Tree Swallows (Tachycineta bicolor) (Leffelaar and Robertson 1986), Pied Flycatchers, (Ficedula hypoleuca) (Alatalo et al. 1988), Great Tits (Parus Major) (Smith et al. 1988) and
Eastern Phoebes (*Sayornis phoebe*) (Conrad and Robertson 1993), and research has shown that up to 40% of nests contain nestlings sired through extra-pair copulations in some species of songbirds (Stutchbury et al. 1997). Future assessments of paternity in Rose-breasted Grosbeak nestlings are needed to determine if high rates of extra-pair copulations can account for the lower contribution to parental care by the males relative to the females of this species.

Rose-breasted Grosbeak males’ contribution to provisioning almost doubled for > 5 day old nestlings (39.5%) relative to < 5 day old nestlings (23%), but differences were not significant in either study year, possibly as a result of small sample sizes and high variation among post-harvest treatments. No significant differences in the proportion of nestling provisioning provided by males between the two stages suggests that male and female Rose-breasted Grosbeaks increase their feeding effort at the same rate during nestling development. In some species, including Great Tits (*Parus major*) (Sanz and Tinbergen 1999), Eastern Kingbirds (*Tyrannus tyrannus*) (Morehouse and Brewer 1968), Gray Catbirds (*Dumetella carolinensis*) (Johnson and Best 1982), and Eastern Phoebes (*Sayornis phoebe*) (Conrad and Robertson 1993) males contribute more to nestling provisioning during the early stages, while the females brood. Rose-breasted Grosbeak males contributed significantly more to nest attendance during the early stages (when nestlings were < 5 days old) than later on, but did not alter their relative contribution to nestling provisioning. This suggests that when females cannot adequately meet the conflicting demands of brooding and foraging, Rose-breasted Grosbeak males will contribute proportionally more to nest attendance rather than to nestling provisioning.
Age of Male Parent

Nestling provisioning rates were lower at nests attended by younger, less experienced males than at nests with older males, and the younger adults were unable to compensate by providing larger prey load sizes. As a result, nestlings raised by younger males weighed less at the time of fledging than nestlings reared by older males. Other studies have found that the age of both male and female parents can influence the date of clutch initiation, clutch size (Reynolds 1997), number of fledglings produced (Préault et al. 2005, Brown and Roth 2009), nestling condition (Préault et al. 2005, but see Wheelwright and Schultz 1994), and quality of parental care (Préault et al. 2005). The body condition of nestlings at the time of fledging can influence their ability to find suitable habitats for foraging and predator avoidance, and as a result, fledglings in poorer condition may have lower chances of survival (Magrath 1991, Naef-Daenzer et al. 2001, Vitz and Rodewald 2010; but see Anders et al. 1997). The correlation between body condition and fledgling survival suggests that for Rose-breasted Grosbeaks, the offspring of first-time breeders, which weigh less at the time of fledging, may have a fitness disadvantage relative to offspring raised by more experienced adults.

Several hypotheses have been proposed to explain differences in reproductive success between SY and ASY adults (reviewed in Curio 1983, Forslund and Pärt 1995, Martin 1995). The selection hypothesis suggests that reproductive success appears higher in older individuals because inferior phenotypes, which would have lower success, experience high mortality at young ages. The recruitment hypothesis proposes that younger individuals may postpone breeding in order to accumulate sufficient resources to successfully breed later in life. According to the restraint hypothesis, older individuals should have higher reproductive
output because survival and reproductive value decrease with age. Finally, the constraint hypothesis suggests that older individuals have higher reproductive success because parental skills such as nest-site selection, foraging ability, coordination between partners, and offspring defence improve with age (Forslund and Part 1995, Martin 1995, Espie et al. 2000, Balbontin et al. 2007). These hypotheses are not mutually exclusive (Curio 1983, Forslund and Pärt 1995, Martin 1995, Brown and Roth 2009), and I did not specifically test any of them. The lack of difference I observed between habitat characteristics at nests with older and younger Rose-breasted Grosbeaks suggests that lack of experience (constraint hypothesis) was more likely a cause of differences in nestling provisioning rates than unequal habitat quality, but further research is required to clarify the causes of lower reproductive success in less experienced Rose-breasted Grosbeaks.

Previous studies have found that younger birds of many species cannot forage as efficiently as older, more experienced adults (e.g. Janson 1990, Wunderle 1991, Daunt et al. 1999, Limmer and Becker 2009; but see Heise and Moore 2003). Differences in foraging ability (Daunt et al. 1999), diet choice (Rutz et al. 2006), the ability to capture large (Catterall et al. 1989, Desrochers 1992) or energy rich (Limmer and Becker 2009) prey items, timing of nest initiation (Stutchbury and Roberston 1988, Hatch and Westneat 2007; but see Daunt et al. 1999) and access to high quality foraging territories (Catterall et al. 1989, Pärt 2001) may contribute to the positive relationship between age and the amount or quality of food obtained. Evidence that the foraging skills and reproductive success of young birds improve with age (Stuchbury and Robertson 1988, Desrochers 1992, de Forest and Gaston 1996, Catry and Furness 1999) supports the hypothesis that age-related differences in reproductive
performance can be attributed to a lack of previous experience in younger birds (Yasukawa 1981, Nol and Smith 1987, Wheelwright and Schultz 1994).

As a result of age-related differences in foraging ability, in environments and years when food resources are particularly scarce, younger birds may be more strongly affected than older birds (Hannon and Smith 1984, Bedard and LePointe 1985, Hussell and Quinney 1987, Stutchbury and Robertson 1988) or they may be unable to provide enough food to successfully fledge young (Sydeman et al. 1991). In my study nestlings raised by younger male parents weighed less than nestlings raised by older parents, but differences were only significant in 2008. Most Rose-breasted Grosbeaks have nestlings during June, and there was considerably more rain in 2008 than in 2007 during this month, which suggests that younger Rose-breasted Grosbeak parents may have more difficulty adjusting to adverse weather conditions than more experienced adults.

In addition to age-related differences in nestling provisioning rates, nest attendance and male contribution to nest attendance also varied with the age of the male parent. Overall nest attendance was higher at nests attended by younger, less experienced males than at nests with older, more experienced males. Higher nest attendance could be expected to increase nest survival, but nests with younger males were not more successful on average than nests with older males (Table 1.5, Chapter 1). In addition, while nest attendance was higher at nests with younger males, the SY males contributed less to nestling provisioning than older males did during both stages in the nestlings’ development. This suggests that females who breed with second-year males may provide more parental care than females paired with older, more experienced males. The body condition of female songbirds decreases rapidly at
the onset of brooding and remains low until the young fledge (Curlee and Beissinger 1995, Sanz and Moreno 1995, Chastel and Kersten 2002). Incubation and nestling provisioning are both energetically costly for females (Thomson et al. 1998, Reid et al. 2002), which suggests that female Rose-breasted Grosbeaks who are mated with SY males may have much lower body condition than females mated with more experienced males who provide more parental care.

**Conclusions**

This study suggests that single-tree selection does not negatively influence Rose-breasted Grosbeak’s ability to find food, provision their nestlings, or attend their nests in hardwood forests. None of the response variables differed significantly among post-harvest treatments in either study year, but they differed with stage of nestling development and with age of male parent. Provisioning was less frequent and nest attendance was higher for < 5 day old nestlings than for > 5 day old nestlings. Fledglings from nests attended by younger (SY) males weighed less than offspring from nests attended by older (ASY) males, and may have been at a fitness disadvantage. Further research is needed to determine why younger breeders were less effective at nestling provisioning.
GENERAL CONCLUSIONS

In the predominantly forested landscape of Algonquin Provincial Park, single-tree selection did not appear to have a significant negative effect on the reproductive success of Rose-breasted Grosbeaks. Density, pairing success, and the mean number of fledglings per successful nest were significantly higher in more recently harvested stands than in the > 50 years post-harvest stands, and nest success, fledgling survival, and productivity were also higher in the harvested stands, although not significantly so. These demographic trends partially support my prediction that single-tree selection would benefit Rose-breasted Grosbeaks. However, the proportion of ASY males was slightly higher in the > 50 years post-harvest treatment than in the other stands, which could indicate that the “unharvested” stands provided higher quality territories, assuming that older, more experienced birds select and successfully defend better quality territories than younger, less experienced ones. Since overall density was significantly lower and the proportion of ASY males was not significantly higher in the > 50 years post-harvest treatment, it seems unlikely that the unharvested stands provided significantly better habitat. Rather, ASY males may have been out-competing SY ones for a more limited number of high quality territories in these stands than were available in other treatments.

The lack of agreement among demographic measures indicates that the factors influencing Rose-breasted Grosbeak reproductive success are complex, and as a result, relying on any single demographic measure to assess the effects of habitat management may result in misleading conclusions.

Single-tree selection harvesting may not have a significant negative effect on Rose-breasted Grosbeaks in predominantly forested landscapes, but population
productivity was below replacement levels in all stands except in the 16-20 years post-harvest stands. This suggests that forest management policies should be implemented with caution in areas where the welfare of this species is of concern, at least until the causes of the Rose-breasted Grosbeak’s decline can be identified. My study suggests that the dense understory and sapling layers characteristic of forests regenerating after single-tree selection harvesting may slightly increase Rose-breasted Grosbeak productivity, but some other forest management practices may have more negative consequences. For example, forest management policies intended to suppress natural disturbances such as wildfires, flooding, and insect outbreaks have reduced the amount of early-seral forest across North America (Askins 1993, Brawn et al. 2001, Trani et al. 2001, Brooks 2003, DeGraaf and Yamasaki 2003). Creating forested landscapes which provide access to a range of forest types and successional stages may be beneficial for mitigating the population declines of the Rose-breasted Grosbeak and other disturbance-dependent species, but silvicultural applications should be selected and implemented with caution.

This study was conducted in stands that were regenerating after their first harvest, and some of them were reaching the stage when a second harvest could be carried out. Silvicultural guidelines for tolerant hardwood forests in the states just south of the Great Lakes suggest that a second harvest can be made using single-tree selection 8-15 years after the first (Tubbs 1977), while guidelines for Ontario suggest waiting 15-20 years (OMNR 1998). Although basal area was not significantly lower in the 16-20 or 21-25 years post-harvest stands than in the > 50 years post-harvest treatment, other measures of forest structure were significantly different. Rose-breasted Grosbeak density and pairing success were significantly higher in the 16-20 years post-harvest treatment than in the >
50 years post-harvest stands, and pairing success was significantly higher in the 21-25 years post-harvest stands than in the “unharvested” stands. This suggests that neither forest structure nor Rose-breasted Grosbeak demography had completely returned to “pre-harvest” conditions even by 25 years after harvesting, and that shorter harvest rotations may lead to cumulative changes in forest structure and avian ecology. Specifically, basal area, which was positively associated with nest survival, was still slightly lower in the 21-25 years post-harvest stands than in the > 50 years post-harvest treatment. However, further study of forest structure and Rose-breasted Grosbeak demography following the second cutting would be necessary to test for cumulative changes.

Although the first single-tree selection harvest rotation did not appear to have a significant effect on nest survival, my study suggests that basal area, sampling year, and timing of nest initiation were important variables explaining nest survival, with nests built in areas with higher basal area and started earlier in the season having a greater chance of survival. The tendency for older, more experienced birds, which typically have higher reproductive success, to begin nesting earlier may partially explain the positive association between early breeding and nest survival. However, it is possible that the hatching dates of young from nests initiated earlier in the season are more closely synchronized with the emergence of insect prey, and parents at these nests may be able to devote more time to nest defence rather than foraging. Many studies have observed a positive correlation between earlier egg-laying dates and increasing temperatures (i.e., Crick et al. 1997, Crick and Sparks 1999, Dunn 2004, Torti et al. 2005). If nests that are initiated earlier allow birds to take advantage of earlier insect peak abundances, this could
indicate that Rose-breasted Grosbeaks may be flexible enough to adapt to climate change as well as to changes in forest structure resulting from forest management practices. However, as this species is currently declining across its breeding range, potentially negative effects of climate change, such as more variable weather conditions (IPCC 2002) or changes in the emergence time of insect prey should not be ignored.

When assessing the influence of climate change, habitat loss or degradation, forest management practices, or other factors it is important to study both nest and fledgling survival and habitat requirements. Although single-tree selection harvesting did not significantly alter nest or fledgling survival, habitat characteristics at nests sites and locations used by fledglings were significantly different, and patterns of nest and fledgling survival among the post-harvest treatments were not strongly correlated. This suggests that conclusions regarding the influence of various factors on the growth rates of avian populations should not be based solely on estimates of nest survival.

My study also suggests that population age structure should be taken into consideration in future studies of avian demography and population growth rates. Overall productivity of after-second-year males was significantly higher than that of second-year males, nestling provisioning was more frequent at nests with older, more experienced males, and nestlings weighed more on average at the time of fledging in nests with older males. After-second-year males also contributed more to nestling provisioning and nest attendance than second-year males did. The density of ASY males was significantly higher than the density of SY males in all post-harvest treatments, but if management practices or other factors altered these proportions to favour more SY adults at the expense of ASY breeders, there could be negative consequences for population
productivity. Variation in reproductive success between more and less experienced parents should be taken into consideration when investigating the consequences of management practices because all species may not exhibit the same patterns or responses.

There are several areas for improvement in this study. First, the population models I used relied on estimates of annual adult mortality from the literature, which may not have been appropriate for this particular species. Although accurate estimates of annual survival are extremely difficult to obtain, future research should focus on improving these estimates to allow more reliable assessments of population growth rates. Second, increased sample sizes and a larger number of study sites would have improved the statistical power of my results, and may have provided additional insight into suggested results. Finally, investigations of nestling provisioning rates and considerations of prey availability would have been complimented by direct measurement of insect and fruit abundance.

Future research should focus on areas outside of Ontario, and should aim to identify habitat types and areas where Rose-breasted Grosbeak populations are above replacement levels. Although the population estimates derived in this study suggested Rose-breasted Grosbeak populations were sinks in most post-harvest treatments, and similar results were reported for forest fragments (Smith et al. 2006, Moore et al. 2010), single-tree selection harvesting did not appear to be having a negative effect on Rose-breasted demography. Future studies could also consider factors that might affect this species during migration and on the wintering grounds, such as weather, climate change, land-use change, and habitat loss or degradation. Long-term studies should also be a priority for future research, to allow a better understanding of temporal variation in nest
survival and productivity, and determine how these parameters respond to selection harvesting over the long-term.

This study suggests that single-tree selection harvesting can maintain and even improve habitat for Rose-breasted Grosbeaks in predominantly forested landscapes if it is strictly implemented according the guidelines set out by the Ontario Ministry of Natural Resources. It should be emphasized that single-tree selection is not equally beneficial for all migratory songbirds, and may even be detrimental to some forest interior species. Nonetheless, for species such as the Rose-breasted Grosbeak, which benefit from habitat features characteristic of regenerating forests, this system can provide an economically and ecologically sustainable system of timber harvesting. These findings should be of value to municipalities, conservation authorities, landowners, land managers, and consultants involved in assessing or developing forest management plans, silvicultural prescriptions, or stewardship plans.
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