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Nest predation on forest songbirds in a western boreal forest landscape altered by energy-sector linear features.

by

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Abstract

Nest predation is a major source of reproductive failure for many species of songbirds. Habitat fragmentation by human land use creates edge habitat that can alter predator-prey dynamics, create ecological traps, and reduce the amount of high quality habitat available for sustaining bird populations. I studied the nesting success of boreal forest songbirds in two regions of western Canada fragmented by pipelines, seismic lines, and service roads. These linear features result in relatively little forest loss but create vast amounts of edge. Our ability to predict the effect of these edges is hampered by incomplete or inaccurate knowledge about what predators depredate nests and how those predators respond to edges. My objective was to determine if edges were negatively impacting songbird nest success through increased rates of nest predation and whether birds were preferentially using habitats with higher reproductive potential. Using video monitoring, I identified 11 species of nest predators at 71 songbird nests. Red squirrels were the dominant nest predator in both regions and all predators were endemic boreal species rather than non-forest species. I did not find strong evidence that the spatial distribution or probability of nest predation by the majority of nest predators was strongly affected by edge proximity. Of all the predators monitored, only bears and deer mice were more common near edges but they depredated few nests. I also did not find strong support for a negative edge effect of linear features on songbird nest fate (n = 571 nests) relative to forest interiors. Ground nest survival was marginally higher near edges and ground and shrub nest survival was marginally higher where squirrels were absent. In contrast, the survival of canopy nests was higher away from the edge and in the presence of squirrels. Abundance of singing males and nest fate of each guild responded similarly to edges and squirrels indicating birds are preferentially using habitats with higher reproductive potential. Uncertainties in field-based estimates of nesting success and other important demographic parameters prevent me from concluding that higher quality habitats are capable of sustaining the local population.

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Table of Contents

List of Tables

List of Figures

List of Appendices

Glossary

Term	Description
3MAIN	Categorical measure of MAIN proximity, 0 m, 200 m, and 400 m.
ALTHAVEDATA	Categorical variable indicating whether alternate nest data were available for the nest.
ALTNEST	Number of alternate nest sites (number of stems of same species as nest shrub within 5 m^2).
CAM	Camera present at a nest.
CANOPY	Categorical canopy closure in 25% increments. Canopy nest concealment.
CLOSED	Linear feature <10 m wide, extensive woody regrowth.
COVER	Nest concealment.
DAY, DAYINT	Day of point count survey and day of nest initiation, respectively.
EDGE	Categorical measure of MAIN proximity, edge (0 m) and interior (400 – 500 m).
ER	Evidence ratio, model support relative to one other model.
GNDCOVN, GNDCOVP	Nest concealment (i.e., cover) at ground level (0 – 0.5 m high) at the nest and patch scales, respectively.
INC	Incubation nesting stage.
IRR	Incident rate ratio compares magnitude of predicted counts.
M100	Categorical measure of MAIN proximity, ≤100 m and > 100 m.
MAIN	Linear feature >10 m wide with no woody regrowth dissecting continuous forest. Distance to the nearest MAIN.
MAIN|OPEN	Distance to nearest MAIN or OPEN edge.
MAXCLUTCH	Potential maximum clutch size per species.
MO100	Categorical measure of MAIN|OPEN proximity, ≤100 m and > 100 m.
NESTL	Nestling nest stage.
NULL	Base model without explanatory variables of interest.
OPEN	Linear feature <10 m wide, little to no woody regrowth.
OR	Odds ratio compares magnitude of predicted probabilities.
PTREE	Proportion of conifer trees in the canopy based on stem density.
RESQ, RESQ01	Continuous and categorical measures of nest predation risk by red squirrels, respectively.
RSHAVEDATA	Categorical variable indicating whether red squirrel predation risk values were available for the nest.
SHBCOVN, SHBCOVP	Nest concealment (i.e., cover) at shrub level (0 – 3 m high) at the nest and patch scales, respectively.
SITE	Study site, northern or southern.

Term	Description
SUBSTRATE	Nest location, ground or above-ground.
TREE	Density of canopy trees >3 m tall (m^{-2}). Canopy nest concealment.
WIND	Ordinal Beaufort wind category 1 - ≥5.
w	Akaike weight, model support relative to all models in set.

Chapter 1. Introduction to Thesis

1.1. Nest predation and habitat quality for nesting songbirds

Every spring in North America, billions of birds migrate north to breed. Reproduction is an important stage in the annual avian life cycle that has implications for individual fitness and population demography (Donovan and Thompson 2001, Saether et al. 2004). Habitat selection is a fundamental component of the breeding process because where an individual chooses to settle can affect their probability of being successful (Johnson 2007). Nest predation is a major source of reproductive failure for many species of birds (Ricklefs 1969, Martin 1992, Newton 1998) and, therefore, is an important force shaping the reproductive strategies of birds in both evolutionary and ecological time. For example, species with inherently high rates of nest predation have evolved smaller clutch sizes and shorter nesting periods to minimize cues that could attract predators to the nest and to reduce the length of time that eggs and nestlings are exposed to predators (Skutch 1949, Slagsvold 1982, Martin 1993, 1995). Reduced nest investment also allows adults to retain sufficient resources to renest should they fail and to increase their own probability of survival and their opportunities to breed in subsequent years (Martin 1995, Santos and Nakagawa 2012). Behavioural flexibility enables adults to further reduce their risk of nest predation by selecting territories with fewer predators (Fontaine and Martin 2006a, Schmidt et al. 2006, Emmering and Schmidt 2011, Hua et al. 2013), by selecting nest sites that have a lower probability of being discovered (Martin and Roper 1988, Martin

1992, Eggers et al. 2006, Chalfoun and Martin 2009), and by adjusting their provisioning and nest attendance strategies in areas of higher risk (Martin et al. 2000, Fontaine and Martin 2006b, Schmidt and Whelan 2005). Therefore, the risk of nest predation and capacity for adults to mitigate that risk can be considered important components defining habitat quality for breeding birds.

Factors that define the quality of breeding habitat, including the risk of nest predation, vary both spatially and temporally. As a result, demographic rates vary across the landscape (Pulliam 1988). Some habitats are reproductive sources that produce a surplus of individuals over and above local adult mortality. Conversely, some habitats are reproductive sinks that produce too few individuals to compensate for local adult mortality and whose numbers are maintained by constant immigration from sources (Pulliam 1988). Although habitat quality varies, it is not unpredictable. Given the importance of nest success to fitness, it is expected that individuals have evolved habitat selection criteria to maximize their fitness potential (Fretwell and Lucas 1970). This does not imply that individuals are capable of assessing habitat quality as it pertains to lifetime reproductive success. Rather, individuals select habitats based on cues that on average are expected to optimize fitness (Kristans 2003). The ability of individuals to recognize and select high quality habitats is contingent on the relationship between habitat quality and the cues evolved to assess quality being maintained and on having sufficient amounts of high quality habitat available (Fretwell and Lucas 1970).

1.2. Habitat fragmentation and predator-prey dynamics

Habitat fragmentation by human land use has the potential to alter predator-prey dynamics and the proportions of source and sink habitats on the landscape. Fragmentation results in several changes in landscape structure. However, deleterious effects of habitat fragmentation are frequently attributed to increased amounts of edge habitat (Harrison and Bruna 1999, Fletcher et al. 2007). Fragmentation creates edge habitat along the interface between the newly created matrix and the remnant landscape. Creating edge habitat was once considered a useful management tool to bolster populations by providing edge-dwelling individuals access to additional resources (Leopold 1933, Ries et al. 2004). However, nest predators also may respond positively to edge habitats (Chalfoun et al. 2002) such that edge-nesting songbirds experience increased nest predation. For this reason, anthropogenic edges are widely regarded as having negative effects on songbirds (Batary and Baldi 2004). However, of greater concern to individual fitness and to conservation is that anthropogenic edges may create an ecological trap (Gates and Gysel 1978). In the presence of a trap, individuals preferentially settle in habitats that appear to be of high quality based on evolved habitat assessment cues but subsequently experience poor reproductive success because of some habitat characteristic(s) they were unable to predict (Dwernychuk and Boag 1972, Donovan and Thompson 2001).This maladaptive habitat choice leads to a potentially unstable system because a large number of the best individuals are preferentially selecting habitats that are incapable of sustainable productivity (Kristans 2003). Increased habitat fragmentation, therefore, has important implications for the fitness potential of individuals that require reliable habitat assessment cues. Increased fragmentation also has important implications for the dynamics of the greater population that requires sufficient amounts of source habitat be maintained on the landscape (Pulliam 1988, Donovan and Thompson 2001, Shustack and Rodewald 2010).

Habitat fragmentation and degradation are considered to be the primary threats to sustaining bird populations in North America (Johnson 2007, Wells 2011, North American Bird Conservation Initiative 2012) and increased rates of nest predation in fragmented habitats have been implicated in some population declines (Askins 1995, Robinson et al. 1995, Lloyd et al. 2005). While edges are widely regarded to have negative effects on the reproductive success of songbirds, evidence in support of increased predation near edges is equivocal because results vary across species, habitats, landscapes, and regions (Lahti 2001, Sisk and Battin 2002). Negative edge effects are more commonly reported in eastern North America (George and Dobkin 2002), at forest-field ecotones (Batary and Baldi 2003), or when avian, rather than mammalian species, are the predominant nest predator (Chalfoun et al. 2002). The potential for local edge effects also may be positively correlated with the amount of habitat fragmentation at a larger landscape scale (Donovan et al. 1997, Chalfoun et al. 2002, Thompson et al. 2002, Stephens et al. 2003, Driscoll and Donovan 2004, Falk et al. 2011). This has led to the suggestion that western landscapes, which have a history of natural fragmentation, and currently are less fragmented by human land uses than eastern landscapes, are less susceptible to negative edge effects (George and Dobkin

2002; but see Hames et al. 2002). Studies conducted in western North America frequently report decreased rates of nest predation in fragmented landscapes or near edges presumably because of reduced numbers of nest predators (Tewksbury et al. 1998, 2006, Cavitt and Martin 2002, Hannon et al. 2009). However, numerous exceptions to these general patterns exist (reviewed by Lahti 2001, Batary and Baldi 2004).

Perhaps one conclusion that can be made concerning edge effects and nest predation is that they are not a universal phenomenon (Lahti 2001). Failure to achieve some coherent understanding about the effects of edges is hampered by incomplete or inaccurate knowledge about what predators are depredating nests and how those predators respond to edges (Lahti 2001, 2009, Thompson 2007). To date, the majority of edge studies have used artificial nests to identify nest predators and to quantify edge-related differences in nest predation risk. Results from these studies have come under increasing scrutiny for not accurately representing the magnitude or spatial patterns of real nest survival, or the composition or relative importance of species depredating real nests (Zanette 2002, Faaborg 2010). To improve our understanding of factors affecting nest fate, including the potential for negative edge effects, it is necessary that sources of nest failure and the composition of the nest predator community are identified (Lahti 2009, Benson et al 2010, Reidy and Thompson 2012).

1.3. Predator-prey dynamics in the boreal forest

The boreal forest is an important resource to North American avifauna (Blancher and Wells 2005). The natural capital of the boreal region also is an important source of revenue for the Canadian economy (Anielski and Wilson 2009). As a result, this landscape is rapidly being fragmented by multiple land uses. Of particular concern in the west is oil and gas development, which creates hundreds of thousands of kilometers of pipelines, seismic lines, and associated service roads through the forest (Schneider 2002). These linear features result in relatively little forest loss but they create vast amounts of edge habitat. Abundance studies suggest boreal birds are resilient to at least moderate levels of habitat fragmentation by linear features (Bayne et al. 2005a, b, Machtans 2006). However, ecological traps are most commonly reported in western North America and in areas with anthropogenic disturbance (Bock and Jones 2004). Because energy sector linear features are predicted to be dominant edge type in the boreal forest over the next 50 years (Schneider et al. 2003), it is important that we determine whether nesting success is lower near edges and whether birds are capable of identifying and selecting high quality habitats in landscapes highly dissected by linear features.

1.4. Objectives and study design

My primary goal was to determine the potential for negative edge effects on nesting songbirds in the boreal forest of western Canada. I conducted a mensurative experiment in several mixed wood forest plots in each of two study areas fragmented by energy sector linear features. One site, which was bisected by a single pipeline, was located near Fort Simpson, Northwest Territories. (61°52′N, 121°20′W; Fig. 1.1). The second site, which was bisected by several pipelines, seismic lines, and service roads, was located in the Chinchaga Forestry Region in northwest Alberta near Manning (57°18′N, 118°23′W). Both sites are characterized by mature, closed stands of mixed wood forest. Canopy composition was a mixture of coniferous white spruce (*Picea glauca*), black spruce (*P. mariana*), and balsam fir (*Abies balsamea*), and deciduous trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*). The understory typically consisted of low-to-moderate densities of shrubs < 0.5 m tall (e.g., *Rosa acicularis*, *Rubus idaeus*, and *Viburnum edule*) with scattered patches of dense alder (*Alnus* spp.) and willow (*Salix* spp.) up to 3 m in height. A sub-canopy was normally absent. The Fort Simpson site was located in the Mackenzie River valley in the Hay River Lowland Ecoregion (Environment Canada 2005). The Chinchaga site was located in the Clear Hills Upland Ecoregion of the Boreal Plains Ecozone, which is characterized by gently rolling hills and broad, gently undulating valleys. The mean summer temperature in both sites is 13°C. The mean winter temperature in Chinchaga and Fort Simpson is -17.5°C and -19°C, respectively. Mean annual precipitation is higher in the Chinchaga (400-600 mm) compared to Fort Simpson (350-450 mm).

Although the Chinchaga site was further south and closer to forestry and to agriculture (approximately 40 km away) than the Fort Simpson site, neither activity occurred in the immediate vicinity of this site. I excluded other anthropogenic edge types from my study design to avoid confounding the effect of edges with effects associated with reduced patch size and patch isolation (Fletcher et al. 2007), effects associated with interspecific competition with species that might occupy a contrasting adjacent habitat type (e.g., cut blocks or agricultural fields; Fagen et al. 1999, Sisk and Battin 2002, Ries et al. 2004), and additional effects related to roads (e.g., vehicle mortalities) that are not edge effects per se. In both sites, larger linear features were periodically cleared of vegetation (pipelines) or were surfaced in gravel (service roads) whereas seismic lines ranged from herbaceous cover only to heavily overgrown with woody vegetation. Study plots in each site were established adjacent to one or two (Chinchaga only) large linear features and extended 400 – 500 m into the forest. This plot size and configuration provided a wide range of edge proximities over which to assess edge effects.

My first objective was to identify which predators were chiefly responsible for nest failure (Chapter 2). Our current understanding of the boreal nest predator community is based almost entirely on artificial nests (e.g., Bayne and Hobson 1997, Hannon and Cotterill 1998, Song 1998, Cotterill and Hannon 1999). Studies that have identified the predators of real nests have been conducted along the southern fringe of the boreal forest in forest fragments surrounded by an extensive agriculture matrix (e.g., McCallum and Hannon 2001, Hannon et al. 2009). These landscapes do not reflect conditions in much of the western boreal forest, which is far removed from agriculture, and these studies did not consider linear feature edges. I designed an infrared digital video camera system to identify nest predators and to provide detailed information on actual nest fate and nest productivity of real songbird nests. Each system was capable of simultaneously providing 24-hr surveillance at four nests. Camera placements were targeted at Swainson’s Thrush (*Catharus ustulatus*), a mature forest species (Mack and Yong

2000), and Chipping Sparrow (*Spizella passerina*), a disturbance-tolerant forest species (Middleton 1998). Cameras were also placed opportunistically at nests of other species when target nests were unavailable. Each camera was small (8 cm x 3.5 cm) and was mounted in vegetation 0.5 – 1.0 m from the nest. Observer disturbance at camera-monitored nests was limited to camera installation and battery changes every 6 days, approximately 10 m from the nest. I compared the identities and relative contributions of predators at depredated real nests and at depredated artificial nests from three separate artificial nest studies conducted in Saskatchewan, Alberta, and the Northwest Territories (Fig 1.1) to determine whether our previous understanding of the boreal nest predator community was accurate.

Negative edge effects on nesting success commonly result from positive functional or numerical responses by nest predators to edges. My second objective was to determine whether the spatial distribution of nest predators responded to edges and whether each species of nest predator was more likely to depredate nests nearer to edges (Chapter 3). I used several different survey methods to quantify the spatial distribution of the potential nest predator community on each study plot and across each study site. Doing so gave me greater insight into the potential mechanisms that might be responsible for an edge effect in this study.

My third objective was to determine what habitat factors best explained variation in nesting success, and whether individuals were capable of accurately assessing and using habitats with greater reproductive potential (Chapter 4.) Assessments of habitat quality for birds are commonly based on estimates of abundance on the assumption that birds will be more abundant in high quality habitats. This assumption is seldom tested and may not be valid in some cases (van Horne 1983, Morrison 1986, Temple and Wiens 1989, Vickery et al. 1992, Bock and Jones 2004). I considered edge proximity, predation risk, nest concealment, and the availability of alternate nest sites as potentially important factors describing habitat quality. I then determined whether each of these variables similarly explained variation in nest fate, nest productivity, and songbird abundance to determine if abundance was a reliable indicator of habitat quality.

For practitioners, identifying high quality habitat (i.e., sources vs. sinks) requires accurate assessments of nest fate and nest productivity. While video monitoring may be the most accurate solution, these systems are expensive and impractical for monitoring large numbers of nests and for monitoring nests of some species (e.g., canopy nesters). Instead, the majority of nest studies rely on observer estimates of success based on repeat nest visits and the available cues at completed nests. This approach may over-estimate nest success if older nestlings have a higher probability of being depredated and if the dominant predators do not disturb the nest structure (Thompson 2007). In addition, it can be assumed that productivity will always be overestimated to the extent that late-stage partial predations occur. The objective of Chapter 5 was to assess the accuracy of observer estimates of nest fate and nest productivity and the utility of cues commonly used to assess fate. Given that reproductive output is a key demographic parameter in defining source and sink habitats and in models of population dynamics, quantifying observer inaccuracies in estimating nesting success will provide additional realism to these estimates. In Chapter 6, I evaluate whether edges are sources or sink habitats for songbirds and discuss the number of challenges in making this assessment.

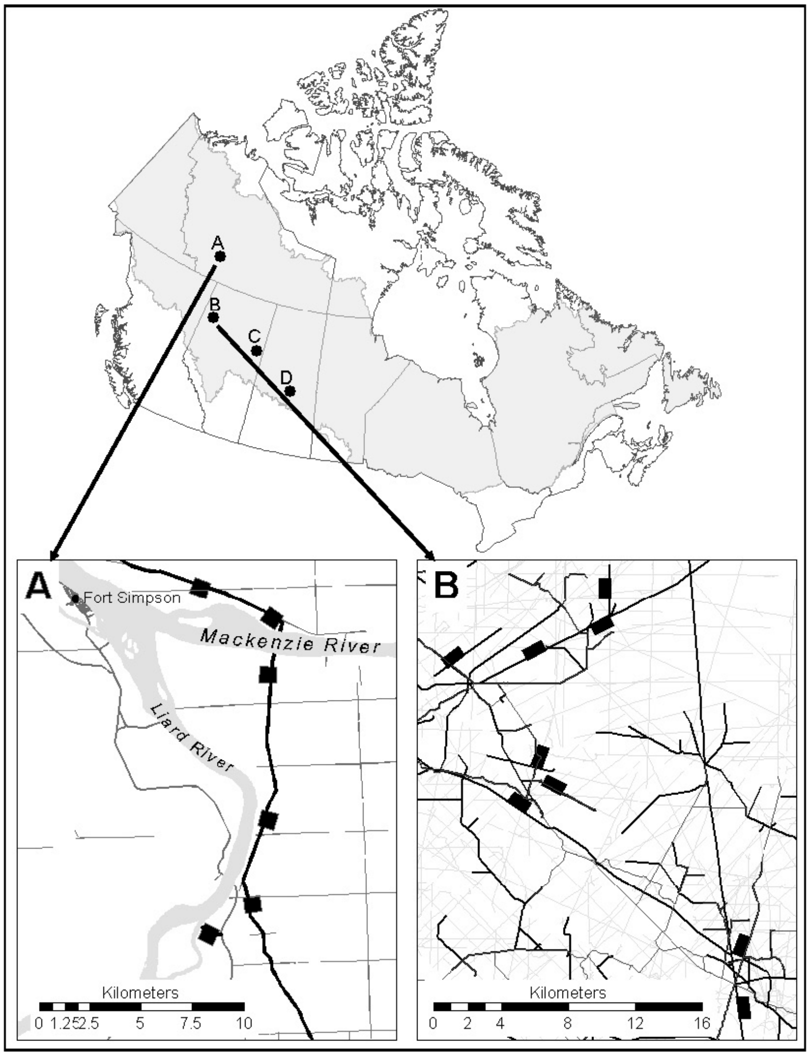

Figure 1.1. Data on real nests were collected from two study sites, Fort Simpson, NT (A), and from the Chinchaga Forestry Region near Manning, AB (B). Study plots are indicated by black boxes on the lower two panels. Dark lines represent pipelines and/or service roads. Light lines represent seismic lines. All seismic lines in Fort Simpson had extensive woody vegetation regrowth in the understory). Artificial nest data (Chapter 2) were collected from Fort Simpson, NT (A), NE Alberta between Lac la Biche and Fort McMurray (C), and Prince Albert National Park, SK (D). The spatial extent of the hemiboreal forest in Canada (shaded portion of the upper panel; Brandt 2009) is from The Boreal Avian Modelling Project (URL: http://www.borealbirds.ca/index.php/scope; accessed 21 July 2013).

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Chapter 2. Video identification of boreal forest songbird nest predators and discordance with artificial nest studies.[1]

2.1. Introduction

Nest predation is a primary cause of reproductive failure for many species of songbirds (Martin 1992). Increased rates of nest predation in fragmented habitats are considered a major cause of population declines in some North American songbird species (Robinson et al. 1995, Lloyd et al. 2005). Fragmentation creates edge habitat along the interface of the newly created matrix and the remnant landscape. Some studies have demonstrated that the diversity, density, foraging intensity, and/or foraging efficiency of some nest predators respond positively to increased fragmentation, particularly in edge habitats (reviewed by Chalfoun et al. 2002). As a result, edge nesting birds may experience higher rates of nest predation.

Evidence of a negative edge effect on nesting birds is equivocal because results vary across species, habitats, landscapes, and regions (Lahti 2001, Sisk and Battin 2002, Batary and Baldi 2004). Predictions concerning the potential effects of edges are often hampered by inadequate knowledge of the identities and relative contributions of predators depredating nests and how those predator species respond to edges (Thompson 2007, Lahti 2009). Much of our current

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understanding about the effects of edges on nesting birds is based on artificial nests (Batary and Baldi 2004). Artificial nests likely do not reflect the relative importance of each nest predator species to the survival of real nests and, therefore, they are not expected to accurately measure the effects of edges on the survival of real nests (Zanette 2002). Information on the identity of nest predators and how they respond to edges is necessary to develop testable hypotheses about when, where, and why negative edge effects on nesting birds may occur (Thompson and Ribic 2012).

We studied the nest predator community in two western boreal forest landscapes fragmented by energy sector linear features (pipelines, seismic lines, and industrial service roads). These features are becoming increasingly common in the western boreal forest and are predicted to be the dominant creator of edge habitat in the coming decades (Schneider et al. 2003). Local negative edge effects on nest success tend to be stronger in more fragmented landscapes (Driscoll and Donovan 2004) and in landscapes fragmented by agriculture, which may attract forest- and human-associated predators to edges by providing additional food sources (Chalfoun et al. 2002, Batáry and Báldi 2004). This suggests boreal songbird nest fate may be particularly sensitive to intensive edge development along the southern forest-agriculture transition zone. Negative edge effects also are more commonly reported when avian species are important nest predators (Chalfoun et al. 2002). Our current understanding of the nest predator community in the western boreal forest is based almost entirely on artificial nests (e.g., Bayne and Hobson 1997, Song 1998, Cotterill and Hannon 1999; but see McCallum and

Hannon 2001, Hannon et al. 2009). The role of avian nest predators in this region is unknown. These uncertainties about the nest predator community need to be addressed to enable predictions about the potential impact of future industrial development (Lahti 2001, 2009, Thompson 2007).

We designed an infrared digital video camera system to monitor nests and document the identities of nest predators in two boreal forest landscapes, a northern site with a single linear clearing bisecting otherwise continuous forest, and a more southerly site with multiple linear clearings. We predicted that the nest predator community in the southern landscape would be more diverse and composed of more human-associated predators because it had more edge habitat and was closer to agricultural lands. We compared our predator data from real, video-monitored nests to the predators identified in three separate boreal forest artificial nest studies to determine whether this commonly used technique accurately represents the dominant nest predators' influence on real nest success. Identifying which predators are chiefly responsible for depredating nests is important to understanding the potential impacts of future industrial development on nesting boreal forest songbirds.

2.2. Methods

2.2.1. Study area

All nest predator data presented here were collected in boreal mixed wood forest stands in western Canada. Real nest data were collected as part of a larger research project on the impacts of energy sector activity on forest songbird communities. Study plots were established in association with energy sector linear features (i.e., buried pipeline right-of-ways, seismic lines, and limited-use service roads). We focused on linear features to minimize confounding edge-associated effects with additional effects associated with habitat loss and adjacent habitat type (e.g., forestry cut blocks or agriculture) and additional effects from high-use roads (e.g., vehicle mortalities and vegetation dusting). The energy sector linear features in our study can be generally characterized as open, straight corridors that often extend several kilometers. In regions of high energy-sector activity, these linear features periodically intersect creating a network of open corridors. Pipelines were typically 25 m wide, seismic lines were typically 8 m wide, and service roads ranged between 12 and 25 m in width. Pipelines and service roads were kept free of extensive woody vegetation by periodic clearing. Seismic lines also remained open at canopy height but ranged from herbaceous cover to dense woody vegetation regrowth at ground level.

Real nest data were collected from two regions (Fig. 1.1). Six 42-ha plots were established near Fort Simpson, NT (61˚ 52' N, 121˚ 20' W) in 2005 and 2006 (hereafter northern site). Each northern plot was adjacent to a single linear feature (pipeline or service road). Nine 24-ha plots were established in the Chinchaga Forestry Region, AB (57˚ 18' N, 118˚ 23' W) in 2006 and 2007 (hereafter southern site). Each southern plot was bordered by one or two linear clearings (pipeline or service road) and each was bisected by one or more additional seismic lines. Each plot was located a minimum of 1.2 km (southern site) to 2 km (northern site) from other plots. Plot sizes and inter-plot distances were chosen to minimize the likelihood that smaller predators would depredate all nests on a single plot or that large predators would depredate nests at multiple plots (Donovan et al. 1997, Stephens et al. 2003).

We compiled artificial nest data from three separate studies conducted between 1994 and 2005 (Fig. 1): Prince Albert National Park, SK (Bayne and Hobson 1997); NE Alberta between Lac la Biche and Fort McMurray (E. M. Bayne unpublished data); and Fort Simpson, NT (E. M. Bayne and S. J. Hartfeil unpublished data). We selected a subsample of artificial nests to enable valid comparisons to data collected on real nests. The Prince Albert data included nests from continuous and harvested forests but excluded nests from farm woodlots. The NE Alberta data excluded transects associated with public gravel roads. The Fort Simpson data excluded a large number of additional nests placed directly on the pipeline for a separate experiment comparing forest vs. pipeline nest fate. Compared to all other study sites included here, the NE Alberta sites were dominated by more deciduous habitats.

2.2.2. Real nests

Predators of real nests were identified using an infrared video system that provided 24-hour surveillance at four nests simultaneously, without continual observer interference. Cameras were small (8 cm long x 3.5 cm in diameter), and each was mounted in vegetation approximately 0.5 m from the nest. Cameras were preferentially placed at randomly selected Swainson's Thrush (*Catharus ustulatus*) and Chipping Sparrow (*Spizella passerina*) nests, which were the two most common types of nests found. Cameras were placed at nests of other species when a suitable nest of either target species was unavailable. All video footage was viewed in the lab to determine the fate of each egg and nestling, and to identify nest predators.

2.2.3. Artificial nests

One plasticine egg and one quail egg were placed in a wicker nest basket lined with vegetation. In Prince Albert and NE Alberta, nests were placed every 30 to 40 m along transects established parallel to the forest edge. Nests on edge transects were within 5 m of the forest edge. Nests on interior transects were approximately 300 m from the forest edge. The artificial nest study in Fort Simpson was conducted on the same plots as the real nest study. Nests were placed at randomly selected distances (between 1 and 100 m) and bearings from stations located 0, 200, and 400 m from the forest edge. Unlike Prince Albert and NE Alberta, the Fort Simpson data included some nests that were randomly located directly on a clearing. In all three studies, each nest was alternately assigned to a shrub or ground category and placed in a microhabitat similar to a real nest (Bayne et al. 1997). Nests were placed during the peak breeding season (late May to mid-July) and left in place for approximately 10 days to simulate a typical songbird incubation period.

Because we were interested in comparing the predator communities of real and artificial nests, we focused on the fate of the plasticine egg, which allowed us to identify predators based on the size and shape of impressions left in the plasticine. Predators were classified as sciurid (*Tamiasciurus* and *Tamias* species), corvid, large mammal, small mammal (primarily *Myodes* and *Peromyscus* species), raptor, and unknown. Missing plasticine eggs (44% of depredated nests) were placed into one of these predator categories based on the relative abundance of each predator (determined from the number of confirmed predations by each predator in each study) and the tendency of each predator to remove eggs (Bayne and Hobson 1999).

2.2.4. Statistical Analyses

We used two-tailed z-tests to determine if the proportions of real nests and the proportions of artificial nests depredated by each pair of predators differed. We considered both species-level and category-level comparisons for predators of real nests and category-level comparisons for predators of artificial nests. Predator category comparisons for real nests were analyzed for egg and nestling stages separately and for both stages combined. Artificial nests were analyzed by study site and by all sites combined. We then used multinomial logistic regression to determine if the probability of a nest being depredated by each predator category (dependent variable) varied by nest type (i.e, artificial vs. real nest; independent variable). We grouped real nests containing eggs and nestlings and excluded raptors from this analysis because they do not depredate eggs. We present relative risk ratios and *P*-values to describe the relative change in probability of each predator depredating an artificial nest compared to a real nest. We produced robust standard errors by including study site (n = 4) as a cluster variable to recognize the lack of independence between nests within each site (Froot 1989, Williams 2000).

2.3. Results

2.3.1. Real nests

Video cameras were established at 145 nests, representing 13 songbird species (Appendix 2.1). In total, 97 (67%) monitored nests were above-ground (i.e., shrub or canopy) and the remaining nests were ground nests. The average (± 1 SD) nest distance from the forest edge was 117 ± 118 m (nests on a linear feature have a distance of zero). The majority of cameras (86 of 145; 59%) were established at nests within 100 m of the forest edge. These included 19 nests that were ≤1 m from the forest edge, located either on, or adjacent to a linear clearing.

Seventy-five predators representing 11 species were recorded at 71 nests during four field seasons (Fig. 2.1, Appendix 2.2). Three nests initially depredated by red-backed voles (*Myodes* spp.) were later depredated by American red squirrel (*Tamiasciurus hudsonicus*; two nests) or least chipmunk (*Neotamius minimus*; one nest). A squirrel also depredated one nest initially depredated by a Sharp-shinned Hawk (*Accipiter striatus*). Video monitoring confirmed that all nest predators were species endemic to the boreal forest. Overall, the numbers of species of real nest predators in the northern and southern sites was similar (six vs. eight, respectively). However, only three species were recorded depredating real nests in both study sites. In addition, the number of nests destroyed by some predator species within each site varied between years. For example, in the southern site American marten (*Martes americana*) and Sharp-shinned Hawks destroyed one and zero, respectively, of the 11 video nests where a predator was documented in 2006 but six and eight nests, respectively, of 33 nests in 2007.

Red squirrels were the dominant predator in both study sites, taking nests or eggs in 46% to 83% of the video-monitored nests annually and they depredated a greater proportion of nests overall compared to any other predator (two-tailed z-test; all *P* < 0.0001). Sharp-shinned Hawks were another common nest predator in both study sites, depredating up to 24% of video-monitored nests in the northern site during 2007. Sharp-shinned Hawks depredated a similar number of nests as American marten (two-tailed z-test; *P* = 0.22) but more nests than the remaining predators (two-tailed z-test; all *P* < 0.034). There was no difference in the numbers of nests depredated by the remaining predators (two-tailed z-test; all *P* > 0.35). Based on predator categories, sciurids depredated a greater proportion of real nests that any other predator (two-tailed z-test; all *P* < 0.0001; Fig. 2.2). Corvids depredated fewer real nests than any other predator (two-tailed z-test; all *P* < 0.02). The numbers of real nests depredated by raptors, large mammals, and small mammals did not differ (two-tailed z-test; all *P* > 0.24). We obtained similar results when we analyzed nestling and egg stages for real nests separately. These results are not presented.

2.3.2. Artificial nests

A total of 2849 artificial nests were set out (Prince Albert, SK = 1647, NE Alberta = 607, Fort Simpson, NT = 595). Of these, 1179 nests were destroyed by identifiable predators (Fig. 2.2). Small mammals were the dominant predator of artificial nests in all study areas (all *P* < 0.0001). In Prince Albert and Fort Simpson, sciurids depredated a greater proportion of artificial nests than corvids (two-tailed z-test; all *P* < 0.03), which depredated a greater proportion of artificial nests than large mammals (two-tailed z-test; all $P < 0.0001$). The proportions of artificial nests depredated by sciurids, corvids, and large mammals in NE Alberta did not differ (two-tailed z-test; all $P > 0.76$). The importance of small mammals and near-absence of sciurid predation in NE Alberta compared to the other artificial nest studies (Fig. 2.2) partially reflects the dominant deciduous composition of those forest stands.

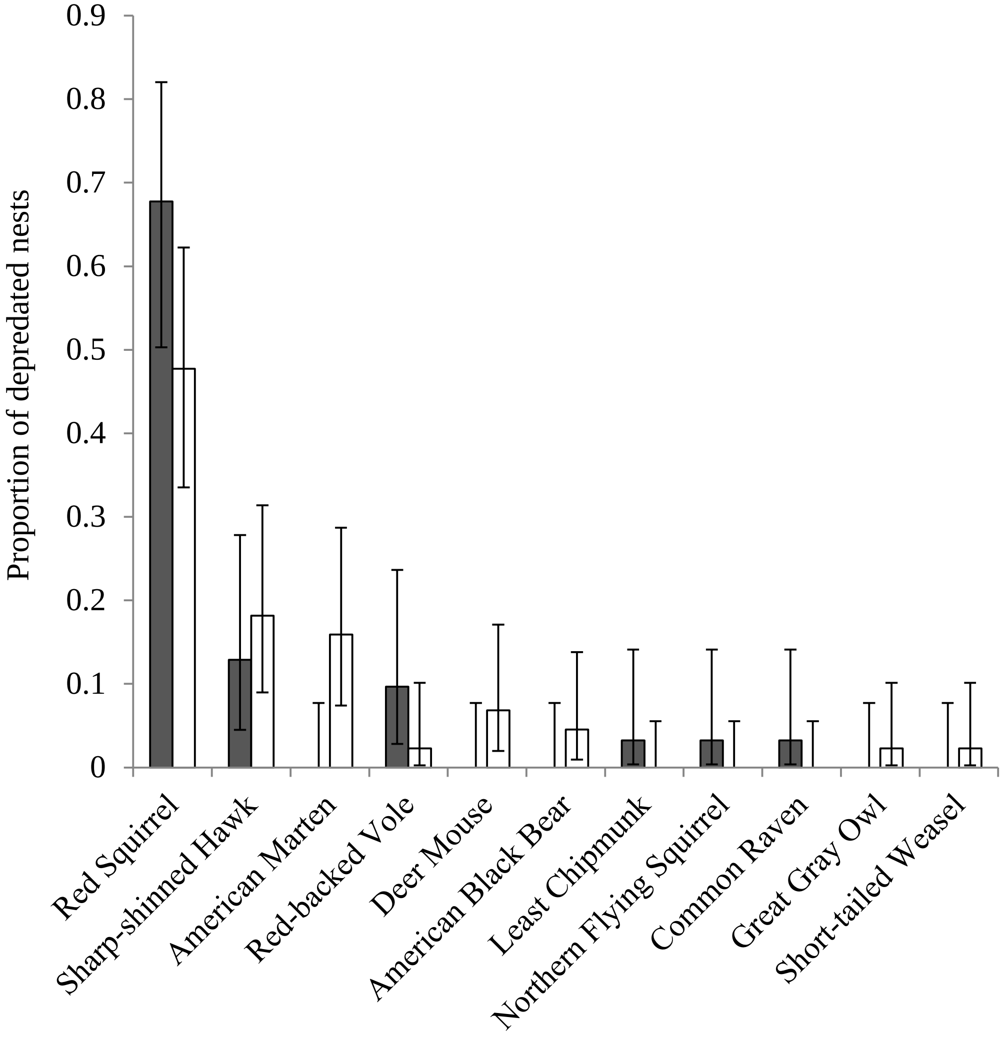

Figure 2.1. Proportion (± 95%) of video-monitored nests depredated by each predator species in Fort Simpson, NT (northern site; grey bars), and the Chinchaga Forestry Region, AB (southern site; white bars). Total numbers of predators recorded by study site and year were north 2005 = 13, north 2006 = 18, south 2006 = 11, and south 2007 = 33.

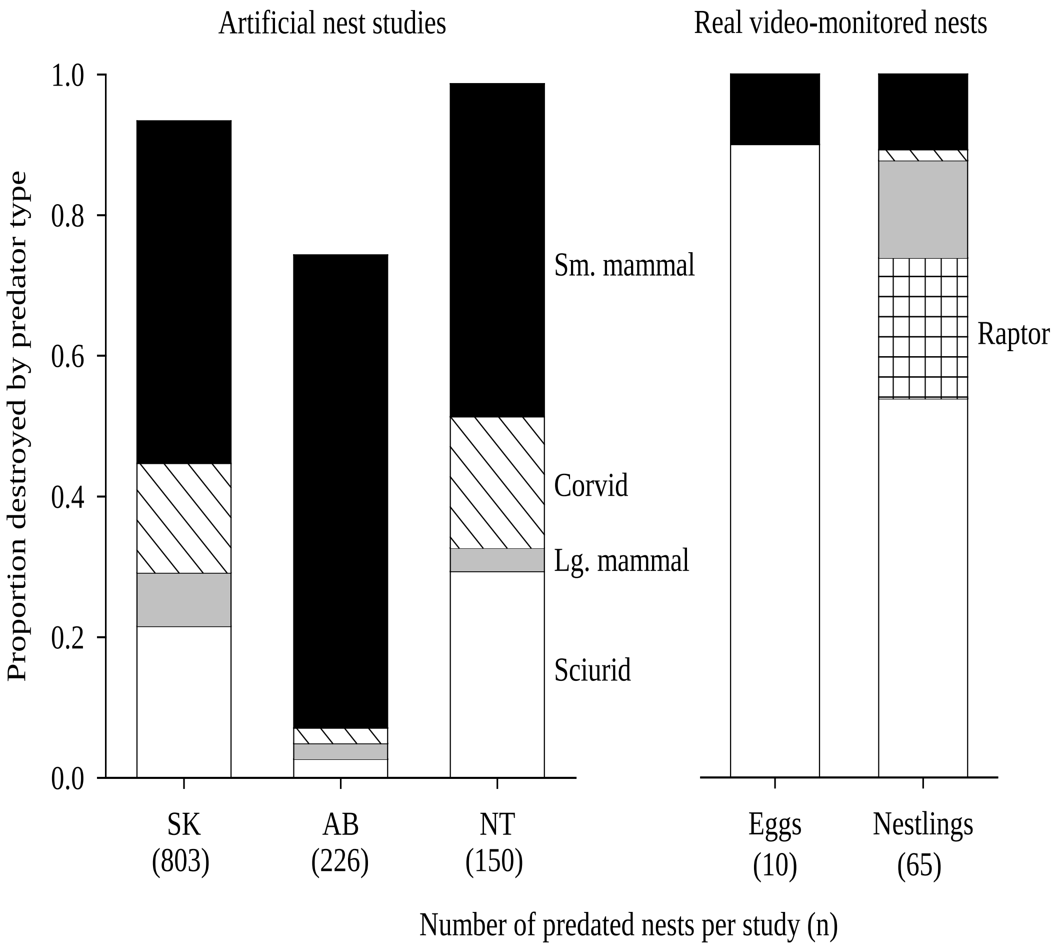

Figure 2.2. Proportion of real nests (containing either nestlings or eggs; total number of nests reported in brackets) or artificial nests (by study location) depredated by each predator species. The difference in height of the artificial nest bars from 1.0 indicates the proportion of nests where the predator was identified as ‘unknown’.

2.3.3. Artificial nests vs. real nests

The composition of the nest predator communities and the relative contribution of each predator category to nest fate differed between real and artificial nests (Fig. 2.2). Small mammals and corvids had a small impact on real nest fate but they had a relatively large impact on artificial nest fate. In contrast, sciurids were the dominant predator of real nests but had comparatively less of an impact on artificial nest fate. Artificial nests also did not identify raptors as important nest predators. As a result, relative to real nests, small mammals and corvids were 9 to 30 times more likely to depredate artificial nests than sciurids or large mammals (Table 2.1). Conversely, the relative risk of small mammals and corvids depredating artificial nests and of sciurids and large mammals depredating artificial nests relative to real nests did not differ.

Table 2.1. Relative risk ratios (RRR) compare the increase in probability of predator 1 depredating an artificial nest compared to a real nest relative to the increase in probability of predator 2 depredating an artificial nest compared to a real nest. RRR > 1 and *P*-values < 0.05 indicate that, relative to a real nest, predator 1 has a greater probability of depredating an artificial nest compared to predator 2.

Predator 1	Predator 2	*P*	RRR
small mammal	sciurid	< 0.0001	15.1928
small mammal	corvid	0.481	0.4873
small mammal	large mammal	0.001	9.7606
corvid	sciurid	< 0.0001	31.1749
corvid	large mammal	0.053	20.0282
sciurid	large mammal	0.563	0.6424

Our approach of assigning missing plasticine eggs to predator categories (see Methods) assumed that the composition of the predator categories and the tendency for each predator to remove eggs was similar across the regions where artificial nest studies were performed. When we excluded missing eggs and only considered identified predators, the differences among predators and between artificial nests and real nests remained and, in most cases, were exaggerated further. More artificial nest depredations were attributed to small mammals and fewer depredations were attributed to sciurids, corvids, and large mammals.

2.4. Discussion

Contrary to our prediction, the identified predator community of real nests in the southern site was similar to that of the northern site, both of which were characterized by species that were endemic to the boreal forest. This result was surprising given the higher density of edge habitat, increased proximity to agricultural areas, and the observed presence of potential human-associated nest predators in the south. For example, we observed coyotes (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), and American Crows (*Corvus brachyrhynchos*) near or within our southern study plots. However, these species were rarely observed compared to forest-associated predators, which suggests our southern study plots may be too far from agricultural areas for these species to have an important role in the local nest predator community or they are not important predators (Lloyd et al. 2005).

Our video data demonstrate that predators of real and artificial nests differed (Fig. 2.2). First, artificial nest studies failed to document raptors as nest predators, because raptors only depredated nestlings (20% of nestling predations). Second, predators differed in relative importance between the two nest types. Our video data confirmed that small mammals can and do depredate real nests. However, together with corvids, their relative importance as real nest predators (10% of eggs and 15% of nestlings) is over-emphasized by artificial nest studies. In contrast, sciurids, which depredated >50% of nestlings and more than triple the number of real eggs compared to artificial eggs, are under-represented by artificial nest studies.

We expected corvids to be important predators in our real nest study. Gray Jays (*Perisoreus canadensis*) are a common corvid in the boreal forest and they are widely considered important boreal nest predators that are attracted to forest edges (Ibarzabal and Desrochers 2004, Strickland and Ouellet 2011). However, their importance as nest predators is based largely on artificial nest studies (summarized by Ibarzabal and Desrochers 2004) and anecdotal observations (Ouellet 1970). We did not record Gray Jay predation of any real video-monitored nests although we identified Gray Jays as important artificial nest predators and we frequently encountered individuals and family groups on our real nest plots (Chapter 3). While some corvids may be deterred from visiting nests where a camera is present (Herranz et al. 2002, Richardson et al. 2009), we commonly recorded Gray Jays on camera traps at bait stations (Chapter 3). The bait cameras were much larger than our nest video cameras, which suggests that jays were unlikely deterred from visiting nests monitored by cameras. Instead, corvids, and Gray Jays in particular, may have less of an impact on nest fate than previously thought. Corvids are visual predators and real nests may be more cryptic than artificial nests. Adult songbirds also may provide an effective defense against corvid predation (Schmidt and Whelan 2005). We join Zanette (2002) in cautioning researchers in drawing conclusions about nest predation rates and predator identity based on artificial nests without validating this technique in their system.

Negative edge effects are more commonly reported along forest-field ecotones (Batáry and Báldi 2004), or when avian, rather than mammalian species, are the predominant nest predator (Chalfoun et al. 2002). We did not identify human-associated species or Gray Jays depredating real video-monitored nests. This suggests that much of Canada's boreal forest may not be vulnerable to some of the more commonly cited negative effects associated with edges because it is sufficiently far from agriculture and because Gray Jays are not as important a nest predator as previously believed. Our nest survival data support this conclusion (Chapters 3 and 4). We did not find strong support for an effect of study site or for a negative effect of edge proximity on nesting success. Instead, the survival probability of ground nests was marginally higher near the edge compared to the forest interior in both sites. This suggests that linear features may affect boreal forest songbird populations primarily through direct loss of forest habitat rather than indirect, edge-induced decreases in reproductive success (Bayne et al. 2005).

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Appendix 2.1. Total number of days of video monitoring (n nests) by species during each year of study in boreal mixed wood forests near Fort Simpson, NT (northern site), and in the Chinchaga Forestry Region, AB (southern site).

		Northern site		Southern site	
Common name	Species name	2005	2006	2006	2007
American Redstart	*Setophaga ruticilla*	4.5 (2)	5.8 (1)	-	1.1 (1)
American Robin	*Turdus migratorius*	3.1 (1)	5.8 (1)	15.6 (1)	12.5 (2)
Chipping Sparrow	*Spizilla passerina*	-	10.9 (1)	92.8 (9)	180.3 (16)
Dark-eyed Junco	*Junco Hyemalis*		-	6.3 (1)	76.6 (6)
Hermit Thrush	*Catharus guttatus*	19.6 (3)	61.3 (7)	-	-
Least Flycatcher	*Empidonax minimus*	15.6 (2)	-	-	14.8 (1)
Magnolia Warbler	*Setophaga magnolia*	-	-	-	17.2 (1)
Northern Waterthrush	*Parkesia noveboracensis*	1.8 (1)	-	-	-
Ovenbird	*Seiurus aurocapilla*	11.8 (1)	-	19.5 (3)	110.5 (9)
Swainson's Thrush	*Catharus ustulatus*	73.8 (11)	171.5 (24)	5.9 (2)	232.9 (19)
Tennesee Warbler	*Oreothlypis peregrina*	20.8 (3)	16.8 (3)	12.0 (2)	61.6 (5)
White-throated Sparrow	*Zonotrichia albicollis*	16.5 (1)	8.2 (1)	7.3 (1)	8.9 (1)
Yellow-rumped Warbler	*Setophaga coronata*		-	2.8 (1)	11.9 (1)
TOTAL		167.5 (25)	280.3 (38)	162.2 (20)	728.4 (62)

Appendix 2.2. Numbers of songbird nests visited by each nest predator species as recorded on video during each year of study in boreal mixed wood forests near Fort Simpson, NT (northern site), and in the Chinchaga Forestry Region, AB (southern site).

		Northern site		Southern site	
Common name	Species name	2005	2006	2006	2007
American Black Bear	*Ursus americanus*	-	-	2	-
Least Chipmunk	*Neotamius minimus*	1	-	-	-
Common Raven	*Corvus corax*	-	1	-	-
Deer Mouse	*Peromyscus maniculatus*	-	-	2	1
Great Gray Owl	*Strix nebulosa*	-	-	-	1
American Marten	*Martes americana*	-	-	1	6
Northern-Flying Squirrel	*Glaucomys sabrinus*	1	-	-	-
Red-backed Vole	*Myodes* spp.	3	-	-	1
American Red Squirrel	*Tamiasciurus hudsonicus*	6	15	6	15
Sharp-shinned Hawk	*Accipiter striatus*	2	2	-	8
Short-tailed Weasel	*Mustela erminea*	-	-	-	1
Total predations		13	18	11	33
Numbers of nests with cameras		25	38	20	62

Chapter 3. Lack of numerical and functional response by nest predators of songbirds in landscapes fragmented by energy sector linear features in the western boreal forest.[2]

3.1. Introduction

Pulliam (1988) recognized the reproductive landscape for most animals is not homogenous. Instead, some habitats act as reproductive sources that produce a surplus of individuals whereas other habitats are reproductive sinks that produce too few individuals to compensate for adult mortality and whose numbers are maintained by immigration. Habitat fragmentation by human land use can alter predator-prey dynamics and the proportion of source and sink habitats in a landscape. Of concern for forest nesting songbirds is the creation of edge habitat. Edge habitat may improve some aspects of territory quality for forest birds (Ries and Sisk 2004) but this benefit can be overwhelmed by increased nest predator activity or density near edges (Chalfoun et al. 2002). Nest predation is the primary source of reproductive failure for many avian species (Ricklefs 1969, Martin 1992, Newton 1998), which has important implications for avian demography in areas where anthropogenic edge creation occurs (Robinson et al. 1995, Sæther and Bakke 2000, Lloyd et al. 2005). Understanding the impacts of anthropogenic fragmentation and whether edges alter the source-sink balance for nesting

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[2] A version of this chapter will be submitted for publication with the following authorship: Jeffrey R. Ball, Erin M. Bayne, and Craig S. Machtans.

songbirds is needed to develop effective land use policies aimed at conserving birds.

Negative edge effects in forest landscapes are commonly reported in landscapes with significant forest loss and/or at forest-agriculture boundaries where increased density and diversity of nest predators often is observed (Donovan et al. 1997, Thompson et al. 2002, Batáry and Báldi 2003, Stephens et al. 2003, Driscoll and Donovan 2004, Lloyd et al. 2005). However, negative edge effects in forests may largely be an “eastern paradigm” owing to the extensive forest matrix and history of wildfires that make western forests more naturally patchy (George and Dobkin 2002; but see Lahti 2001). Studies conducted in western North America frequently report decreased rates of nest predation in fragmented landscapes or near edges presumably because of reduced numbers of nest predators (Tewksbury et al. 1998, 2006, Cavitt and Martin 2002, Hannon et al. 2009; but see Hames et al. 2002). Negative edge effects also are more commonly reported when avian, rather than mammalian species, are the predominant nest predator (Chalfoun et al. 2002). Predictions concerning edge effects on nest predation are hampered by our lack of knowledge about what predators are chiefly responsible for nest failure and how those predators respond to edges (Lahti 2001, 2009, Thompson 2007). Identifying sources of nest failure and composition of the nest predator community is necessary to improve our understanding of factors affecting nest fate, including the potential for negative edge effects and the observed differences in edge effects between eastern and western North America (Lahti 2009, Benson et al 2010, Reidy and Thompson

2012). By identifying who depredates nests and under what conditions nest predation rates become elevated we can begin to develop testable hypotheses about what changes have occurred in the landscape and how those negative effects can be mitigated (Thompson and Ribic 2012).

We studied nesting success of boreal forest songbirds in western Canada. The boreal forest is an important resource to North American avifauna (Blancher and Wells 2005). The natural capital of the boreal region also is an important source of revenue for the Canadian economy (Anielski and Wilson 2009). As a result, this landscape is rapidly being fragmented by forestry, oil and gas development, associated transportation networks, and other less extensive disturbances. The oil and gas industry, in particular, creates hundreds of thousands of kilometers of seismic line and pipeline clearings through the forest (Schneider 2002). These linear features result in relatively little forest loss yet create vast amounts of edge habitat. Abundance studies suggest boreal birds may be resilient to fragmentation caused by such development (Schmiegelow et al. 1997, Norton et al. 2000, Brotons et al. 2003, Bayne et al. 2005a, b, Machtans 2006, Taylor and Krawchuk 2006, Leonard et al. 2008). However, a demographic mechanism for resilience has not been identified, in part, because our current understanding of boreal nest predators is largely based on artificial nests (e.g., Bayne and Hobson 1997, Cotterill and Hannon 1999, Song 1998, Ibarzabal and Desrochers 2005). Results from these studies do not accurately reflect the magnitude or spatial patterns of real nest survival, or the composition and relative importance of the species depredating real nests (Zanette 2002). Given the growing pace of edge creation in the boreal forest (Schneider 2002), when, where, and why negative edge effects occur must be clarified.

We tested the hypothesis that boreal forest birds are negatively impacted by edges associated with energy sector linear features as a result of increased rates of nest predation near edges. We placed video cameras at a suite of boreal forest songbird nests to identify those predator species chiefly responsible for nest predation. We then examined whether different predator species were more or less likely to depredate nests close to a forest edge. A variety of survey techniques were used to determine whether the spatial distribution of each species of nest predator showed a clear response to forest edges.

3.2. Methods

3.2.1. Study sites and linear feature classification.

We studied nesting success in mature mixedwood boreal forest close to versus far from energy sector linear features. Linear features in our system included buried pipeline right-of-ways (~25 m wide), seismic lines (~8 m wide), and limited-use service roads (12 to 25 m wide). Pipelines are periodically cleared of woody vegetation whereas seismic lines ranged from herbaceous ground cover only to entirely overgrown with shrubs or trees. The centre portions of service roads were typically surfaced in gravel. We did not evaluate edges created by forestry, agriculture, or surfaced roads with high traffic volume.

We established several study plots in each of two regions (SITE) with different amounts of linear feature edge (Fig. 1.1). Six 42-ha plots were studied near Fort Simpson, Northwest Territories (61°52′N, 121°20′W; hereafter northern site), in 2005 and 2006. Nine 24-ha plots were studied in the Chinchaga forestry region northwest of Manning, Alberta (57°18′N, 118°23′W; hereafter southern site), in 2006 and 2007. Plots in each site were a minimum 1.2 km apart. Plot sizes and spatial configuration were chosen to minimize the likelihood smaller predators could depredate all nests on a single plot or that large predators could depredate multiple plots (Donovan et al. 1997, Stephens et al. 2003). We categorized all lines in the vicinity of each study plot based on width and amount of woody vegetation regrowth, which may influence the magnitude of edge effects (Rich et al. 1994, Harper et al. 2005). We categorized lines into three types, MAIN, OPEN or CLOSED based on width and amount of woody vegetation regrowth (see Glossary for definitions). Each northern plot was adjacent to a single MAIN line. Each southern plot bordered one or two MAIN lines or a MAIN and an OPEN line and was bisected by one or more OPEN lines. We assumed CLOSED lines were ecologically similar to the adjacent forest and they were not considered as creating an edge effect (Tigner 2012, Lankau et al. 2013).

3.2.2. Nests and nest predator identification.

We visited each plot every 3 days between late May and mid-July to search for and monitor nests. Infrared digital video cameras were placed at randomly selected Swainson’s Thrush (*Catharus ustulatus*) and Chipping Sparrow (*Spizella passerina*) nests and opportunistically at nests of other songbird species when target nests were unavailable. We delayed camera installation until late incubation or the early nestling stage to avoid abandonment. Cameras were left in place until nesting was complete. Cameras were small (8 cm x 3.5 cm), and each was mounted in vegetation 0.5 – 1.0 m from the nest. Observer disturbance was limited to battery changes every 6 days, ~10 m from the nest, unless adults were absent, in which case nests were visited to check contents. We identified all predator species that visited each video-monitored nest. We also recorded nest substrate (SUBSTRATE) and concealment (COVER) of each nest (Glossary). Concealment was the percentage of a 0.5 m wide × 3 m tall cover board obscured by vegetation when viewed from a horizontal distance of 2 m (MacFarlane 2003). COVER was the average of concealment estimates made at four cardinal directions at each of five locations (n = 20 estimates per nest). One location was centered on the nest and the remaining locations were in four cardinal directions each 5 m from the nest.

3.2.3. Spatial distribution of nest predators.

All species in the nest predator community could not be adequately sampled using a single survey method. Therefore, we used five different methods to measure the association between nest predators and linear feature edges. We used 100-m fixed radius point counts to survey nest predators that were relatively common, active, and easily detected during the day. Each nest-study plot contained a systematic grid of nine survey stations (Fig. 3.1). Three stations were located at 0, 200, and 400 m from the edge in each plot. Each station was surveyed twice each year during June between sunrise and 10:00. During each survey observers recorded the initial time period (0 – 3 min, 3 – 5 min, and 5 – 10 min) and distance category (0 – 50 m and 50 – 100 m) of all potential nest predators heard or observed.

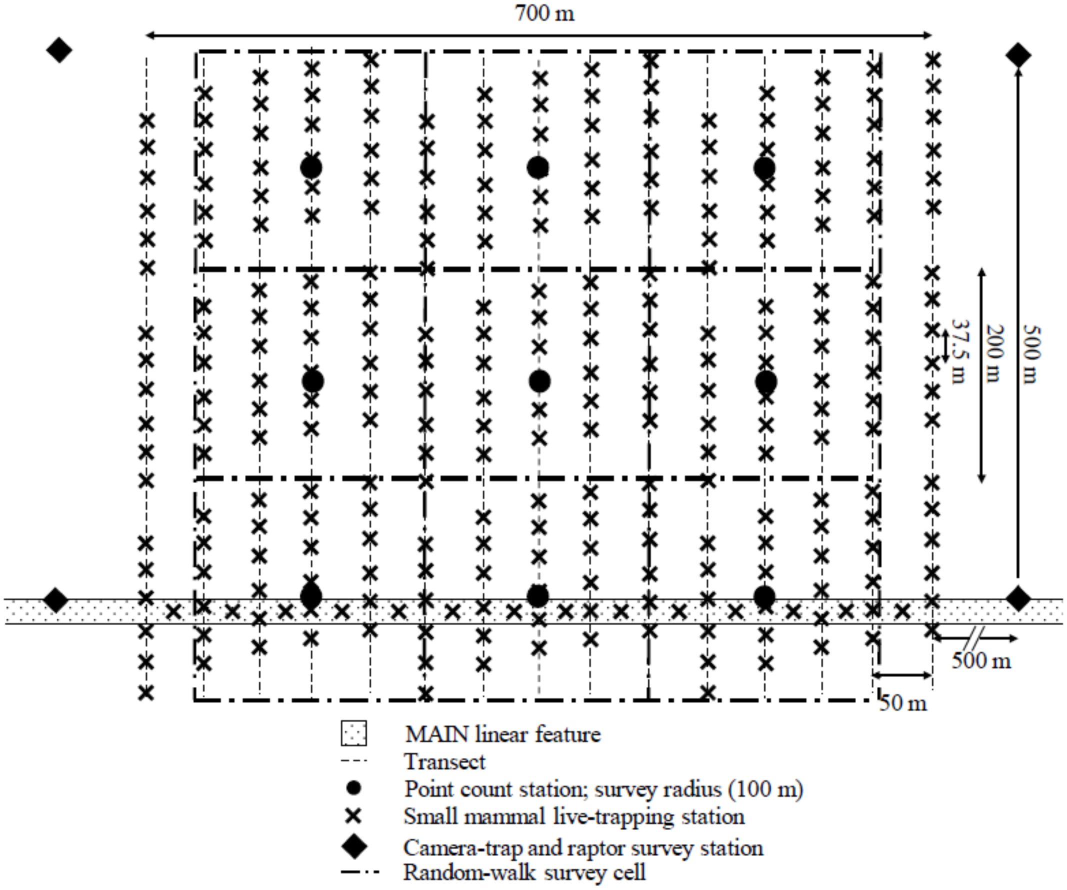

Figure 3.1. Plot layout of survey locations in Fort Simpson, NT (northern site). The layout in Chinchaga, AB (southern site), was similar except the plot dimensions were slightly smaller (400 m × 600 m) and live-trapping transects were spaced 100 m along the MAIN linear feature and did not extend off both sides of linear feature or beyond 400 m from edge.

We used live-capture traps to record the spatial distribution of small mammals on the nest-study plots (Darling 2008). Trap stations were established in a systematic grid of 182 (southern site) and 480 (northern site) stations/plot (Fig. 3.1). Trap stations were a minimum 37.5 m apart and extended 400 m (southern site) to 500 m (northern site) into the forest perpendicular to the MAIN edge. Each plot also had one transect of trap stations spaced 50-m apart along the centre of the MAIN linear feature. A multiple-capture Tincat® trap and a larger single-capture Longworth® trap were placed 10 m apart at each trap station. Two rounds of trapping were performed in the northern site between late May and early August in 2005 and 2006. One round of trapping was conducted on five plots in the southern site between July and early August 2007. Traps were set in the late afternoon and checked the following morning. Traps were baited with peanut butter and carrot. Each plot was trapped for 3 consecutive nights. The numbers of individuals per species were recorded each morning before release.

Observers performed random-walk surveys by recording the potential nest predators they encountered while performing other duties on the nest-study plots. Observers recorded their GPS location and the distance and bearing to each potential predator they observed or heard (Hochachka et al. 2000). Observers recorded all detections unless they were certain an individual was previously recorded during the current visit based on predator location and duration between detections. We assumed individuals were counted multiple times because nest predators were unmarked and often detected aurally. Therefore, these data represent spatial variation in nest predator activity rather than abundance. We accounted for the effect of spatial variation in observer effort on frequency of predator detections by dividing each plot into nine cells with each cell centred on a point count station (Fig. 3.1). Observers were instructed to divide their time evenly among cells and to record their time spent surveying in each cell.

Camera traps and raptor playback surveys were used to document the edge-association of wider-ranging and cryptic species. Camera traps were used in the northern site in 2005 and 2006 and in the southern site in 2007. Playbacks were conducted in the northern site in 2006 and in the southern site in 2006 and 2007. Camera trap stations and playback stations were established in pairs with one station on a MAIN edge 1 – 3 m into the forest and the other station 400 – 500 m into the forest perpendicular to the MAIN edge. A portion of these stations were associated with the nest-study plots (Fig. 3.1). At each camera trap station we attached a motion-activated camera (Bushnell Trail Scout® Digital Camera 11-9835C) to a tree 0.5 m above the ground. We applied a bait mixture of sardines and dog food to an adjacent tree ≤ 3 m from the camera. Cameras were set for 24-hour surveillance and to take one picture every minute in response to movement at the bait station. Camera stations were active for an average (± 1 SE) 8.6 ± 0.25 nights at each location. Playback surveys were performed between late May and late July during daylight hours. Upon arriving at a survey station observers listened for 1 min, played a Sharp-shinned Hawk (*Accipiter striatus*) call for 1 min, listened for 2 min, played a Northern Goshawk (*A. gentilis*) call for 1 min, listened for 2 min, played a Great Horned Owl (*Bubo virginianus*) call for 1 min, and listened for 4 min for a total 12 min per station. Each northern station was visited twice during the summer whereas southern stations were visited once during the summer.

3.2.4. Statistical analyses.

We spatially referenced all video-monitored nests, point count stations, live-trap stations, random-walk predator detections, camera traps, playback stations, and all linear features into a geographic information system (ArcGIS

10.0, Environmental Systems Research Institute, Inc. [ESRI], 2010). We corrected the locations of random-walk predator detections using observer estimates of distance and bearing and the Distance/Azimuth extension (Jenness 2005) in ArcView GIS 3.3 (ESRI, 2002). We also generated a 5 m × 5 m systematic grid of points on each plot that served as 'available' locations in our random-walk analysis (Benson 2013). We used the NEAR tool (ArcGIS 10.0, ESRI, 2010) to calculate two edge metrics for each point associated with a study plot, distance (m) to the nearest MAIN edge and distance to the nearest MAIN or OPEN edge (hereafter, MAIN|OPEN). Points occurring on a linear feature had a distance of 0 m. We excluded random-walk detections from our analyses that were beyond the maximum distance to MAIN of our available points. Because we lacked information about width or vegetation regrowth of lines not associated with our study plots, we classified the edge association of points outside of plot boundaries (i.e., camera trap and playback stations) as edge or interior in our analyses.

Multinomial logistic regression was used to determine the nest-related factors that best explained variation in the probability of daily nest mortality by each predator group (Thompson and Burhans 2003, Cox et al. 2012, Thompson and Ribic 2012). The data consisted of each 24-h interval each nest was filmed. The dependent variable for each interval was predator identity if the nest was depredated or 'other fate' if the nest was active, fledged, or failed by means other than predation. We considered all predator visits as predation attempts regardless of whether the nest was successfully depredated. Predators that depredated ≥ 5% of all nests were identified to species. The remaining predators were pooled into an ‘other predators’ category. We only counted the initial predation event for nests depredated by the same species across multiple intervals (Cox et al. 2012).

We used an information-theoretic approach based on Akaike’s Information Criteria adjusted for small sample size (AIC_c) to select among competing models that considered the effects of SUBSTRATE, COVER, and linear and quadratic forms of nest distance to the nearest MAIN or nearest MAIN|OPEN as independent variables. We did not include study site as a dependent variable in this analysis because not all predator groups were recorded in both sites. We constructed a set of models that considered all additive combinations of our independent variables. We also considered interactions between SUBSTRATE and edge proximity and between COVER and edge proximity that reflect potential differential edge responses by predators related to differences in nest characteristics. We completed our model set by including a constant mortality rate model (NULL) that did not contain any explanatory variables. We compared support among models using AIC_c weights (w) and evidence ratios (ER; Burnham and Anderson 2002, Anderson 2008; Glossary).

We used a common set of models to analyze the edge-related distributions of nest predators recorded by each survey method. Our goal was to determine whether nest predators responded to edges rather than identifying mechanisms for that response. Therefore, we did not include variables that may co-vary with edge proximity (i.e., shrub density) and partially explain predator occurrence as that would affect the magnitude of edge response. Each model set considered all possible additive and interactive combinations of SITE and edge proximity as independent variables. The measure(s) of edge proximity in each model set depended on survey design and the available level of detail regarding linear feature class (i.e., MAIN or OPEN). Camera traps and playback surveys had the simplest design and the least available detail about linear feature class. These models included a single two-category measure of edge proximity (EDGE = edge or interior). The remaining survey models considered two continuous measures of edge proximity (MAIN and MAIN|OPEN) as linear and quadratic relationships. Our point count analyses also considered three additional categorical edge measures. Stations were categorized as occurring within hearing distance (i.e., 100 m) of a MAIN (M100) and a MAIN|OPEN (MO100) edge, and occurring at 0, 200, or 400 m from a MAIN edge (3MAIN; Glossary) as per our study design. Finally, each model set included a NULL model that did not contain SITE or edge variables.

All survey data were analyzed using mixed-effects regression with an underlying statistical distribution appropriate to the dependent variable. This analytical approach provides an index of abundance or presence. Indices are well-suited to test our edge hypothesis so long as variation in detection is minimized by study design and is not biased by edge proximity (Sinclair et al. 2006, Johnson 2008). Edge proximity may bias detectability of observer-based surveys if open linear features enable observers to see or hear predators at greater distances. We determined whether linear features affected detection in our point count surveys by comparing the effective detection radius (EDR; Matsuoka et al. 2012) between edge and interior stations for each potential nest predator. Individuals were pooled at each station across years to achieve a sufficient sample size for analyses. EDR between edge and interior points were compared using mixed-effects linear regression with a random intercept for plot. We also determined whether linear features affected detection during our random-walk surveys. We used Mann-Whitney tests to compare the median distance between the observer and each predator species that was recorded on or within 10 m of a linear feature vs. within the forest. We separated our analyses by detection method (i.e., predators that were heard and predators that were seen) when sample size allowed because linear features may affect these detection methods differently. We used a bootstrap with 1000 replicates to calculate the mean detection distance (± 95% CI) for each species and detection method at edge and interior locations.

Live-capture and baited camera traps remove the human element and are not expected to have a detectability bias with respect to edge proximity. Detection distance was not recorded for raptor playbacks and we are therefore unable to determine if detectability using these methods varies in response to edge. However, both playback stations and camera traps were within the forest and cameras were not pointed towards the edge so neither observers nor cameras had an unobstructed view down the linear feature. Our sampling design also limited variation in detectability by focusing on a single habitat type (mature mixed wood forest), by employing a single observer during each season (point counts) or by randomizing observers with respect to edge proximity (random-walk, raptor playback), and by collecting samples over consecutive days and/or repeated visits to control for potential time and weather effects.

We also accounted for the effects of survey effort and the effects of several nuisance variables (point count models; see below) on detectability in our analyses. The dependent variable in our point count analyses was the number of individuals of each predator species recorded during each survey (Poisson distribution). Survey day (standardized to the earliest day of surveys in each site), survey time (hours post-sunrise), temperature, wind speed, and wetness were included as nuisance variables presumed to be important to detectability. The dependent variable in our live-capture analyses was the number of each species captured at each trap station (negative binomial distribution). Each dependent variable was the sum of all captures per station over all of the years of study in each site. The total number of nights each trap was open was included as an exposure variable to control for the effect of trapping effort on total captures. One trap night was one trap open on one night. A trap that was visited without capture of an animal but that was closed was designated as half a trap night (Beauvais and Buskirk 1999). The dependent variable in our random-walk models was used (i.e., locations where a predator was recorded) vs. available locations (binomial distribution). The exposure variable for each point was ln(survey effort). Survey effort for each used point was the sum duration of all visits to the grid cell in which that point occurred. Survey effort for used locations was centred prior to analysis (mean grid cell survey time – grid cell survey time); effort for unused locations equals zero. The dependent variables in our camera trap and playback analyses was predator presence (yes or no; binomial distribution). We considered a predator to be present at a playback station if it was detected during ≥ 1 visit during a year. The exposure variable for each trap and playback station was ln(survey effort). Survey effort for camera trap station was the number of days a camera was active. Survey effort for playback station was the number of visits to the station. All models included a random intercept for plot or grouping (camera trap and playback stations) to account for the lack of independence between points within a plot or grouping. Point count models also included a random intercept for station to account for multiple visits to each station.

To directly compare the magnitude of edge responses of predators and predation events, we standardized our results into incident rate ratios (IRR; point count, live-capture) or odds-ratios (OR; nest fate, camera trap, playback). The IRR of an interior vs. an edge event was calculated as IR400/IR0 where IR is the expected incident rate (i.e., count per unit effort). The OR of an interior vs. an edge event for each analysis was calculated as ([Pr400/(1-Pr400)]/[Pr0/(1-Pr0)]). We estimated the incident rates and probability of an event at 400 m and 0 m from the top-supported edge models from each of our analyses. Predictions were made based on average values for other model covariates. We used a Monte Carlo simulation to randomly generate 10,000 predicted probabilities on the linear scale based on the estimated coefficient and its SE. Each replicate was backtransformed to an IR or probability before computing the IRR or OR. We report the median ratio and the 2.5 and 97.5 percentiles (95% CI) from the Monte Carlo simulation. All analyses were performed using Stata (Stata/IC 11.2, StataCorp LP).

3.3. Results

3.3.1. Identification of nest predators.

We recorded 448 days of video at 63 songbird nests (10 species) in the northern site and 890 days of video at 82 nests (11 species) in the southern site (average duration ± 1 SE of video/nest = 9.2 ± 0.45 days; Appendix 2.1). We documented 75 predation events by 11 species at 71 nests (Fig. 2.1; Appendix 2.2). Three nests initially depredated by red-backed voles were later depredated by American red squirrel (two nests) or least chipmunk (one nest). A squirrel also depredated the remaining contents of one nest initially depredated by a Sharp-shinned Hawk. The numbers of nest predator species in the northern and southern sites was similar (six vs. eight species, respectively). However, only three species depredated nests in both study sites and only four species depredated ≥ 5% of nests in both study sites combined (Fig. 2.1). We did not record Gray Jays (*Perisoreus canadensis*) depredating our video-monitored nests despite their purported importance as nest predators (Strickland and Ouellet 2011). Gray Jays may be deterred from visiting nests where a camera is present (Herranz et al. 2002, Richardson et al. 2009; but see discussion) and they were, therefore, considered potential nest predators in our survey analyses.

We did not find strong support for a negative effect of edge proximity on the probability of daily nest mortality. Variation in daily nest mortality of video nests was best explained by a model that included SUBSTRATE as the only independent variable, which received 5.7 times (ER) more support than the next best supported NULL model (Table 3.1). Ground nests had a higher daily probability of being successful (0.96 [95% CI: 0.94 – 0.98]) compared to above-ground nests (0.94 [0.93 – 0.96]) because the two most prevalent nest predators, red squirrels and Sharp-shinned Hawks, were more than twice as likely to depredate above-ground nests compared to ground nests (Fig. 3.2). In contrast, American marten (*Martes americana*), red-backed vole, and 'other predators' were 1.21 – 5.46 times more likely to depredate ground nests compared to above-ground nests (Fig. 3.2).

Table 3.1. Top-supported models ($\sum w = 0.90$) explaining variation in the daily probability of video nests being depredated by a Red Squirrel, Sharp-shinned Hawk, American Marten, Red-backed Vole, or 'other predator' compared to nests that were not depredated (n = 145). The NULL model did not contain any explanatory covariates and represents a constant survival model. k is the number of model parameters. $L(\text{model} \mid x)$ is model likelihood given data x (exp[-1/2 ΔAIC$_c$]). w_i is the Akaike weight of model i.

Model	Log likelihood	k	AIC$_c$	ΔAIC$_c$	$L(\text{model} \mid x)$	w_i
SUBSTRATE	-383.13	10	786.41	0.00	1.00	0.52
NULL	-389.93	5	789.90	3.49	0.17	0.09
SUBSTRATE + (MAIN)^2	-374.78	20	790.15	3.74	0.15	0.08
SUBSTRATE + MAIN	-379.95	15	790.24	3.84	0.15	0.08
SUBSTRATE + MAIN|OPEN	-379.98	15	790.29	3.88	0.14	0.07
COVER	-386.02	10	792.20	5.79	0.06	0.03
SUBSTRATE + (MAIN|OPEN)^2	-375.88	20	792.35	5.95	0.05	0.03

The remaining nest mortality models, including all models that considered edge proximity, received less support than the null model (Appendix 3.1). Because each additional independent variable in a multinomial model strongly penalizes model AIC$_c$ (k increases by n – 1 levels of the dependent variable), we report results from the top-supported edge model, SUBSTRATE + (MAIN)^2, which received similar support to the null model (ER = 0.88; Table3.1). The daily

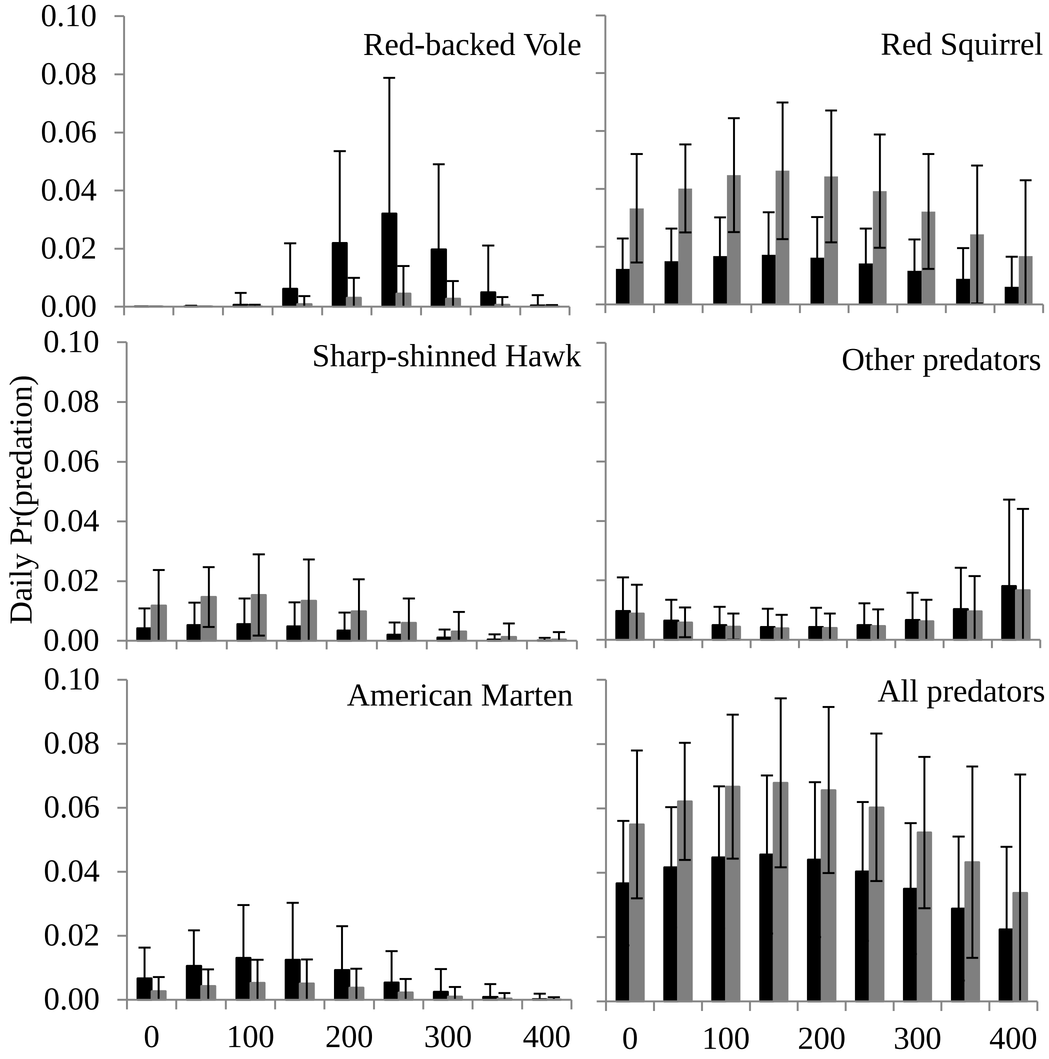

Figure 3.2. Daily probability (± 95% CI) of ground (black bar) and above-ground (grey bar) video-monitored nests being depredated by red-backed vole, American red squirrel, Sharp-shinned Hawk, American marten, 'other predators', or all predators combined with increasing distance from a MAIN edge. 'Other predators', which depredated < 5% of all video nests, include deer mouse, American black bear, least chipmunk, northern flying squirrel, Common Raven, Great Gray Owl, and short-tailed weasel.

probability of a nest being depredated by most predators was highest at intermediate distances from a MAIN edge (50 – 250 m; Fig. 3.2). Only the daily probability of red-backed vole predation was low near the edge compared to forest interiors. Consequently, the daily probability of a nest being successful was lowest at intermediate edge distances. The top model that included COVER was unsupported compared to the top model (ER = 0.06; Table 3.1).

3.3.2. Edge association of nest predators.

We performed 216 point count surveys at 54 stations in the northern site and 254 surveys at 82 stations in the southern site. We recorded sufficient numbers of red squirrels (n = 276) and Gray Jays (n = 77) for analyses. Variation in the numbers of squirrels and jays was best explained by the effects of study site and MAIN proximity (Appendix 3.2). The EDR for squirrels did not differ between edge and interior stations (*P* = 0.286; edge = 44.8 m [95% CI: 38.3 – 52.3 m], interior = 48.9 m [44.0 – 54.4 m]). We did not record sufficient numbers of Grays Jays to statistically test whether EDR differed between edge and interior stations but average EDR values were similar (edge = 49.1 m [43.1 – 55.2 m], interior = 50.5 m [45.1 – 55.9 m]). Therefore, we are confident that our results reflect a functional or numerical response to edge by jays and squirrels rather than edge-related variation in detectability by observers.

The top five squirrel models included distance to the nearest main edge, either as a categorical or continuous variable, and the additive or interactive effects of SITE (Table 3.2). Together these five models received 75% support among all models considered. The top model that did not consider an edge effect (SITE) was unsupported compared to the top model (ER = 0.12). Based on the top model the predicted number of red squirrels per survey was higher in the southern site compared to the northern site and higher at stations 400 m from a MAIN edge compared to stations 0 m and 200 m from the edge (Fig. 3.3). Gray Jays also were more numerous in the southern site but, in contrast to squirrels, the predicted number of jays was higher near MAIN edges (Fig. 3.3). Edge proximity appeared in the top 15 jay models ($\sum w = 0.93$; Table 3.2). The top model without edge effects (SITE) was unsupported compared to the top model (ER = 0.08). The top three models received similar support and included additive effects of SITE and continuous or categorical distance to the nearest main edge ($\sum w = 0.43$).

Table 3.2. Top-supported models ($\sum w \geq 0.90$) explaining variation in the edge-related distribution of a) red squirrels and b) Gray Jays recorded during point count surveys. $L(\text{model}|x)$ is model likelihood given data x (exp[-1/2 ΔAIC_{c}]). w_i is the Akaike weight of model *i*.

Model	Log likelihood	*k*	AIC_c	ΔAIC_c	$L(\text{model}|x)$	w_i
a. American red squirrel						
3MAIN + SITE	-417.64	11	857.85	0.00	1.00	0.31
MAIN + SITE	-419.06	10	858.59	0.74	0.69	0.22
$(\text{MAIN})^2$ + SITE	-418.81	11	860.20	2.35	0.31	0.10
MAIN × SITE	-418.95	11	860.48	2.63	0.27	0.08
3MAIN × SITE	-417.56	13	861.92	4.07	0.13	0.04
SITE	-421.86	9	862.11	4.26	0.12	0.04
MAIN|OPEN + SITE	-420.85	10	862.18	4.33	0.11	0.04
M100 + SITE	-420.94	10	862.35	4.50	0.11	0.03
3MAIN	-421.34	10	863.17	5.31	0.07	0.02
MO100 + SITE	-421.50	10	863.48	5.63	0.06	0.02
b. Gray Jay						
MAIN + SITE	-208.83	10	438.14	0.00	1.00	0.16
M100 + SITE	-208.92	10	438.32	0.18	0.91	0.15
MAIN|OPEN + SITE	-209.11	10	438.71	0.57	0.75	0.12
MAIN × SITE	-208.74	11	440.06	1.92	0.38	0.06
M100 × SITE	-208.74	11	440.07	1.93	0.38	0.06
$(\text{MAIN})^2$ + SITE	-208.82	11	440.22	2.08	0.35	0.06
MAIN|OPEN	-210.94	9	440.26	2.12	0.35	0.06
$(\text{MAIN}|\text{OPEN})^2$ + SITE	-209.10	11	440.78	2.64	0.27	0.04
MAIN|OPEN × SITE	-209.11	11	440.79	2.65	0.27	0.04
3MAIN + SITE	-209.19	11	440.96	2.82	0.24	0.04
MO100 + SITE	-210.33	10	441.13	2.99	0.22	0.04
MAIN	-211.45	9	441.28	3.14	0.21	0.03
M100	-211.51	9	441.41	3.27	0.20	0.03
$(\text{MAIN}|\text{OPEN})^2$	-210.87	10	442.21	4.08	0.13	0.02
MO100 × SITE	-209.82	11	442.22	4.08	0.13	0.02
SITE	-212.43	9	443.26	5.12	0.08	0.01

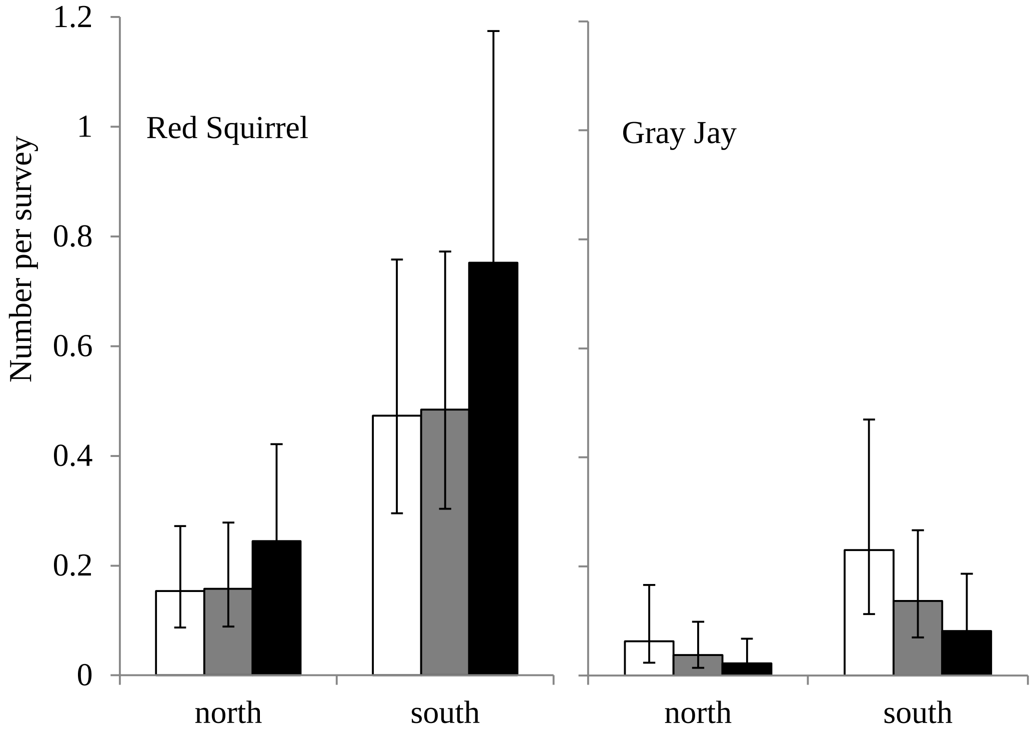

Figure 3.3. Predicted number of American red squirrels and Gray Jays per point count survey (± 95% CI) at stations located 0 m (white bar), 200 m (gray bar), and 400 m (black bar) from the MAIN forest edge in Fort Simpson, NT (north) and Chinchaga Forestry Region, AB (south).

Our live-capture data included 1,440 stations opened for 18,068 trap nights in the northern site (average ± 1 SE = 12.5 ± 0.23 nights/trap) and 455 stations opened for 2694.5 trap nights in the southern site (5.9 ± 0.01 nights/trap). The two species of small mammals we recorded depredating video nests, red-backed vole and deer mouse, also were the two most prevalent small mammal species captured (82% of combined captures; Darling 2008). We captured an average (± 1 SE) of 16.4 (0.53) and 22.2 (0.15) red-backed voles and 3.92 (0.31) and 16.0 (1.48) deer mice per 100 trap nights in the north and south, respectively. These capture rates are sufficiently low that our indices are consistent with detectability-corrected estimates (Watkins et al. 2010). Variation in the numbers of live-captured voles was best explained as a quadratic relationship with MAIN|OPEN proximity and the additive effect of SITE (Table 3.3, Appendix 3.3). Greater numbers of voles were captured in the forest interior compared to the MAIN|OPEN edge and in the southern site compared to the northern site (Fig. 3.4). Variation in deer mouse captures was best explained by the interactive effects of SITE and either the quadratic or linear form of MAIN proximity (Table 3.3; Appendix 3.3). Greater numbers of mice were captured near the forest edge compared to the forest interior in the southern site and in the southern site compared to the northern site (Fig. 3.4).

We performed 3,253 h of random-walk surveys in the northern site and 2,059 h of surveys in the southern site. We recorded sufficient numbers of red squirrels (680 and 1,521 detections in the north and south, respectively), Gray Jays (380, 600), Common Ravens (72, 58), and Sharp-shinned Hawks (10, 9) to consider the main and interactive effects of SITE and edge proximity. We also recorded sufficient numbers of Great Gray Owls (38 detections in both sites combined), least chipmunks (21), American marten (14), and American black bears (13) to consider the effects of edge proximity alone. Survey effort and study area were excluded from these latter models to achieve convergence. Finally, our analyses included 40,349 and 22,545 available locations in the northern and southern sites, respectively. Compared to the forest interior, observers recorded seeing Common Ravens at marginally further distances at the forest edge (P = 0.065) and hearing Gray Jays at marginally further distances at the forest edge (P

Table 3.3. Top-supported models ($\sum w > 0.90$) explaining variation in the edge-related distribution of a) red-backed voles and b) deer mice captured in live-capture traps. *k* is the number of model parameters. *L*(model|*x*) is model likelihood given data x (exp[-1/2 ΔAIC_c]). w_i is the Akaike weight of model *i*.

Model	Log likelihood	*k*	AIC_c	ΔAIC_c	*L*(model|*x*)[a]	w_i
a. Red-backed vole						
$(MAIN\|OPEN)^2$ + SITE	-3291.74	6	6595.52	0.00	1.00	0.84
$(MAIN\|OPEN)^2$ × SITE	-3291.37	8	6598.81	3.29	0.19	0.16
b. Deer mouse						
$(MAIN)^2$ × SITE	-1704.80	8	3425.68	0.00	1.00	0.61
MAIN × SITE	-1707.27	6	3426.59	0.91	0.63	0.39

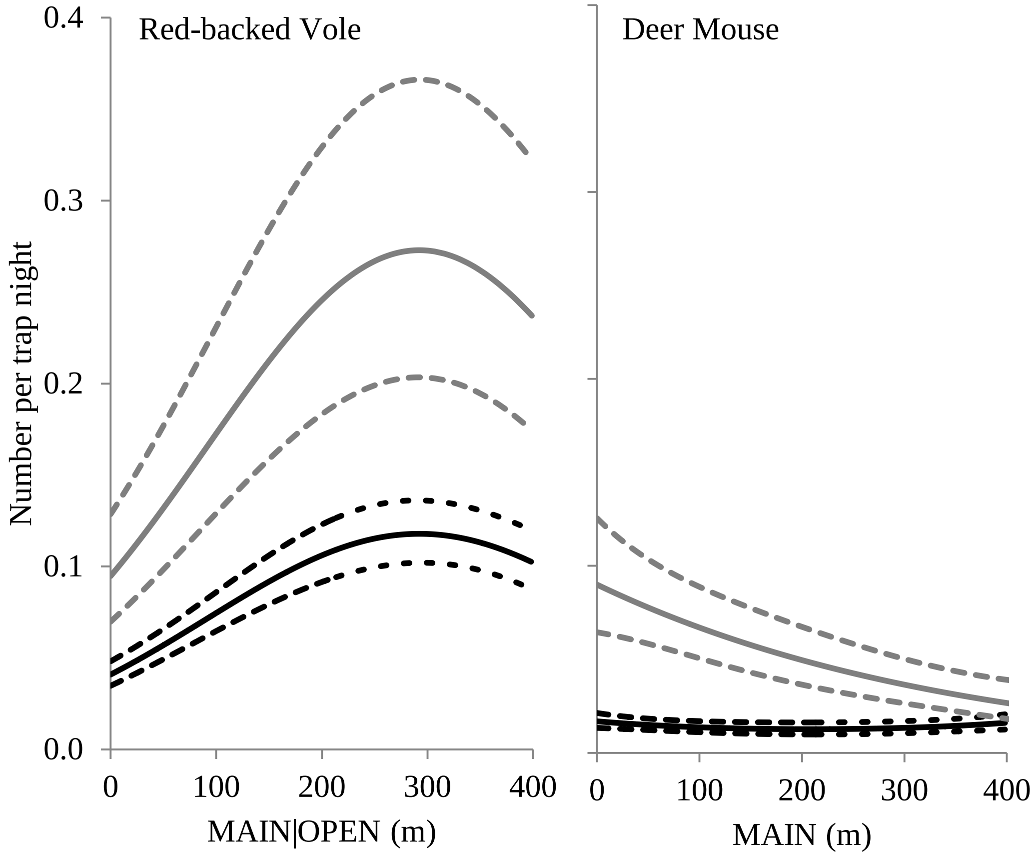

Figure 3.4. Predicted numbers of red-backed voles and deer mice per trap night in live-capture traps at increasing distance from the nearest linear feature edge in Fort Simpson, NT (northern site; black lines), and the Chinchaga Forestry Region, AB (southern site; grey lines). Dashed lines represent ± 95% CI.

= 0.078; Fig. 3.5). Detection distances did not differ for the remaining species and did not vary consistently between the edge and interior among species (all *P* > 0.19).

The encounter probability for the majority of species (7of 8) was best explained by proximity of the nearest MAIN or MAIN|OPEN edge (Table 3.4, Appendix 3.4). Only the encounter probability of chipmunks was unexplained by edge proximity. The majority of species (7 of 8) also were more likely to be detected nearer to MAIN or MAIN|OPEN edges (Fig. 3.6). Only ravens were more likely to be detected in the forest interior and only in the southern site. The top edge model was strongly supported for squirrels, jays, ravens, and bears whereas the top edge model received only moderate support for Great Gray Owls, marten, and Sharp-shinned Hawks. For marten, the top edge model received 35 times the support of the NULL and the top three edge-containing models received a cumulative 97% support among all models considered. For hawks and owls, the top edge model only received approximately 4.5 times the support of the NULL. We established 61 and 135 pairs of baited camera stations in the northern and southern sites, respectively. We had sufficient numbers of stations with red squirrels (45 stations), Gray Jays (81), American marten (43), and American black bears (74) for analyses. We also counted 7 Sharp-shinned Hawks during 80 raptor playback surveys at 20 edge and 20 interior stations in the northern site, and 8 hawks during 138 surveys at 76 edge and 62 interior stations in the southern site. Edge proximity received some support for explaining variation in encounter probability for all species except Gray Jay (Table 3.5, Appendix 3.5). An edge

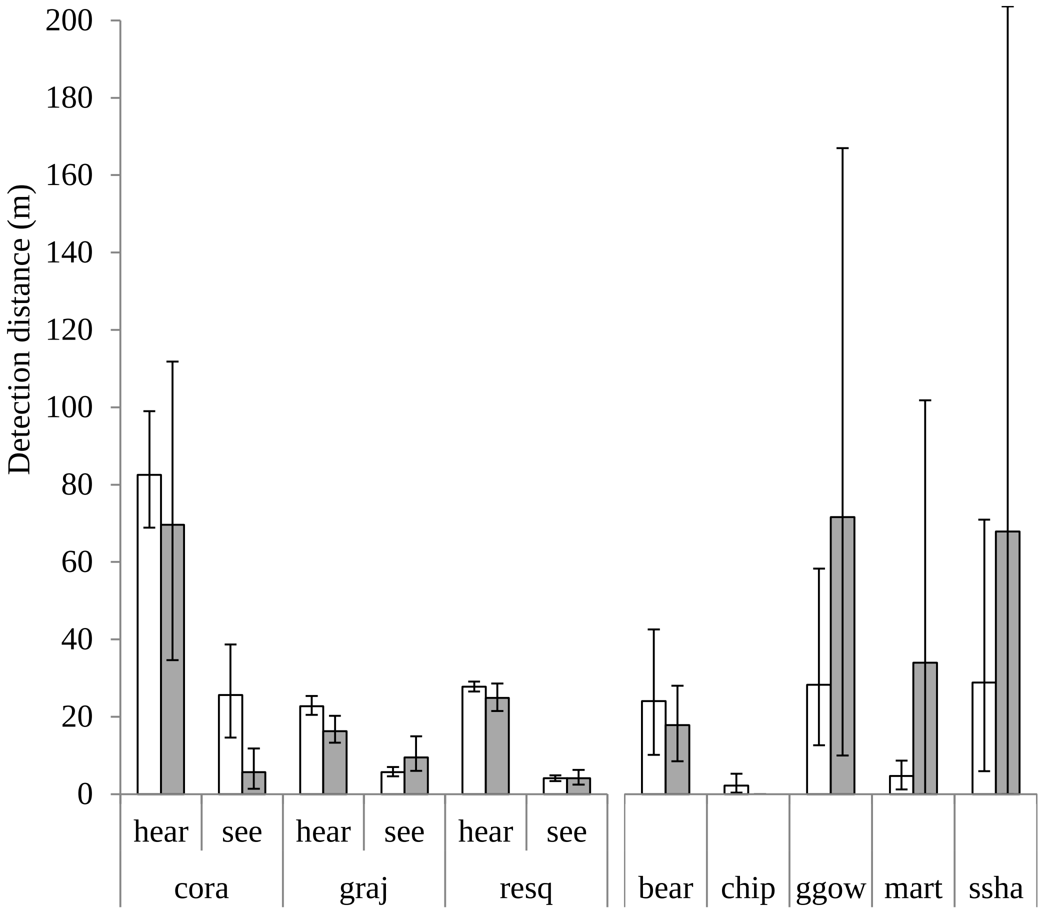

Figure 3.5. Average (± 95% CI) distance from the observer at the forest edge (white bars) and in the forest interior (grey bars) that nest predators were heard or observed, or were detected by either method during random-walk surveys. Nest predators include Common Raven (cora), Gray Jay (graj), American red squirrel (resq), American black bear (bear), least chipmunk (chip; all interior distances = 0 m), Great Gray Owl (ggow), American marten (mart) and Sharp-shinned Hawk (ssha).

Table 3.4. Top-supported models ($\sum w > 0.90$) explaining variation in the encounter probability of a) red squirrel, b) Gray Jay, c) Common Raven, d) Sharp-shinned Hawk, e) Great Gray Owl, f) least chipmunk, g) American black bear, and h) American marten during random-walk surveys. The NULL model did not contain any explanatory covariates and represents a constant encounter probability model. k is the number of model parameters. $L(\text{model}|x)$ is model likelihood given data x (exp[-1/2 $\Delta\mathrm{AIC}_{\mathrm{c}\,]}$). w_i is the Akaike weight of model i.

Model	Log likelihood	k	AIC_c	$\Delta\mathrm{AIC}_\mathrm{c}$	$L(\text{model}\|x)^{\mathrm{a}}$	w_i
a. Red squirrel						
(MAIN|OPEN)^2 × SITE	-8776.27	7	17566.55	0.00	1.00	1.00
b. Gray Jay						
(MAIN|OPEN)^2 × SITE	-4673.55	7	9361.10	0.00	1.00	1.00
c. Common Raven						
(MAIN|OPEN)^2 × SITE	-880.89	7	1775.77	0.00	1.00	1.00
d. Sharp-shinned Hawk						
(MAIN|OPEN)^2	-169.19	4	346.39	0.00	1.00	0.22
MAIN|OPEN	-170.33	3	346.66	0.27	0.87	0.19
MAIN|OPEN × SITE	-168.40	5	346.80	0.41	0.81	0.18
(MAIN|OPEN)^2 + SITE	-169.03	5	348.06	1.67	0.43	0.09
MAIN|OPEN + SITE	-170.22	4	348.44	2.06	0.36	0.08
NULL	-172.72	2	349.44	3.05	0.22	0.05
(MAIN|OPEN)^2 × SITE	-167.73	7	349.46	3.07	0.22	0.05
MAIN	-171.87	3	349.74	3.35	0.19	0.04
e. Great Gray Owl						
MAIN	-261.63	3	529.26	0.00	1.00	0.36
MAIN|OPEN	-262.13	3	530.26	1.00	0.61	0.22
(MAIN|OPEN)^2	-261.25	4	530.50	1.24	0.54	0.19
(MAIN)^2	-261.55	4	531.09	1.84	0.40	0.14
f. Least chipmunk						
NULL	-172.01	2	348.02	0.00	1.00	0.43
MAIN|OPEN	-171.96	3	349.92	1.90	0.39	0.17
MAIN	-171.99	3	349.97	1.95	0.38	0.16
(MAIN)^2	-171.26	4	350.52	2.50	0.29	0.12
(MAIN|OPEN)^2	-171.30	4	350.59	2.57	0.28	0.12
g. American black bear						
(MAIN|OPEN)^2	-110.16	4	228.33	0.00	1.00	0.84
(MAIN)^2	-111.83	4	231.66	3.33	0.19	0.16
h. American marten						
MAIN|OPEN	-121.36	3	248.73	0.00	1.00	0.65
(MAIN|OPEN)^2	-121.18	4	250.36	1.63	0.44	0.29

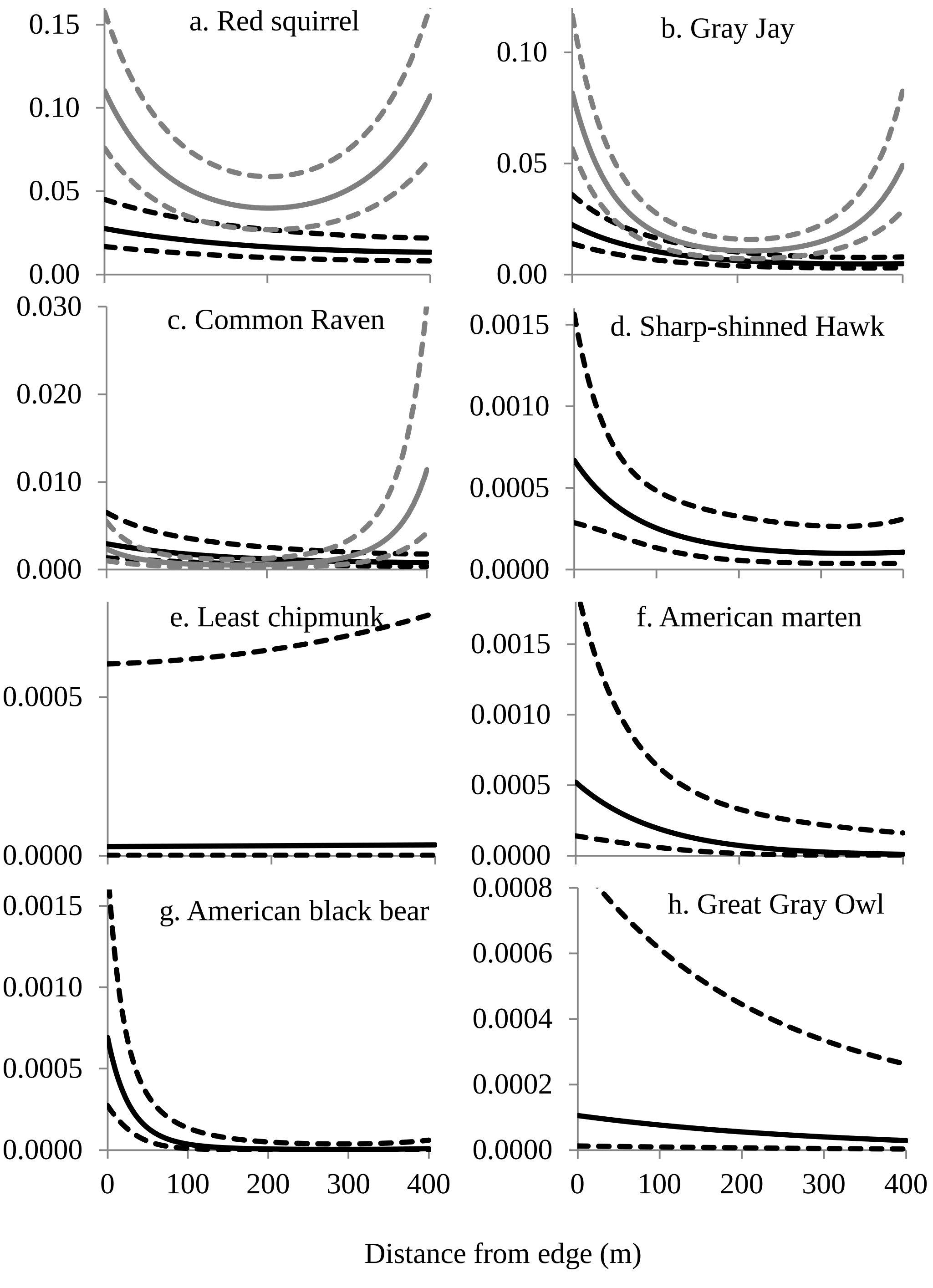

Figure 3.6. Predicted probability (± 95% CI) of recording each nest predator during one day of random-walk surveys at increasing distance from the nearest MAIN or OPEN edge (MAIN edge only for owls) in the northern and southern sites (a – c; northern = black line, southern = grey line), or in either site (d – h).

effect was strongly supported for marten, receiving 29 times the support of the NULL model. The top edge model received moderate support for squirrels (ER = 6.5) but was weakly supported for bears and hawks (ER = 2.7 and 1.3, respectively). Only bears responded positively to edges (Fig. 3.7). The remaining species were more likely to be encountered at interior stations.

3.4. Discussion

Concerns about a dramatic increase in risk of nest predation close to anthropogenic edges appears unwarranted for our study sites. The nest predator community in both our northern and southern sites was composed of endemic boreal forest species rather than invasive, human-associated species. We did not find support for a negative effect of increased edge proximity on the probability of nest predation by each nest predator species. We also failed to find strong support for a positive effect of increased edge proximity on the spatial distribution of most nest predator species. Instead, most showed neutral or weakly negative edge-associated distributions across survey methods. Red squirrels, Sharp-shinned Hawks, American marten, and red-backed voles were the dominant nest predators in our sites and we did not find evidence than any of these species were strongly attracted to edges. We only found strong support for a positive edge response by black bears and deer mice but they destroyed few video nests. Consequently, the daily survival rate of edge nests was not lower near edges as the overall predator community seems to be widely distributed relative to anthropogenic edges.

Table 3.5. Top-supported models ($\sum w \geq 0.90$) explaining variation in the encounter probability of a) red squirrel, b) Gray Jay, c) American marten, d) American black bear, and e) Sharp-shinned Hawk at baited camera trap stations (a – d) and playback survey stations (e). The NULL model did not contain any explanatory covariates and represents a constant encounter probability model. *k* is the number of model parameters. *L*(model|*x*) is model likelihood given data x (exp[-1/2 ΔAIC_{c}]). w_i is the Akaike weight of model *i*.

Models	Log likelihood	*k*	AIC_c	ΔAIC_c	*L*(model|*x*)[a]	w_i
a. Red squirrel						
SITE	-131.56	3	269.18	0.00	1.00	0.46
SITE + EDGE	-130.87	4	269.85	0.67	0.72	0.33
SITE × EDGE	-130.83	5	271.82	2.64	0.27	0.12
b. Gray Jay						
NULL	-215.16	2	434.35	0.00	1.00	0.48
EDGE	-214.89	3	435.84	1.49	0.47	0.23
SITE	-215.14	3	436.34	1.99	0.37	0.18
SITE + EDGE	-214.87	4	437.84	3.49	0.17	0.08
c. American marten						
SITE + EDGE	-124.78	4	257.66	0.00	1.00	0.54
SITE × EDGE	-124.61	5	259.37	1.71	0.42	0.23
SITE	-127.3	3	260.66	3.00	0.22	0.12
EDGE	-127.67	3	261.40	3.74	0.15	0.08
d. American black bear						
EDGE	-186.01	3	378.08	0.00	1.00	0.48
SITE + EDGE	-185.85	4	379.81	1.73	0.42	0.20
NULL	-188.02	2	380.07	1.99	0.37	0.18
SITE	-187.86	3	381.78	3.71	0.16	0.07
e. Sharp-shinned Hawks						
EDGE	-46.68	3	99.50	0.00	1.00	0.27
SITE + EDGE	-45.74	4	99.71	0.21	0.90	0.24
NULL	-47.99	2	100.05	0.55	0.76	0.21
SITE	-47.05	3	100.24	0.74	0.69	0.19

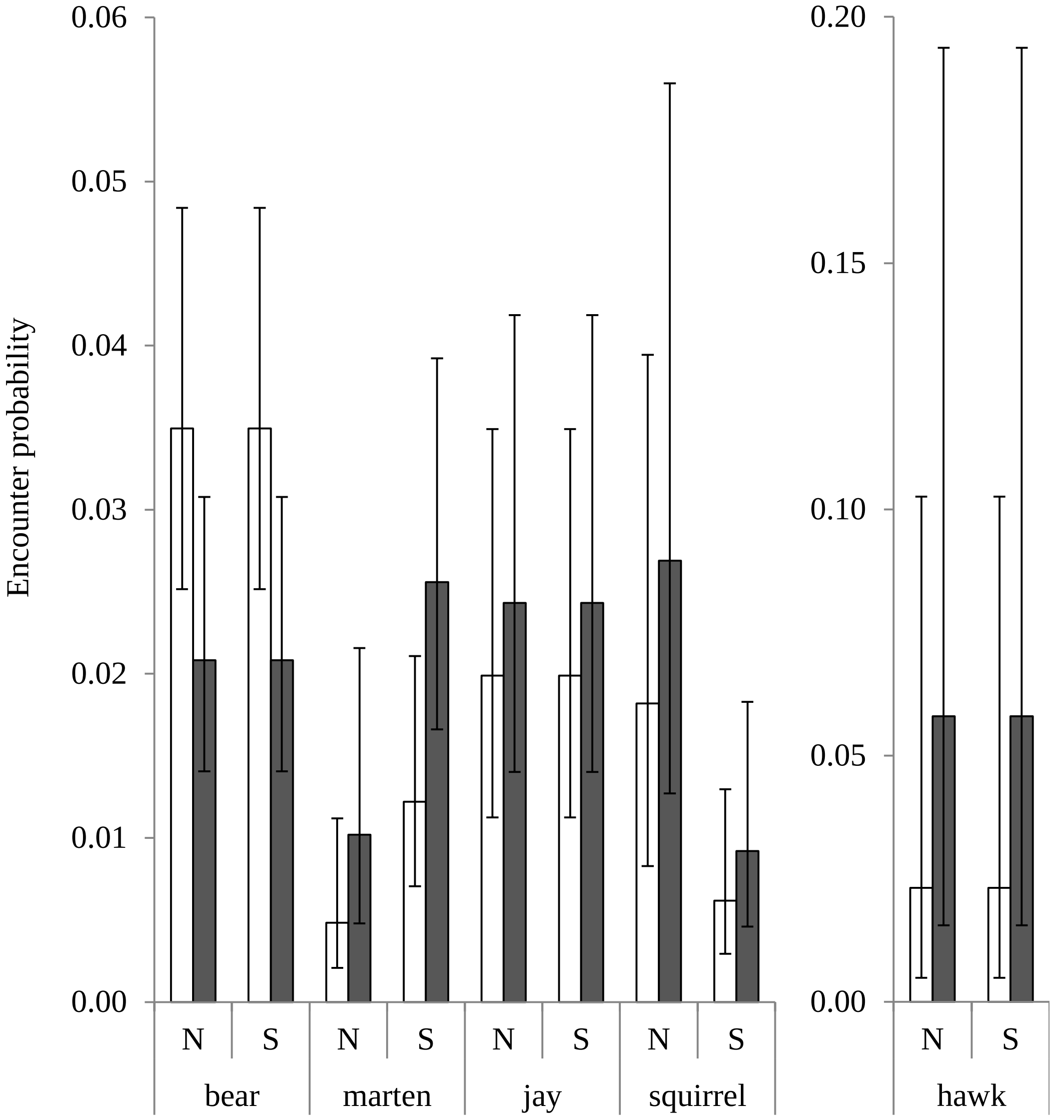

Figure 3.7. Predicted probability (± 95% CI) of encountering American black bears, American marten, American red squirrels, and Gray Jays at forest edge (white bar) and forest interior (i.e., 400 – 500 m; grey bar) camera trap stations (left panel) during one day of monitoring and the predicted probability of encountering a Sharp-shinned Hawks at each playback survey station (right panel) in Fort Simpson, NT (N) and the Chinchaga forestry region, AB (S).

We found limited agreement in the direction of edge response between survey-types for species surveyed by multiple methods. Random walk surveys generally had higher odds of encountering predators at edges compared to interiors whereas camera traps and playbacks generally had higher odds of encountering predators in the forest interior (Table 3.6). We did not find strong support for an edge-related detectability bias in our random walk survey data. Ravens tended to be observed at further distances when the observer was near the edge but they had greater odds of being encountered in the interior, which contradicts an observer bias in our result. Jays tended to be heard at further distances at the edge compared to the forest interior, which might partly explain the higher detection probability of jays near the edge during random walk surveys. However, jays were also more frequently encountered near the edge during point count surveys, which did not appear to have an edge-related detectability bias.

Although detectability does not seem to have been strongly biased by edges, open linear features may create a travel bias for observers. Predators may have had greater odds of being encountered near an edge because observers spend a disproportionate amount of time surveying near edges. We were unable to control for fine-scale variation in survey effort in our analyses and, therefore, we are unable to determine if an observer travel bias may have affected our results. However, the edge responses of predators detected during random walk surveys were more consistent with the corresponding edge-related effects on daily nest mortality compared to other survey methods, which suggests they may be unbiased (Table 3.6). Alternatively, the detection probability of one or more species at our camera traps may have been biased by negative indirect interactions between species (Lazenby and Dickman 2013). For example, bears were recorded at ~25% of camera traps with greater odds of being recorded at edge vs. interior locations (Table 3.6). Bears may have depleted the bait available to attract squirrels, marten, and/or jays to edge cameras, which could explain why these species had greater odds of being recorded at interior camera traps. A study designed to simultaneously consider multiple survey methods (e.g., Nichols et al. 2008) may prove useful in identifying whether one or more methods are better suited for surveying each species. Unfortunately, our study design was not designed with such an analytical approach in mind. Camera trap and raptor surveys were not used within the boundaries of the study plots and, therefore, they do not sample the same area as point counts and random walks. Random walks also were conducted over much longer periods than point count surveys and effort was measured over a large area such that occupancy would equal one for most of the landscape.

Our findings for squirrels, marten, and voles are in general agreement with previous studies from eastern and western forests, which report neutral or negative edge responses for these species (Mills 1995, Sekgororoane and Dilworth 1995, Bayne and Hobson 1998, Chapin et al. 1998, Harris and

Reed 2002, Markelvitz 2003, Tallmon and Mills 2004, Tigner 2012). To our knowledge, no previous study has documented the edge response of Sharp-shinned Hawks. Our results suggest that hawks tended to avoid edges. Because Sharp-shinned Hawks prefer to hunt in mature, closed-canopy forests to capture

Table 3.6. The odds of daily nest mortality by each predator species or of detecting each nest predator species at a forest interior relative to a forest edge (i.e., 400 m vs. 0 m). Point count and live-capture models report change in the encounter rate as incident rate ratios (IRR = IR400/IR0, where IR is the expected count per unit of survey effort; ± 95% CI). The remaining models report odds ratios (OR = $[Pr_{400}/(1\text{-}Pr_{400})]/[Pr_0/(1\text{-}Pr_0)]$; ± 95% CI). An IRR or OR equal to 1.0 (or a CI that includes 1.0) indicates that a nest predation or a species encounter was equally likely to occur at an interior as at an edge location. Values and lower CI greater than 1.0 indicate that encounter rate (IRR) or probability of detection or nest predation (OR) was greater at an interior location than at an edge.

Species	Daily nest mortality[a]	Point count[a]	Live-capture[b]	Random walk[c]	Camera trap/ Playback[a]
American red squirrel	0.51 (0.08 – 5.42)	1.59 (0.72 – 3.53)		0.68 (0.33 – 1.40)	1.49 (0.49 – 4.50)
American marten	0.04 (3.42×10^{-5} – 62.1)			0.02 (8.87×10^{-4} – 0.42)	2.12 (0.67 – 6.60)
Sharp-shinned Hawk	0.04 (2.04×10^{-4} – 12.3)			0.16 (0.04 – 0.62)	2.65 (0.33 – 20.6)
Red-backed vole	626 (4.87×10^{-6} – 7.43×10^{10})		2.49 (1.99 – 3.13)		
Deer mouse	1.93[d] (0.28 – 20.8)		0.53 (0.37 – 0.77)		
Least chipmunk	1.93[d] (0.28 – 20.8)			1.19 (0.01 – 91.0)	
American black bear	1.93[d] (0.28 – 20.8)			0.01 (1.34×10^{-3} – 0.11)	0.59 (0.35 – 0.99)
Common Raven	1.93[d] (0.28 – 20.8)			1.16 (0.36 – 3.63)	
Great Gray Owl	1.93[d] (0.28 – 20.8)			0.27 (0.01 – 5.52)	
Gray Jay		0.35 (0.08 – 1.55)		0.35 (0.17 – 0.73)	1.23 (0.55 – 2.76)

[a] Comparisons refer to MAIN edge.

[b] Red-backed vole comparisons refer to MAIN|OPEN edge. Deer mouse comparison refers to MAIN edge.

[c] All species comparisons refer to MAIN|OPEN edge except Great Gray Owls, which refer to MAIN edge.

[d] Lumped into a single ‘other predators’ category for nest fate analysis.

avian prey by surprise, they may be disadvantaged near open edges (Bildstein and Meyer 2000). Based on our results we would not predict to find negative edge-related fragmentation effects by oil and gas development on nesting songbirds in areas with habitat and predator community attributes similar to our sites. However, we caution against uncritically extrapolating our results to other boreal systems. For example, Pelech (1999) found a positive edge association by Red Squirrels in a conifer-dominated forest in the Yukon. Songbirds nesting near edges in this system may subsequently experience increased rates of nest predation. The identity and edge response of the predator community and the potential for negative edge effects on nesting songbirds needs to be evaluated for other boreal forest types.

Negative edge effects are more commonly reported when avian species, particularly Corvidae, are the predominant nest predator (Chalfoun et al. 2002). Gray Jays are purported to be important nest predators (Strickland and Ouellet 2011) with an affinity for edge habitat (this study; Ibarzabal and Desrocher 2004). We were surprised to not record a single Gray Jay predation on our nest cameras. Some corvids may be deterred from depredating nests with cameras (Herranz et al. 2002, Richardson et al. 2009). However, our results suggest camera wariness does not apply to Gray Jays. We recorded jays at >20% of our camera-trap stations. These cameras are much larger and were not placed much further from their target than our nest video cameras. We also recorded successive images of jays at several stations, which further suggest these jays were not camera shy.

Gray Jays have a broad diet that includes eggs, nestlings, and recently fledged young (Ouellet 1970) but their role as a nest predator is based on artificial nest studies (see references in Strickland and Ouellet 2011). Our data indicate that the importance of Gray Jays as a nest predator is overstated by these studies (Ball et al. 2009; see also Hannon et al. 2009). Jays are visual predators and real nests may be more cryptic than artificial nests. Alternatively, adult songbirds may be capable of deterring nest predation by Gray Jays (*sensu* Schmidt and Whelan 2005). Although we did not record jays depredating video nests, they may represent a substantial risk of nest predation. Jays are occasionally mobbed by songbirds, presumably when they are near a nest, suggesting they do present some risk (Strickland and Ouellet 2011; pers. obs.). Adults may experience reduced fecundity if they alter their nesting behaviours in areas where the perceived risk of predation by jays is high, such as edge habitats (Cresswell 2008). Further study is required to determine the potential for non-lethal edge effects on boreal songbirds.

Negative edge effects are also more commonly reported in highly fragmented forests in an agriculture matrix. These conditions did not exist in our study areas nor do they exist across much of the western boreal landscape. Our southern site was sufficiently close to agriculture to record the presence of coyotes (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), American Crows (*Corvus brachyrhynchos*), and Brown-headed Cowbirds (*Molothrus ater*) near our study plots. However, we did not record a predation event by any non-forest predators or brood parasitism by cowbirds. These species were rarely observed compared to forest-associated predators, which suggests our southern site was sufficiently intact and far from agriculture to prevent these species from having important impacts on nest fate.

A negative edge effect on nest fate may not occur in highly fragmented areas because most of the boreal forest is far from agriculture. Nest survival may actually increase in highly fragmented landscapes due to reduced numbers of boreal predators. Numbers of Red Squirrels, Sharp-shinned Hawks, marten, and

Red-backed Voles are predicted to show neutral or negative responses to loss of forest cover and increased edge density (Bayne and Hobson 1997, 1998, Chapin et al. 1998, Hargis et al. 1999, Tewksbury et al. 1998, Poole et al. 2004, Ibarzabal and Desrocher 2005, Hannon et al. 2009, Tigner 2012). Only Gray Jays are expected to increase abundance in fragmented habitats (Bayne and Hobson 1997, Thompson et al. 2008; but see Ibarzabal and Desrocher 2005). A negative edge effect on nest fate also may not occur with increased proximity to agriculture. For example, Hannon et al. (2009) also recorded only forest-associated predators in a moderately fragmented forest-agriculture landscape in the southern boreal fringe in Alberta. Increased nest predation and negative edge effects might only occur at very high levels of fragmentation in a predominantly agricultural matrix due to increased predation pressure by Red Squirrels and corvids (*C. brachyrhynchos* and *Pica hudsonia*), and by Deer Mice in edge habitats (Sekgororoane and Dilworth 1995, Bayne and Hobson 1997, 2000, Tewksbury et al. 1998). Brood parasitism by Brown-headed Cowbirds also may negatively impact nest fate nearer to agriculture (Hannon et al. 2009).

Land use policies aimed at conserving birds must ensure sufficient source habitats are retained on the landscape. We did not find support for a strong negative effect of edges created by industrial oil and gas development on the nesting success of boreal forest songbirds. This result is consistent with an apparent lack of a positive edge response by the dominant nest predators. Because territory selection by individuals is positively related to the success of prior nesting attempts and the presence of congeners (Haas 1998, Ahlering et al. 2010), edge habitats in the boreal forest are unlikely to be avoided during settlement. Therefore, the apparent lack of a positive edge response by the dominant nest predators provides a potential mechanism for the resilience of boreal bird communities to edge related fragmentation observed in other studies. Our results also support the hypothesis that negative edge effects on nesting songbirds are an ‘eastern paradigm’ (George and Dobkin 2002). However, further study is needed to identify the thresholds of forest cover and agriculture proximity necessary to prevent negative edge effects from developing in the western boreal forest.

3.5. Literature Cited

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Appendix 3.1. Candidate set of models used to explain variation in the daily probability of video nests being depredated by an American red squirrel, Sharp-shinned Hawk, American marten, red-backed vole, or ‘other predator’ compared to nests that were not depredated (n = 145). Predator identity or ‘other fate’ (active, fledge, failed for reasons other than predation) were the dependent variables assessed during each 24-h interval that each nest was monitored by video camera. The independent variables included nest substrate (SUBSTRATE; n = 2; ground or above-ground), percent concealment by vegetation (COVER), and distance (m) to the nearest MAIN or MAIN|OPEN edge. *k* is the number of model parameters. w_i is the Akaike weight of model *i*.

Model	Log likelihood	*k*	AIC_c	ΔAIC_c	*L*(model|*x*)[a]	w_i
SUBSTRATE	-383.13	10	786.41	0.00	1.00	0.52
NULL	-389.93	5	789.90	3.49	0.17	0.09
SUBSTRATE + $(\text{MAIN})^2$	-374.78	20	790.15	3.74	0.15	0.08
SUBSTRATE + MAIN	-379.95	15	790.24	3.84	0.15	0.08
SUBSTRATE + MAIN|OPEN	-379.98	15	790.29	3.88	0.14	0.07
COVER	-386.02	10	792.20	5.79	0.06	0.03
SUBSTRATE + $(\text{MAIN|OPEN})^2$	-375.88	20	792.35	5.95	0.05	0.03
MAIN|OPEN	-386.60	10	793.36	6.95	0.03	0.02
COVER + $(\text{MAIN})^2$	-376.53	20	793.64	7.23	0.03	0.01
SUBSTRATE + COVER	-381.74	15	793.81	7.40	0.02	0.01
MAIN	-386.85	10	793.86	7.45	0.02	0.01
$(\text{MAIN})^2$	-381.83	15	793.99	7.59	0.02	0.01
COVER + MAIN|OPEN	-382.41	15	795.15	8.75	0.01	0.01
COVER + MAIN	-382.43	15	795.20	8.80	0.01	0.01
COVER + $(\text{MAIN|OPEN})^2$	-377.54	20	795.67	9.27	0.01	0.01
$(\text{MAIN|OPEN})^2$	-382.68	15	795.69	9.28	0.01	0.01
SUBSTRATE + COVER + $(\text{MAIN})^2$	-372.80	25	796.52	10.11	0.01	0.00
SUBSTRATE + COVER + MAIN	-378.43	20	797.44	11.04	0.00	0.00
SUBSTRATE + COVER + MAIN|OPEN	-378.50	20	797.59	11.19	0.00	0.00
SUBSTRATE × MAIN|OPEN	-378.65	20	797.88	11.48	0.00	0.00
SUBSTRATE × MAIN	-378.91	20	798.42	12.01	0.00	0.00
SUBSTRATE + COVER + $(\text{MAIN|OPEN})^2$	-373.82	25	798.55	12.14	0.00	0.00
COVER × MAIN	-380.98	20	802.56	16.15	0.00	0.00
COVER × MAIN|OPEN	-381.56	20	803.71	17.30	0.00	0.00

[a] Model likelihood given data *x* = exp(-1/2 ΔAIC_c)

Appendix 3.2. Model sets explaining the edge-related distribution of a) American red squirrels and b) Gray Jays recorded during point count surveys. The dependent variable in each model set was the number of each predator counted during each survey. The independent variables included study site (SITE; n = 2), distance (m) to the nearest MAIN edge, distance to the nearest MAIN|OPEN edge, two-category edge proximity M100 and MO100 based on whether the point count location was within 100 m of a MAIN or a MAIN|OPEN edge, respectively, and three-category edge proximity 3MAIN based on whether the point count was located 0 m, 200 m, or 400 m from a MAIN edge as per the study design. All models, including the NULL, controlled for variation in detectability by including survey-specific parameters for date, time, temperature, wind speed, and wetness. k is the number of model parameters. w_i is the Akaike weight of model i.

Model	Log likelihood	k	AIC$_c$	ΔAIC$_c$	L(model|x)^a	w_i
a. Red squirrel						
3MAIN + SITE	-417.64	11	857.85	0.00	1.00	0.31
MAIN + SITE	-419.06	10	858.59	0.74	0.69	0.22
(MAIN)^2 + SITE	-418.81	11	860.20	2.35	0.31	0.10
MAIN × SITE	-418.95	11	860.48	2.63	0.27	0.08
3MAIN × SITE	-417.56	13	861.92	4.07	0.13	0.04
SITE	-421.86	9	862.11	4.26	0.12	0.04
MAIN|OPEN + SITE	-420.85	10	862.18	4.33	0.11	0.04
M100 + SITE	-420.94	10	862.35	4.50	0.11	0.03
3MAIN	-421.34	10	863.17	5.31	0.07	0.02
MO100 + SITE	-421.50	10	863.48	5.63	0.06	0.02
MAIN|OPEN × SITE	-420.49	11	863.56	5.70	0.06	0.02
MAIN	-422.61	9	863.60	5.75	0.06	0.02
(MAIN)^2 × SITE	-418.48	13	863.76	5.91	0.05	0.02
M100 × SITE	-420.80	11	864.18	6.33	0.04	0.01
(MAIN|OPEN)^2 + SITE	-420.82	11	864.22	6.36	0.04	0.01
MO100 × SITE	-421.18	11	864.93	7.07	0.03	0.01
(MAIN)^2	-422.37	10	865.23	7.37	0.03	0.01
NULL	-425.56	8	867.43	9.58	0.01	0.00
M100	-424.54	9	867.47	9.62	0.01	0.00
(MAIN|OPEN)^2 × SITE	-420.35	13	867.50	9.65	0.01	0.00
MAIN|OPEN	-424.67	9	867.73	9.87	0.01	0.00
MO100	-425.18	9	868.74	10.89	0.00	0.00
(MAIN|OPEN)^2	-424.67	10	869.81	11.96	0.00	0.00
b. Gray Jay						
MAIN + SITE	-208.83	10	438.14	0.00	1.00	0.16
M100 + SITE	-208.92	10	438.32	0.18	0.91	0.15
MAIN|OPEN + SITE	-209.11	10	438.71	0.57	0.75	0.12
MAIN × SITE	-208.74	11	440.06	1.92	0.38	0.06
M100 × SITE	-208.74	11	440.07	1.93	0.38	0.06
(MAIN)^2 + SITE	-208.82	11	440.22	2.08	0.35	0.06
MAIN|OPEN	-210.94	9	440.26	2.12	0.35	0.06
(MAIN|OPEN)^2 + SITE	-209.10	11	440.78	2.64	0.27	0.04
MAIN|OPEN × SITE	-209.11	11	440.79	2.65	0.27	0.04
3MAIN + SITE	-209.19	11	440.96	2.82	0.24	0.04
MO100 + SITE	-210.33	10	441.13	2.99	0.22	0.04
MAIN	-211.45	9	441.28	3.14	0.21	0.03
M100	-211.51	9	441.41	3.27	0.20	0.03
(MAIN|OPEN)^2	-210.87	10	442.21	4.08	0.13	0.02
MO100 × SITE	-209.82	11	442.22	4.08	0.13	0.02

Model	Log likelihood	k	AIC_c	ΔAIC_c	$L(\text{model}\|x)$[a]	w_i
SITE	-212.43	9	443.26	5.12	0.08	0.01
MO100	-212.44	9	443.27	5.13	0.08	0.01
$(\text{MAIN})^2$	-211.44	10	443.36	5.22	0.07	0.01
$(\text{MAIN})^2$ × SITE	-208.52	13	443.84	5.70	0.06	0.01
3MAIN	-211.70	10	443.88	5.74	0.06	0.01
$(\text{MAIN}\|\text{OPEN})^2$ × SITE	-208.62	13	444.04	5.90	0.05	0.01
3MAIN × SITE	-208.86	13	444.52	6.38	0.04	0.01
NULL	-214.96	8	446.23	8.09	0.02	0.00

[a] Model likelihood given data $x = \exp(-1/2\ \Delta AIC_c)$

Appendix 3.3. Model sets explaining the edge-related distribution of a) red-backed voles and b) deer mice. The dependent variable in each model set was the total number of each predator captured at each trap location during all years of study (i.e., 2 years in the northern site and 1 year in the southern site). All models included the parameter ln(trap nights) as an exposure variable to control for the effect of total number of trap nights on the dependent variable The independent variables included additive and interactive combinations of study site (SITE; n = 2) and distance (m) to the nearest MAIN or nearest MAIN|OPEN edge, which were modelled as linear and quadratic functions. All models also included study plot as a random intercept. *k* is the number of model parameters. w_i is the Akaike weight of model *i*.

Model	Log likelihood	*k*	AIC$_c$	ΔAIC$_c$	*L*(model|*x*)[a]	w_i
a. Red-backed vole						
(MAIN|OPEN)^2 + SITE	-3291.74	6	6595.52	0.00	1.00	0.84
(MAIN|OPEN)^2 × SITE	-3291.37	8	6598.81	3.29	0.19	0.16
(MAIN)^2 × SITE	-3302.12	8	6620.31	24.79	0.00	0.00
(MAIN)^2 + SITE	-3306.21	6	6624.46	28.94	0.00	0.00
(MAIN|OPEN)^2	-3308.78	5	6627.59	32.07	0.00	0.00
(MAIN)^2	-3318.19	5	6646.41	50.89	0.00	0.00
MAIN|OPEN × SITE	-3329.54	6	6671.12	75.60	0.00	0.00
MAIN|OPEN + SITE	-3331.60	5	6673.23	77.71	0.00	0.00
MAIN × SITE	-3342.86	6	6697.75	102.23	0.00	0.00
MAIN + SITE	-3344.61	5	6699.25	103.73	0.00	0.00
MAIN|OPEN	-3352.50	4	6713.02	117.49	0.00	0.00
MAIN	-3355.70	4	6719.42	123.89	0.00	0.00
SITE	-3400.29	4	6808.61	213.08	0.00	0.00
NULL	-3417.29	3	6840.58	245.06	0.00	0.00
b. Deer mouse						
(MAIN)^2 × SITE	-1704.80	8	3425.68	0.00	1.00	0.61
MAIN × SITE	-1707.27	6	3426.59	0.91	0.63	0.39
(MAIN|OPEN)^2 × SITE	-1713.02	8	3442.12	16.44	0.00	0.00
MAIN|OPEN × SITE	-1715.63	6	3443.31	17.63	0.00	0.00
MAIN + SITE	-1717.31	5	3444.66	18.98	0.00	0.00
(MAIN)^2 + SITE	-1716.98	6	3446.00	20.32	0.00	0.00
(MAIN|OPEN)^2 + SITE	-1717.31	6	3446.66	20.98	0.00	0.00
MAIN|OPEN + SITE	-1721.01	5	3452.05	26.37	0.00	0.00
SITE	-1722.61	4	3453.25	27.57	0.00	0.00
(MAIN|OPEN)^2	-1745.32	5	3500.68	75.00	0.00	0.00
MAIN	-1747.40	4	3502.83	77.15	0.00	0.00
MAIN|OPEN	-1747.72	4	3503.46	77.78	0.00	0.00
(MAIN)^2	-1746.94	5	3503.91	78.23	0.00	0.00
NULL	-1750.17	3	3506.36	80.68	0.00	0.00

[a] Model likelihood given data *x* = exp(-1/2 ΔAIC$_c$)

Appendix 3.4. Model sets explaining variation in the detection probability of a) red squirrel, b) Gray Jay, c) Common Raven, d) Sharp-shinned Hawk, e) Great Gray Owl, f) least chipmunk, g) American black bear, and h) American marten during random-walk surveys. The dependent variable in each model set was site occupancy (used vs. available) by a predator. Available sites are represented by a systematic 5 m × 5 m grid of points on each study plot. The independent variables include study site (SITE; n = 2) and distance (m) to the nearest edge (MAIN, MAIN|OPEN) as linear or quadratic terms. Models e – h include edge effects only. All models included ln(survey effort) as an exposure variable to control for the effect of effort on the dependent variable. All models also included a random intercept for study plot to account for the repeat visits to each plot. *k* is the number of model parameters. w_i is the Akaike weight of model *i*.

Model	Log likelihood	*k*	AIC_c	ΔAIC_c	*L*(model|*x*)[a]	w_i
a. Red squirrel						
$(MAIN\|OPEN)^2$ × SITE	-8776.27	7	17566.55	0.00	1.00	1.00
$(MAIN\|OPEN)^2$ + SITE	-8810.35	5	17630.69	64.15	0.00	0.00
$(MAIN\|OPEN)^2$	-8815.15	4	17638.30	71.75	0.00	0.00
MAIN|OPEN × SITE	-8834.76	5	17679.53	112.98	0.00	0.00
$(MAIN)^2$ × SITE	-8832.87	7	17679.75	113.20	0.00	0.00
MAIN|OPEN + SITE	-8835.93	4	17679.86	113.31	0.00	0.00
$(MAIN)^2$ + SITE	-8838.18	5	17686.36	119.82	0.00	0.00
MAIN|OPEN	-8840.37	3	17686.73	120.18	0.00	0.00
$(MAIN)^2$	-8843.47	4	17694.95	128.40	0.00	0.00
MAIN × SITE	-8852.58	5	17715.17	148.62	0.00	0.00
MAIN + SITE	-8855.97	4	17719.94	153.39	0.00	0.00
MAIN	-8860.91	3	17727.83	161.28	0.00	0.00
SITE	-8876.39	3	17758.77	192.23	0.00	0.00
NULL	-8881.50	2	17767.01	200.46	0.00	0.00
b. Gray Jay						
$(MAIN\|OPEN)^2$ × SITE	-4673.55	7	9361.10	0.00	1.00	1.00
$(MAIN)^2$ × SITE	-4694.30	7	9402.61	41.51	0.00	0.00
$(MAIN)^2$ + SITE	-4696.96	5	9403.92	42.83	0.00	0.00
$(MAIN\|OPEN)^2$ + SITE	-4699.85	5	9409.70	48.60	0.00	0.00
$(MAIN)^2$	-4701.94	4	9411.88	50.79	0.00	0.00
$(MAIN\|OPEN)^2$	-4703.80	4	9415.60	54.50	0.00	0.00
MAIN|OPEN × SITE	-4749.25	5	9508.50	147.41	0.00	0.00
MAIN|OPEN + SITE	-4759.94	4	9527.87	166.77	0.00	0.00
MAIN|OPEN	-4763.24	3	9532.47	171.38	0.00	0.00
MAIN + SITE	-4772.53	4	9553.06	191.96	0.00	0.00
MAIN × SITE	-4772.48	5	9554.96	193.86	0.00	0.00
MAIN	-4776.77	3	9559.54	198.45	0.00	0.00
SITE	-4847.92	3	9701.84	340.74	0.00	0.00
NULL	-4852.48	2	9708.95	347.85	0.00	0.00
c. Common Raven						
$(MAIN\|OPEN)^2$ × SITE	-880.89	7	1775.77	0.00	1.00	1.00
MAIN|OPEN × SITE	-896.01	5	1802.01	26.24	0.00	0.00
$(MAIN)^2$ × SITE	-896.44	7	1806.89	31.12	0.00	0.00
MAIN × SITE	-899.43	5	1808.87	33.09	0.00	0.00
$(MAIN)^2$	-900.74	4	1809.49	33.72	0.00	0.00
$(MAIN)^2$ + SITE	-900.67	5	1811.33	35.56	0.00	0.00
MAIN	-902.77	3	1811.54	35.76	0.00	0.00
MAIN + SITE	-902.65	4	1813.31	37.53	0.00	0.00
$(MAIN\|OPEN)^2$	-903.27	4	1814.55	38.77	0.00	0.00

Model	Log likelihood	k	AIC$_c$	ΔAIC$_c$	L(model|x)[a]	w_i
MAIN|OPEN	-904.86	3	1815.73	39.96	0.00	0.00
NULL	-906.03	2	1816.07	40.29	0.00	0.00
(MAIN|OPEN)^2 + SITE	-903.12	5	1816.25	40.47	0.00	0.00
MAIN|OPEN + SITE	-904.68	4	1817.36	41.59	0.00	0.00
SITE	-905.93	3	1817.87	42.09	0.00	0.00
d. Sharp-shinned Hawk						
(MAIN|OPEN)^2	-169.19	4	346.39	0.00	1.00	0.22
MAIN|OPEN	-170.33	3	346.66	0.27	0.87	0.19
MAIN|OPEN × SITE	-168.40	5	346.80	0.41	0.81	0.18
(MAIN|OPEN)^2 + SITE	-169.03	5	348.06	1.67	0.43	0.09
MAIN|OPEN + SITE	-170.22	4	348.44	2.06	0.36	0.08
NULL	-172.72	2	349.44	3.05	0.22	0.05
(MAIN|OPEN)^2 × SITE	-167.73	7	349.46	3.07	0.22	0.05
MAIN	-171.87	3	349.74	3.35	0.19	0.04
(MAIN)^2	-171.06	4	350.12	3.73	0.15	0.03
SITE	-172.31	3	350.62	4.23	0.12	0.03
MAIN + SITE	-171.48	4	350.96	4.57	0.10	0.02
(MAIN)^2 + SITE	-170.56	5	351.11	4.72	0.09	0.02
MAIN × SITE	-171.47	5	352.94	6.55	0.04	0.01
(MAIN)^2 × SITE	-170.26	7	354.52	8.13	0.02	0.00
e. Great Gray Owl						
MAIN	-261.63	3	529.26	0.00	1.00	0.36
MAIN|OPEN	-262.13	3	530.26	1.00	0.61	0.22
(MAIN|OPEN)^2	-261.25	4	530.50	1.24	0.54	0.19
(MAIN)^2	-261.55	4	531.09	1.84	0.40	0.14
NULL	-264.13	2	532.26	3.00	0.22	0.08
f. Least chipmunk						
NULL	-172.01	2	348.02	0.00	1.00	0.43
MAIN|OPEN	-171.96	3	349.92	1.90	0.39	0.17
MAIN	-171.99	3	349.97	1.95	0.38	0.16
(MAIN)^2	-171.26	4	350.52	2.50	0.29	0.12
(MAIN|OPEN)^2	-171.30	4	350.59	2.57	0.28	0.12
g. American black bear						
(MAIN|OPEN)^2	-110.16	4	228.33	0.00	1.00	0.84
(MAIN)^2	-111.83	4	231.66	3.33	0.19	0.16
MAIN	-117.87	3	241.73	13.40	0.00	0.00
MAIN|OPEN	-118.65	3	243.30	14.98	0.00	0.00
NULL	-123.18	2	250.37	22.04	0.00	0.00
h. American marten						
MAIN|OPEN	-121.36	3	248.73	0.00	1.00	0.65
(MAIN|OPEN)^2	-121.18	4	250.36	1.63	0.44	0.29
(MAIN)^2	-123.35	4	254.70	5.97	0.05	0.03
NULL	-125.93	2	255.86	7.13	0.03	0.02
MAIN	-125.62	3	257.24	8.51	0.01	0.01

[a] Model likelihood given data x = exp(-1/2 ΔAIC$_c$)

Appendix 3.5. Model sets explaining variation in encounter probability (i.e., present or absent, dependent variable) by a) red squirrel, b) Gray Jay, c) American marten, d) American black bear, and e) Sharp-shinned Hawk at baited camera trap stations (a – d) and playback survey stations (e). Study site (SITE: northern or southern) and edge proximity (EDGE: edge or interior) were categorical independent variables. All models include study plot as a random intercept. All models, including the NULL model, also include the parameter ln(survey effort) as an exposure variable to control for the effect of total number of survey days (a – d) or survey visits (e) on the dependent variable. *k* is the number of model parameters. w_i is the Akaike weight of model *i*.

Models	Log likelihood	k	AIC$_c$	ΔAIC$_c$	L(model|x)[a]	w_i
a. Red squirrel						
SITE	-131.56	3	269.18	0.00	1.00	0.46
SITE + EDGE	-130.87	4	269.85	0.67	0.72	0.33
SITE × EDGE	-130.83	5	271.82	2.64	0.27	0.12
NULL	-134.78	2	273.58	4.41	0.11	0.05
EDGE	-134.11	3	274.28	5.10	0.08	0.04
b. Gray Jay						
NULL	-215.16	2	434.35	0.00	1.00	0.48
EDGE	-214.89	3	435.84	1.49	0.47	0.23
SITE	-215.14	3	436.34	1.99	0.37	0.18
SITE + EDGE	-214.87	4	437.84	3.49	0.17	0.08
SITE × EDGE	-214.76	5	439.68	5.33	0.07	0.03
c. American marten						
SITE + EDGE	-124.78	4	257.66	0.00	1.00	0.54
SITE × EDGE	-124.61	5	259.37	1.71	0.42	0.23
SITE	-127.3	3	260.66	3.00	0.22	0.12
EDGE	-127.67	3	261.40	3.74	0.15	0.08
NULL	-130.18	2	264.40	6.74	0.03	0.02
d. American black bear						
EDGE	-186.01	3	378.08	0.00	1.00	0.48
SITE + EDGE	-185.85	4	379.81	1.73	0.42	0.20
NULL	-188.02	2	380.07	1.99	0.37	0.18
SITE	-187.86	3	381.78	3.71	0.16	0.07
SITE × EDGE	-185.85	5	381.86	3.78	0.15	0.07
e. Sharp-shinned Hawks						
EDGE	-46.68	3	99.50	0.00	1.00	0.27
SITE + EDGE	-45.74	4	99.71	0.21	0.90	0.24
NULL	-47.99	2	100.05	0.55	0.76	0.21
SITE	-47.05	3	100.24	0.74	0.69	0.19
SITE × EDGE	-45.62	5	101.58	2.08	0.35	0.10

[a] Model likelihood given data $x = \exp(-1/2\ \Delta\text{AIC}_c)$

Chapter 4. Abundance is not a mis-leading indicator of habitat quality in landscapes dissected by linear features in the western boreal forest.[3]

4.1. Introduction

Maintaining biodiversity is the goal of conservation biology (Balmford et al. 2005, Rudd et al. 2010). To achieve this goal practitioners require an efficient yet effective means of assessing habitat quality and quantifying changes in quality within habitats in response to natural and anthropogenic stressors. Habitat assessments for songbirds typically use point count surveys, which are an efficient and reliable method of evaluating bird abundance (Toms et al. 2006). The assumption underlying this approach is that abundance and habitat quality are positively correlated, which is seldom tested. Several researchers have questioned this assumption, particularly when anthropogenic habitat alteration creates an ecological trap (Gates and Gysel 1978, van Horne 1983, Morrison 1986, Temple and Wiens 1989, Vickery et al. 1992). In the presence of a trap, individuals selectively settle in lower quality habitats. These low quality habitats are subsequently misidentified by the researcher as being high quality based on the above assumption (Donovan and Thompson 2001, Hannah et al. 2008). For this reason, reproductive success can be a more reliable indicator of local habitat quality than abundance (Morrison 1986, Temple and Wiens 1989). While

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[3] A version of this chapter will be submitted for publication with the following authorship: Jeffrey R. Ball, Erin M. Bayne, and Craig S. Machtans.

reproductive success may be more costly to measure, failure to quantify the link between abundance and a metric of fitness like reproductive success can lead to ineffective or counter-productive conservation strategies (Johnson 2007, Griesser and Lagerberg 2012).

Negative correlations between abundance and reproductive success are most commonly reported in western North American and in areas with high levels of anthropogenic disturbance (Bock and Jones 2004). In western Canada, industrial development is rapidly fragmenting the boreal landscape, which is an important resource to North American avifauna (Blancher and Wells 2005). Concern has been raised about the impact continued development may have on North America's songbird populations (Wells and Blancher 2011). Of particular concern in the west is the proliferation of linear features (seismic lines, buried pipeline right-of-ways, and associated transportation networks) associated with oil and gas development (Schneider 2002). These linear features result in relatively little forest loss yet create vast amounts of edge habitat that may alter biotic and abiotic conditions in the adjacent forest that are important elements defining habitat quality (Murcia 1995, Harper et al. 2005). There is growing pressure to conserve the boreal forest by applying conservation-based land use planning, by creating sustainable development practices, and by expanding and establishing new protected areas (Canadian Boreal Initiative 2003, IUCN 2005). These initiatives need efficient and effective monitoring tools.

We evaluated whether songbird abundance was a reliable surrogate for assessing local differences in habitat quality in a boreal forest landscape in western Canada fragmented by linear features. We compared support among a common set of hypotheses for explaining variation in abundance, daily nest survival rate (hereafter, nest fate), and number of young fledged from successful nests (hereafter, productivity). We considered proximity to the nearest forest edge (edge hypothesis), risk of nest predation (predation hypothesis), nest concealment (cover hypothesis), and number of alternate nest sites (alternate nest site hypothesis) to be important components of habitat quality for boreal forest songbirds. Edge habitats may offer improvements in reproductive potential if edge-nesting songbirds gain access to additional resources (Ries et al. 2004). However, nest predators also may respond positively to edge habitats such that edge-nesting songbirds experience an increased risk of nest predation (Chalfoun et al. 2002, Batary and Baldi 2004). Nest predation is a major source of reproductive failure for many avian species (Ricklefs 1969, Martin 1992, Newton 1998) and several studies have shown that birds attempt to reduce their risk of nest predation by selecting habitats and placing their nests in areas with fewer predators (Fontaine and Martin 2006a, Schmidt et al. 2006, Thomson et al. 2006, Emmering and Schmidt 2011, Hua et al. 2013), selecting nest sites with greater amounts of cover (Martin 1992, Eggers et al. 2006, Matsui and Takagi 2012), or nesting in areas with large numbers of alternate nest sites (Martin and Roper 1988, Chalfoun and Martin 2009). While we defined habitat quality as the reproductive success of individuals, management priorities are based on population–level productivity, which is the combination of reproductive success and abundance (Pidgeon et al. 2006). Congruence between these two metrics would identify habitats or habitat components that should be the focus of conservation and land-use planning in the western boreal.

4.2. Methods

4.2.1. Study areas and edge classification

This study was conducted in two boreal regions in western Canada, near Fort Simpson, Northwest Territories (61°52′N, 121°20′W; hereafter northern site), and in the Chinchaga forestry region northwest of Manning, Alberta (57°18′N, 118°23′W; hereafter southern site). Both sites were located in mature stands of mixedwood forest that had similar composition and structure. The canopies were dominated by deciduous trees (primarily trembling aspen [*Populus tremuloides*] with lesser amounts of balsam poplar [*P. balsamifera*]). Scattered trees or small stands of conifers (primarily white spruce [*Picea glauca*] but black spruce [*P. mariana*], balsam fir [*Abies balsamea*], and jack pine [*Pinus banksiana*]) also were present. The understories in both regions typically consisted of low-to-moderate densities of shrubs < 0.5 m tall (e.g., *Rosa acicularis, Rubus idaeus*, and *Viburnum edule*) with scattered patches of dense alder (*Alnus* spp.), willow (*Salix* spp.) and conifer (primarily white spruce) up to 3 m in height. A sub-canopy was normally absent.

Both regions had edge habitat associated with energy sector linear features. Pipeline right-of-ways were ~25 m wide and were periodically cleared of woody vegetation. Seismic lines were ~8 m wide and ranged from herbaceous ground cover only to entirely overgrown with shrubs or saplings. Service roads were 12 to 25 m wide and the centre portion was typically surfaced in gravel. Average (± 1SE) linear feature density was higher in the south (2.43 ± 0.13 km/km^2) compared to the north (1.05 ± 0.03 km/km^2). Forestry and agriculture did occur in the south but not in the vicinity of our study and we did not evaluate edges created by forestry, agriculture, or surfaced roads with high traffic volume. Red squirrels (*Tamiasciurus hudsonicus*) were the dominant nest predator in both sites destroying ~50 to 70% of nests monitored with video cameras in each site (Chapter 2). Squirrels were ~3 times more abundant in the south compared to the north.

We established six 42-ha plots in the north in 2005 and 2006 and nine 24-ha plots in the south in 2006 and 2007. Plots in each site were a minimum 1.2 km apart. Plot sizes and spatial configuration were chosen to minimize the likelihood that smaller predators would affect all songbirds on a single plot or that large predators would affect multiple plots (Donovan et al. 1997, Stephens et al. 2003; a typical red squirrel territory is < 1 ha; Rusch and Reeder 1978). We categorized all lines in the vicinity of each study plot as MAIN, OPEN or CLOSED (see Glossary for definitions) based on width and amount of woody vegetation regrowth, which may influence the magnitude of edge effects (Rich et al. 1994, Harper et al. 2005). Each northern plot was adjacent to a single MAIN line. Each southern plot bordered one or two MAIN lines or a MAIN and an OPEN line and was bisected by one or more OPEN lines. We assumed CLOSED lines were ecologically similar to the adjacent forest and they were not considered as creating an edge effect (Tigner 2012, Lankau et al. 2013).

4.2.2. Nest fate and nest productivity

We visited each plot every 3 days between late May and mid-July to search for and monitor nests. Nest stage (building, laying, incubating, nestling) and contents were recorded during the initial visit. When a nest was too high to observe its contents, nest stage was determined from adult behavior (Martin et al. 1997). Subsequent nest checks were performed from a distance using binoculars when possible to minimize disturbance. If adults were absent or inadvertently flushed the nest was approached and the contents recorded. Adults were not intentionally flushed from the nest unless a stage change was expected (clutch initiation, clutch completion, hatch, or just prior to fledge) and were never flushed during inclement weather. Video cameras were placed at a subset of nests to identify nest predators as part of a concurrent study. Observer disturbance at video-monitored nests was limited to battery changes every 6 days, ~10 m from the nest, unless adults were absent, in which case nests were visited to check and count contents.

We consider active nests to have contained ≥ 1 egg and successful nests to have fledged ≥ 1 chick. A nest was deemed successful when a) behavioral cues of the parent birds suggested one or more fledglings were in the immediate area; b) the physical state of the nest was not visibly disturbed; and c) the median date between the last nest check and the present was within two days of the predicted fledging date (Martin et al. 1997, Ball and Bayne 2012). We assumed all failed nests were depredated if nest contents were missing or damaged. Nests were considered abandoned if adults were absent and cold, undamaged eggs or nestlings remained. Nest productivity (the number of young fledged from each nesting attempt) was recorded as the maximum number of young present on the last active visit. For nests that were assumed to have partially fledged on the last active visit (based on adult behavior) the maximum number of young fledged was the number present on the second-to-last visit. Observers did not have time to locate adults that were not in the immediate vicinity of the nest to determine if and how many fledglings were present. Successful pairs in our study are believed not to renest.

4.2.3. Songbird abundance

We used 10-minute fixed-radius point counts of 100 m to quantify bird abundance. Each plot contained nine survey stations. Three stations were established on each of three transects spaced every 200 m perpendicular to the MAIN edge of each plot. Stations were 0, 200, and 400 m from the forest edge on each transect. We chose a distance of 200 m between stations to reduce the probability of double-counting the same individual. Surveys were conducted during June between sunrise and 10:00. During each survey observers recorded the initial time period (0 – 3 min, 3 – 5 min, and 5 – 10 min) and distance category (0 – 50 m and 50 – 100 m) for all songbirds and red squirrels heard or observed. White-winged Crossbills (Loxia leucoptera) were frequently encountered in flocks that were difficult to quantify or distinguish from territorial pairs. Therefore, we recorded their presence rather than their abundance. Each station was visited twice annually by the same observer. One observer performed all surveys in the southern site whereas surveys in the northern site were performed by a different observer in each year.

4.2.4. Nest concealment and alternate nest sites

Available cover (i.e., concealment by vegetation) for ground and shrub nests was estimated as the percentage of a 0.5 m wide cover board obscured by vegetation when viewed from 2 m (MacFarlane 2003). We considered two vertical levels of cover. Ground cover included all vegetation up to 0.5 m in height and shrub cover included all vegetation up to 3 m in height. We also considered two spatial scales of cover for ground and shrub nests. Nest-scale cover estimates were centered on the nest or point count station. Patch-scale cover included the central point and four points 5 m from the center in four cardinal directions. Four cover estimates were made from opposing directions at each point. These estimates (4 per nest-scale, 20 per patch-scale) were averaged to obtain two nest-scale (GNDCOVN, SHBCOVN; see Glossary) and two patch-scale (GNDCOVP, SHBCOVP) cover estimates for each ground and shrub nest. We quantified the number of alternate nest sites (ALTNEST) available to each shrub nest that had an obvious association with a willow, conifer, or alder shrub. We counted the number of stems of the same shrub species in five 1-m quadrats centered on the points used to estimate patch-scale cover. We considered two measures of cover available for canopy nests measured in an 11.3 m radius around the nest tree or point count station. Canopy closure (CANOPY) was estimated in quartiles as the percentage of sky obscured by tree branches and foliage at the canopy level. Tree density (TREE, m^{-2}) was quantified by counting the number of trees > 3 m tall.

4.2.5. Predator surveys

We quantified the risk of predation by red squirrels at nests. Squirrels are active and frequently vocal during the day and defend non-overlapping territories of similar size to songbirds (Rusch and Reeder 1978), which should allow nesting adults to assess spatial variation in squirrel encounter probability (Emmering and Schmidt 2011). Observers performed random-walk surveys by recording the squirrels they encountered while performing other duties on each study plot. Observers recorded their GPS location and the distance and bearing to each squirrel they observed or heard (Hochachka et al. 2000). Observers were instructed to record all detections unless they were certain an individual was previously recorded during the current visit. We assumed squirrels were counted multiple times because individuals were unmarked and often detected aurally. Therefore, these data represent spatial variation in activity rather than abundance. We accounted for the effect of spatial variation in observer effort on detection frequency by dividing each plot into nine cells with each cell centered on a point count station. Observers were instructed to roughly divide their time evenly among cells and to record their time spent surveying in each cell.

4.2.6. Statistical Analyses

To quantify edge and predation risk covariates we spatially referenced all nests, point count stations, random-walk predator detections, and all linear features into a geographic information system (ArcGIS 10.0, Environmental

Systems Research Institute, Inc. [ESRI], 2010). We used the NEAR tool (ArcGIS 10.0, ESRI, 2010) to measure distance (km) to the nearest MAIN linear feature edge and distance to the nearest MAIN or OPEN linear feature edge (hereafter, MAIN|OPEN) for each nest and point count station. Nests occurring on a linear feature had a distance of 0 km. We also generated three additional categorical edge measures for each point count station. Stations were categorized as occurring within hearing distance (i.e., 100 m) of a MAIN (M100) and a MAIN|OPEN (MO100) edge, and occurring at 0, 200, or 400 m from a MAIN edge (3MAIN; (see Glossary) as per our study design.

We used random-walk survey data (Chapter 3) to estimate predation risk by squirrels for each nest. We restricted our detections to the nest searching period to avoid inclusion of dispersing juvenile squirrels later in the summer (Larsen and Boutin 1994, Haughland and Larsen 2004). We assumed squirrel predation risk at a nest varied as function of squirrel detection probability. We standardized the probability of each squirrel detection (P_i) by dividing each detection by the total time (t_i) spent searching the sector (i) in which it was detected and multiplying by 200 h of surveying ($P_i = 1/t_i \times 200$ h). We further assumed the probability of nest (j) being encountered declined as a function of the inverse distance ($1/D_{ij}$) to each squirrel detection. We used the Distance/Azimuth extension (Jenness 2005) in ArcView GIS 3.3 (ESRI, 2002) to correct the locations of red squirrel detections based on observer estimates of distance and bearing. We then used the NEAR tool (ArcGIS 10.0, ESRI, 2010) to measure distance between each nest and each predator detected within 100 m during each year of study. All distances < 1 m were changed to 1 m to eliminate outliers. We calculated a continuous measure of risk (RESQ) for each nest as the sum of the individual detection probabilities in each year multiplied by the encounter probability of each detection ($RESQ_j = \sum P_i \times [1/D_{ij}]$). For each point count station we determined RESQ to be the maximum number of squirrels detected at that point during each year of study. We also considered a categorical measure of risk (RESQ01) that identified squirrels as present or absent. For both nests and point count stations, RESQ01 = 1 where RESQ > 0.

Our analyses considered three dependent variables, nest fate (i.e., daily nest survival rate), nest productivity (i.e., number of young fledged from successful nests), and abundance for all ground-nesting songbirds, all shrub-nesting songbirds, and all canopy-nesting songbirds. We separated our analyses by nesting substrate due to inherent differences in predation risk (Martin 1993). We did not consider cavity-nesting songbirds because our field methods did not provide reliable fate and productivity estimates for this group. We considered four hypotheses for explaining variation in our dependent variables. Each hypothesis is represented by a subset of candidate models (Appendix 4.1). The first subset of models considered the effects of edge proximity. Fate and productivity models considered linear and quadratic relationships with MAIN and MAIN|OPEN. Abundance models considered linear relationships with MAIN, M100, MO100, and 3MAIN. The second subset of models considered encounter risk by red squirrel (RESQ, RESQ01) for all dependent variables. The third subset model considered vegetation concealment. Fate and productivity models considered both nest and patch-scale measures of cover whereas abundance models considered patch-scale cover only. For ground-nesting species we considered both ground-level (GNDCOVN, GNDCOVP) and shrub-level (SHBCOVN, SHBCOVP) concealment. For shrub-nesting species we only considered shrub-level concealment. For canopy-nesting species we considered canopy closure (CANOPY) and tree density (TREE) for all dependent variables. The fourth subset of models considered the effect of the number of alternate nest sites (ALTNEST) on fate and productivity and was applied to shrub-nesting species only.

Each model subset considered all possible additive and interactive combinations of SITE (north or south) and the variable of interest. We used Akaike's information criterion corrected for small sample size (AIC_c) and evidence ratios (ER) to identify the top supported model containing a parameter of interest for each hypothesis (Burnham and Anderson 2002, Anderson 2008). ER indicate model support compared to a BASE model that did not contain a parameter of interest (see below). We considered two additional hypotheses by generating interactions between the top predation risk and the top vegetation models to determine whether the effect of predation risk on the dependent variable varied as a function of concealment (risk × cover) or the number of alternate nest sites (risk × alternate nests). Finally, we combined the top supported models from each subset and the risk × cover and risk × alternate nest interactions to identify the top supported combination of parameters that explained variation in our dependent variables. We considered all additive permutations of the independent variables and the risk-vegetation interactions. Shrub and ground cover estimates, ALTNEST, and RESQ were square root transformed, and TREE was log transformed (productivity models only) to improve normality and these and all continuous edge variables were centered (X – mean) prior to analyses.

Seven ground nests, 15 shrub nests, and 4 canopy nests did not have a measure of predation risk and 34 shrub nests did not have a measure of alternate nests sites. Rather than exclude these nests from analyses in their respective subsets, which would preclude comparison of support for each hypothesis across subsets using AIC_c, we accounted for the missing data in one of two ways. For canopy nests, we substituted average risk values for the missing data. For ground and shrub nests, which had more missing values, we created indicator variables RSHAVEDATA and ALTHAVEDATA to identify those nests where predation risk and alternate nest site, respectively, were unknown. We then replaced the missing data with zeros and generated an interaction between the indicator variable and its associated parameter of interest We included both the indicator variable and the interaction, which was the updated variable of interest, in all models that would have contained the missing data (the original variable of interest was dropped from each model due to multicollinearity). This process retained the original sample of nests but removed any influence of those nests missing data (see Appendix 4.2 for further details). To avoid over-penalizing the AIC_c value of those models containing both the indicator variable and the updated variable of interest, we included the indicator variable(s) in all models regardless of whether the updated variable of interest was present.

We used logistic exposure models (PROC NLMIXED; SAS, version 9.1.3 SAS Institute, Cary, North Carolina; Rotella et al. 2004, Shaffer 2004) to analyze variation in nest fate, zero-truncated Poisson regression models (ztp; Stata/IC 11.2, StataCorp LP), to analyse variation in nest productivity, and mixed-effects Poisson regression models to analyze variation in abundance (xtmepoisson; Stata/IC 11.2, StataCorp LP). The logistic exposure procedure uses a binomial response distribution to model the probability of a nest surviving the interval between nest checks. The probability of surviving an interval depends on interval length, which is equal to the number of days between nest checks for successful intervals and equal to 1 for failed intervals (Rotella et al. 2004). Nests without a minimum of one interval (i.e., found failed or fledged) were not included in our fate analyses. We also excluded those nests from our fate analyses that were abandoned due to camera placement or failed due to extreme weather or a collapsed nest structure because these failures were unrelated to the hypotheses considered. We did not use video to correct our field-based estimates of nest fate or productivity, or the length of the terminal exposure interval for nests with cameras. We expect these sources of error to be minimal because of the short interval duration and the reasonably high accuracy of our fate estimates (Stanley 2000, Ball and Bayne 2012).

All models in each model set accounted for the lack of independence between sampling units within each study plot by including plot as a random effect (fate and abundance models) or by including plot as a clustering variable to produce robust variance estimates (productivity; Froot 1989, Williams 2000).

Abundance models also included a random intercept for point count station to account for multiple visits to each station. All models also included independent nuisance variables to account for variation in the dependent variable that was unrelated to the hypotheses being considered. We used model selection and AIC_c to select the most parsimonious combination of nuisance variables for all nesting substrates combined and these variables together with SITE, RSHAVEDATA (fate and productivity models only), and ALTHAVEDATA (shrub fate and productivity models only) were the only covariates in our NULL models. The final set of fate and productivity nuisance variables included linear and quadratic forms of DAYINIT (standardized to 1 = 16 May), nest stage (INC, NESTL; reference level = lay; fate models only), CAM (reference level = no), and MAXCLUTCH (productivity models only). SITE, INC, and CAM were excluded from canopy nest models due to limited sample size. The final set of abundance nuisance variables included linear and quadratic forms of DAY (standardized to the earliest day of sampling per site: north = 5 June, south = 30 May), WIND, and PTREE (see Glossary). All continuous nuisance variables except MAXCLUTCH and WIND were centered (X – mean) prior to analyses.

Our analyses of abundance provide an index of relative abundance with respect to the dependent variables considered. Indices are well-suited to test our hypotheses regarding abundance as long as variation in detectability is minimized by study design and is not biased by the variable(s) of interest (Johnson 2008). Detectability is defined as the product of two probabilities: 1) the probability that a bird provides a cue (i.e., sings or makes itself visible) during the survey, and 2) the probability that the observer detects that cues given that it is provided (Farnsworth 2002). Several analytical approaches have been developed to account for variability in one or more components of detectability (e.g., Buckland 1987, Farnsworth et al. 2002, Solymos et al. *in press*). However, these methods are intended for analyses of single-species with large numbers of detections rather than guilds (Johnson 2008). The adjusted counts produced by different methods also can vary substantially such that they themselves are (adjusted) indices of abundance (Johnson 2008, Reidy et al. 2011). Therefore, we did not attempt to directly adjust our counts for detectability. Instead we controlled for many of the factors purported to affect detectability by restricting our study to a single habitat-type (i.e., mature mixed wood forest), using a single observer during each season, visiting each sampling station twice per season at a different time of day during each sampling round, and halting counts during persistent rain and high winds. We also accounted for variable detectability by including several nuisance variables in our abundance models (see above).

Of particular concern in this study was whether detectability was higher at edge stations compared to interior stations and whether detectability was higher at stations where squirrels were absent compared to stations where squirrels were present. Observers may be capable of detecting cues at further distances at edge stations if songs are scattered and attenuated more rapidly in the forest compared to along an open linear feature (Schieck 1997). We used binomial distance sampling based on two distance classes, 0 – 50 m and 50 – 100 m, to estimate the effective detection radius (EDR; Buckland et al. 1987, Matsuoka et al. 2012) at edge and interior stations. In fixed radius sampling, the number of individuals available to be detected increases with increasing distance from the observer. However, the probability of the observer detecting those individuals declines with increasing distance. EDR is estimated from the rescaled probability detection function as the distance at which as many birds are detected beyond the EDR as are missed within the EDR. We used mixed-effects linear regression to compare EDR between edge and interior points. Different nesting guilds may have inherently different attenuation rates if they typically sing at different heights in the forest (Marten and Marler 1977). Therefore, we calculated EDRs for each nesting guild, for each of the most commonly recorded species in our study, and for red squirrels. Individuals were pooled at each sampling station during each year (ground and shrub nesters), at stations across years (canopy nesters, Tennessee Warbler, red squirrel), or across edge and interior stations on each study plot during each year (Swainson’s Thrush, Yellow-rumped Warbler, Chipping Sparrow, Ovenbird; see Appendix 3.4 for species names) to achieve a sufficient sample size for analyses. Regression models included a random intercept for plot and station depending on level of grouping and SITE as a fixed effect.

Detection also may be influenced by predation risk if birds reduce the frequency that they sing when predators are present (Fontaine and Martin 2006a). We used the removal method of Farnsworth et al. (2002) and Program SURVIV (White 1992) to determine whether detectability of the most commonly recorded species in our study varied due to differences in singing rates between stations where squirrels were absent and stations where squirrels were present. This method is not appropriate for modeling guilds due to differences in singing rates between species within guilds (Farnsworth et al. 2002). Removal models estimate detectability based on the decline in numbers of individuals recorded during successive time intervals of a 10-minute survey. We used model selection based on AIC_c to select the most parsimonious detectability model (heterogeneous or constant detectability among individuals within a species; Farnsworth et al. 2002), which we then used to calculate the predicted detection probability during a 10-minute count (± 1 SE) between stations with and without squirrels. We used the estimates of mean and SE for each species and a Monte Carlo simulation with 2000 replicates to determine whether the probability of detection in the absence of squirrels was greater than that in the presence of squirrels. We calculated average EDR and detection probabilities weighted by 1/SE for all guilds and for all species combined.

To assess the magnitude of response of each dependent variable to each hypothesis we standardized the results of our nest fate analyses into odds-ratios (OR) and the results of our productivity and abundances analyses into incident rate ratios (IRR; Glossary). Each ratio was calculated as $\exp^{(\beta \times \Delta)}$ where β is the coefficient of the parameter of interest and Δ is the magnitude of change in the corresponding variable. We considered a 100 m increase in distance from an edge as Δ for all edge variables. For all other continuous variables Δ equals the difference between the10th and the 90th percentile of observed values. All categorical variables were increased from 0 to 1. OR and IRR equal to one or that include one in their CI indicate no difference in expected probability or count, respectively, between each level of the variable of interest. Ratios and lower CI greater than one indicate an increase in the expected outcome with an increase in the variable of interest.

4.3. Results

4.3.1. Nest fate and nest productivity

Our fate analyses included 334 nests in the northern site and 237 nests in the southern site representing a total of 23 species or 19 species per site (Appendix 4.3). The majority (64%) were shrub nests. Ground and canopy nests comprised 29% and 7% of nests, respectively. A total of 203 nests were successful in the northern site and 144 nests were successful in the southern site (Appendix 4.4). The proportion of nests that were successful was highest for canopy nests (78%) and lowest for shrub nests (57%). Sixty-seven percent of ground nests were successful.

We found limited support for our hypotheses, either individually or in combination, for explaining variation in nest fate (Table 4.1, Appendix 4.6). Overall, red squirrel presence (RESQ01) was the top supported nest fate model. RESQ01 appeared in the top supported model for all nesting guilds and was the only model to receive any support for explaining variation in fate of shrub nests. The odds of a ground and shrub nest surviving each day decreased approximately one half to one third, respectively, in the presence of squirrels (Table 4.2, Figs. 4.1, 4.2). The CI of the OR for both nesting guilds included 1.0 in their estimates and the ERs indicate these models were not strongly supported. Support for an effect of predation risk on the fate of canopy nests did not exceed that of the NULL when considered independently but RESQ01 was included in the top supported model when included as an interaction with nest cover (TREE; discussed below). Edge proximity was the second most frequently supported hypothesis for explaining variation in nest fate and edge appeared in the top supported models for both ground and canopy nests (Table 4.2). The probability of canopy nests surviving increased 55% with a 100 m increase in distance from the nearest MAIN|OPEN edge (Fig. 4.3). In contrast, the probability of ground nests surviving decreased 14% over the same distance from a MAIN edge (Fig. 4.1). For ground nests the edge proximity hypothesis received 1.18 times the support of the predation risk hypothesis and the additive effects of edge proximity and predation risk received 1.63 times the support of edge alone. However, the edge-plus-predation model received only 2.39 times the support of the NULL and the OR for both the edge and predation parameters included 1.0 in their CI indicating their effects were weak. The edge hypothesis was did not have strong support for shrub nests.

The cover hypothesis only received support for explaining variation in the survival probability of canopy nests and it was the top supported hypothesis for this group (Table 4.2). Contrary to expectations, survival probability of canopy nests decreased with an increase in cover (TREE). However, a model that considered an interaction between predation risk and cover (RESQ01 × TREE) received 1.5 times the support of cover alone and 3.24 times the support of a

Table 4.1. Models that received more support than a Null model without covariates of interest for explaining variation in daily nest survival rate of (A) ground, (B) shrub, and (C) canopy nests. Independent variables are described in the Glossary. *k* is the number of model parameters. w_i is the Akaike weight of model *i*.

Models	Log likelihood	*k*	AIC_c	ΔAIC_c	w_i
A. Ground nests [a]					
+ MAIN + RESQ01	-191.12	10	402.339	0.00	0.15
+ MAIN	-192.61	9	403.31	0.97	0.09
+ RESQ01	-192.78	9	403.64	1.30	0.08
+ MAIN|OPEN	-192.78	9	403.65	1.31	0.08
+ MAIN + RESQ01 + GNDCOVP	-190.84	11	403.8	1.46	0.07
B. Shrub nests [b]					
+ RESQ01	-496.82	10	1013.67	0.00	0.12
+ SITE × RESQ01	-495.21	12	1014.49	0.82	0.08
+ RESQ01 + SITE × SHBCOVP	-495.30	12	1014.66	0.99	0.07
C. Canopy nests [c]					
+ MAIN|OPEN + RESQ01 × TREE	-31.14	8	78.48	0.00	0.23
+ RESQ01 × TREE	-32.39	7	78.94	0.46	0.19
+ TREE	-34.83	5	79.74	1.26	0.12
+ MAIN|OPEN	-35.28	5	80.65	2.17	0.08
+ MAIN|OPEN + TREE	-34.34	6	80.80	2.32	0.07
+ RESQ01 + TREE	-34.58	6	81.29	2.81	0.06
+ MAIN	-35.85	5	81.78	3.30	0.04

[a] NULL: SITE + DAYINIT + $DAYINIT^2$ + INC + NESTL + CAM + RSHAVEDATA; Null AIC_c = 404.08; n = 167 nests.

[b] NULL: SITE + DAYINIT + $DAYINIT^2$ + INC + NESTL + CAM + RSHAVEDATA + ALTHAVEDATA; NULL AIC_c = 1014.78; n = 364 nests.

[c] NULL: DAYINIT + $DAYINIT^2$ + NESTL; NULL AIC_c = 81.85; n = 40 nests.

Table 4.2. The top supported model that contained a parameter of interest for the hypotheses edge proximity, predation risk, cover, and alternate nests sites, and for all hypotheses combined (Overall) for explaining variation in the dependent variables nest fate , nest productivity, and abundance of ground-nesting, shrub-nesting, and canopy-nesting boreal forest songbirds in Fort Simpson, NT (north), and Chinchaga, AB (south). AIC$_c$ weights (*w*) reflect model support compared to all models in each hypotheses' subset of candidate models or in all models combined (Overall). Evidence ratios (ER) indicate model support compared to a null model that did not contain a parameter of interest. Models in bold text and with ER > 1 indicate greater support than the null. The ratio of ER within each nest substrate indicates relative model support. For fate models odd ratios (OR ± 95% CI) represent the relative likelihood of a nest surviving an increase in the parameter of interest. For productivity and abundance models incidence rate ratios (IRR ± 95% CI) are the relative change in the predicted number of young fledged and predicted number individuals detected per survey, respectively, with an increase in the parameter of interest. Each ratio was calculated as exp$^{(\beta \times \Delta)}$ where β is the coefficient of the parameter of interest and Δ is the magnitude of change in the corresponding variable. Continuous distance to edge variables used $\Delta = 100$ m, the remaining continuous variables used Δ = 90th percentile - 10th percentile of the observed values, and categorical variables were increased from 0 to 1. Abundance data represent 470 point count surveys.

Nest substrate (n Fate, n Prod.)	Hypothesis	Dependent variable					
		Fate		Productivity		Abundance	
		Top model (*w*, ER)	OR (± 95% CI)	Top model (*w*, ER)	IRR (± 95% CI)	Top model (*w*, ER)	IRR (± 95% CI)
Ground	Edge	**MAIN**	0.86 (0.72 – 1.02)	MAIN	1.02 (0.99 – 1.04)	**SITE**	0.85 (0.66 – 1.09)
(167, 112)		**(0.22, 1.47)**		(0.16, 0.35)		**+ M100**	0.94 (0.79 – 1.11)
						+ SITE × M100	0.79 (0.61 – 1.01)
						(0.46, 34.4)	
	Predation	**RESQ01**	0.54 (0.23 – 1.31)	RESQ01	1.04 (0.92 – 1.17)	**RESQ**	0.79 (0.67 – 0.92)
		(0.42, 1.25)		(0.19, 0.33)		**(0.41, 24.9)**	
	Cover	GNDCOVP	1.36 (0.65 – 2.83)	GNDCOVN	0.93 (0.83 – 1.04)	SHBCOVP	1.10 (0.93 – 1.32)
		(0.30, 0.55)		(0.13, 0.36)		(0.24, 0.65)	

Nest substrate (n Fate, n Prod.)	Hypothesis	Dependent variable Fate Top model (*w*, ER)	 OR (± 95% CI)	 Productivity Top model (*w*, ER)	 IRR (± 95% CI)	 Abundance Top model (*w*, ER)	 IRR (± 95% CI)
	Overall	**MAIN** **+ RESQ01** **(0.15, 2.39)**	0.84 (0.69 – 1.03) 0.51 (0.21 – 1.24)	NULL (0.20, 1.00)		**SITE** **+ M100** **+ SITE × M100** **+ RESQ** **(0.42, 553)**	0.91 (0.72 – 1.16) 0.94 (0.79 – 1.12) 0.79 (0.62 – 1.01) 0.79 (0.67 – 0.93)
Shrub (364, 206)	Edge	MAIN (0.34, 0.43)	0.97 (0.86 – 1.09)	MAIN (0.15, 0.34)	1.00 (0.97 – 1.03)	**MO100** **(0.17, 3.07)**	0.88 (0.78 – 1.00)
	Predation	**RESQ01** **(0.35, 1.74)**	0.69 (0.43 – 1.10)	RESQ01 (0.35, 0.85)	1.14 (1.05 – 1.23) ^{a}	**RESQ** **(0.38, 2.27)**	0.89 (0.77 – 1.03)
	Cover	SITE + SHBCOVP + SITE × SHBCOVP (0.19, 0.52)	0.90 (0.60 – 1.34) 1.11 (0.61 – 2.02) 0.52 (0.20 – 1.34)	SHBCOVP (0.20, 0.40)	0.94 (0.84 – 1.05)	**SITE** **+ SHBCOVP** **+ SITE × SHBCOVP** **(0.71, 14.3)**	0.63 (0.50 – 0.80) 1.36 (1.09 – 1.70) 0.72 (0.51 – 1.01)
	Alternate	ALTNEST (0.22, 0.40)	0.91 (0.57 – 1.48)	ALTNEST (0.28, 0.41)	1.07 (1.00 – 1.13) ^{a}	-	-
	Overall	**RESQ01** **(0.12, 1.74)**	0.69 (0.43 – 1.10)	NULL (0.14, 1.00)		**MO100** **+ RESQ** **+ SITE** **+ SHBCOVP** **+ SITE × SHBCOVP** **(0.34, 61.1)**	0.89 (0.79 – 1.01) 0.89 (0.78 – 1.02) 0.64 (0.50 – 0.81) 1.34 (1.08 – 1.66) 0.71 (0.52 – 1.00)
Canopy (40, 29)	Edge	**MAIN|OPEN** **(0.37, 1.83)**	1.55 (0.86 – 2.81)	MAIN|OPEN (0.21, 0.42)	0.92 (0.87 – 0.96) ^{a}	**SITE** **+ MO100** **+ SITE × MO100** **(0.49, 44.6)**	0.47 (0.26 – 0.86) 0.65 (0.44 – 0.97) 1.86 (1.07 – 3.21)
	Predation	RESQ01 (0.25, 0.46)	1.65 (0.31 – 8.69)	RESQ (0.16, 0.24)	1.07 (0.84 – 1.35)	**RESQ** **(0.48, 92.5)**	1.38 (1.05 – 1.84)

Nest substrate (n Fate, n Prod.)	Hypothesis	Dependent variable					
		Fate		Productivity		Abundance	
		Top model (*w*, ER)	OR (± 95% CI)	Top model (*w*, ER)	IRR (± 95% CI)	Top model (*w*, ER)	IRR (± 95% CI)
	Cover	**TREE** **(0.68, 2.87)**	0.19 (0.03 – 1.15)	TREE (0.20, 0.33)	1.27 (1.13 – 1.43) [a]	**SITE** **+ TREE** **+ SITE × TREE** **(0.86, 35.7)**	0.57 (0.32 – 1.01) 0.79 (0.64 – 0.98) 1.32 (1.01 – 1.73)
	Overall	**MAIN|OPEN** **+ RESQ01** **+ TREE** **+ RESQ01 × TREE** **(0.23, 5.40)**	1.65 (0.77 – 3.52) 3.14 (0.41 – 24.0) 23.6 (0.09 – 9106) 0.004 (0.00 – 2.63)	NULL (0.29, 1.00)		**SITE** **+ MO100** **+ SITE × MO100** **+ RESQ** **+ TREE** **+ SITE × TREE** **(0.50, 9504)**	0.39 (0.20 – 0.74) 0.71 (0.48 – 1.03) 1.76 (1.03 – 1.36) 1.40 (1.07 – 1.85) 0.84 (0.68 – 1.04) 1.28 (0.99 – 1.68)

[a] Does not exceed support of BASE and IRR includes zero when robust standard error grouped on PLOT is excluded from model.

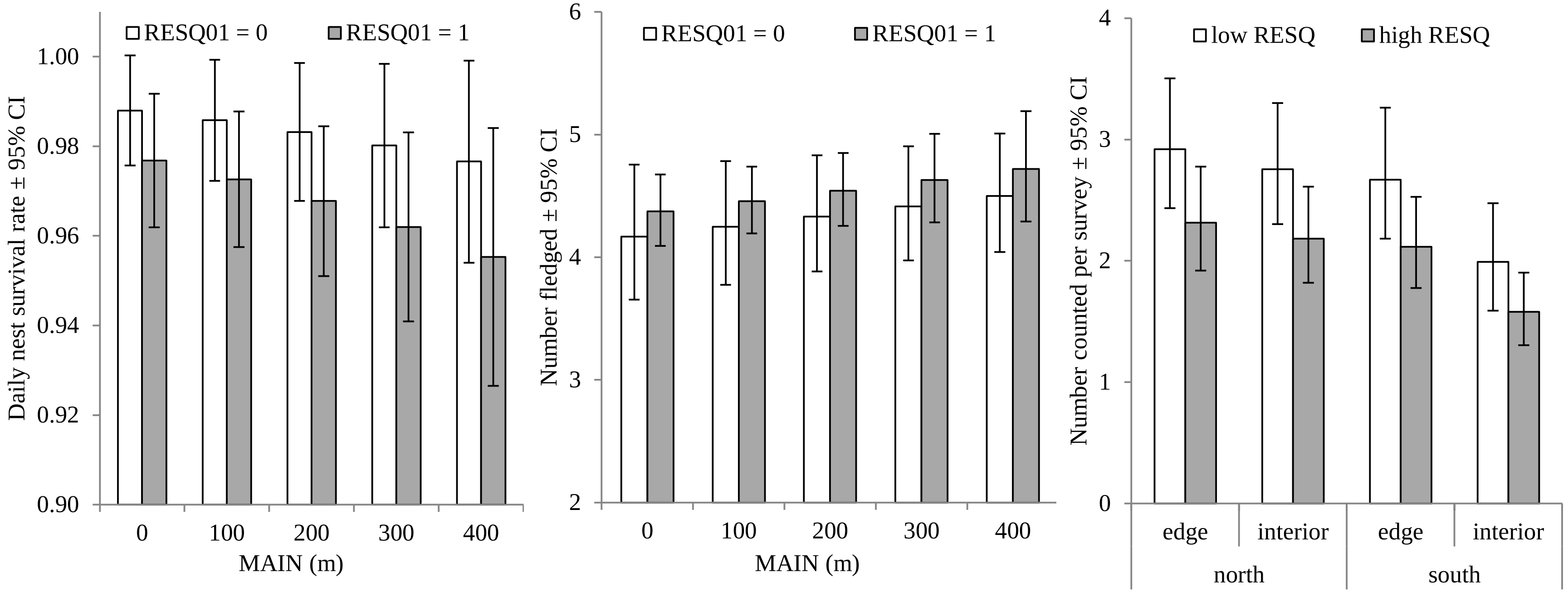

Figure 4.1. Predicted daily survival rate of ground nests (left panel), predicted number of young fledged from successful ground nests (middle panel), and predicted number of ground-nesting individuals counted per 10-minute point count survey (right panel) as a function of edge proximity, red squirrel presence (fate and productivity) or abundance (abundance; white and gray bars represent low and high predation risk, respectively), and study site (abundance). All predicted values (± 95% CI) are based on the top supported model that included edge and predator covariates. Variance estimates account for the lack of independence within plots and for multiple visits to each point count station.

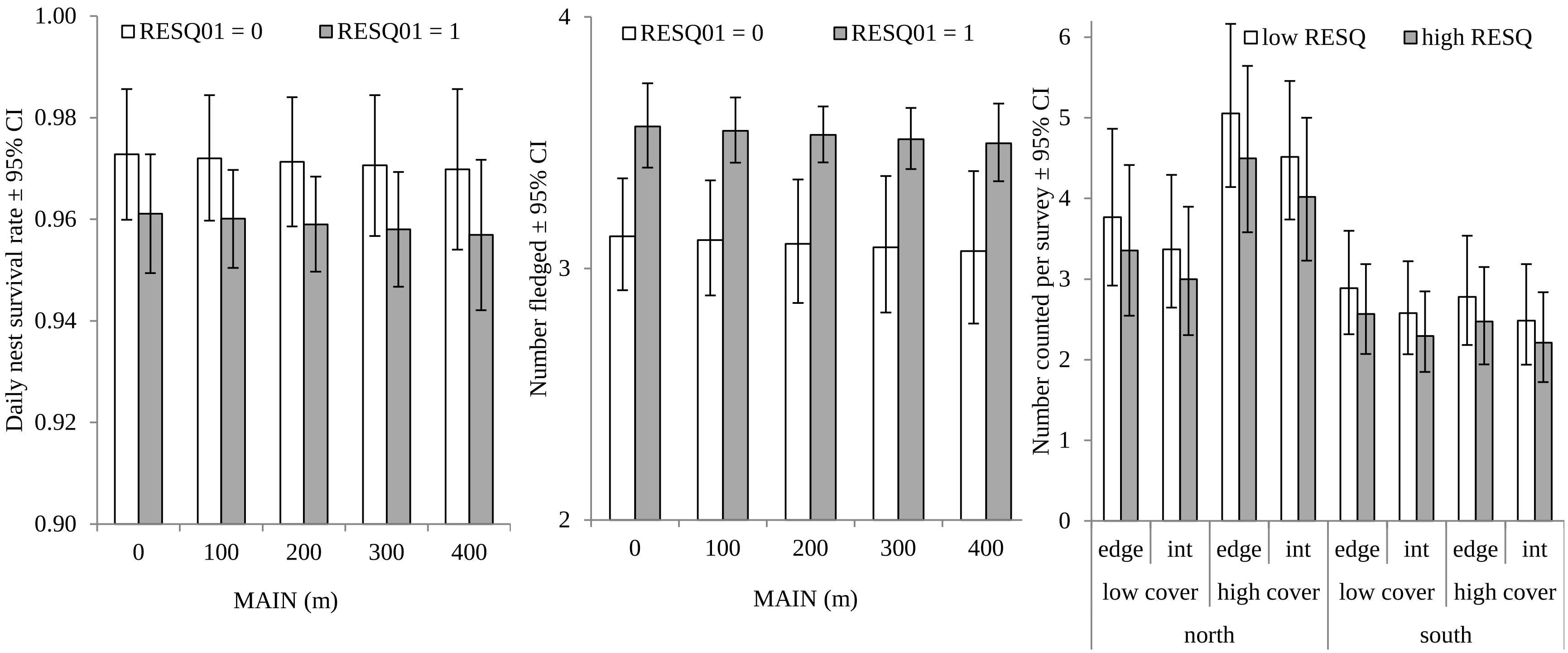

Figure 4.2. Predicted daily survival rate of shrub nests (left panel), predicted number of young fledged from successful shrub nests (middle panel), and predicted number of shrub-nesting individuals counted per 10-minute point count survey (right panel) as a function of edge proximity, red squirrel presence (fate and productivity) or abundance (abundance; white and gray bars represent low and high predation risk, respectively), and study site and cover (abundance). All predicted values (± 95% CI) are based on the top supported model that included edge and predator covariates. Variance estimates account for the lack of independence within plots and for multiple visits to each point count station.

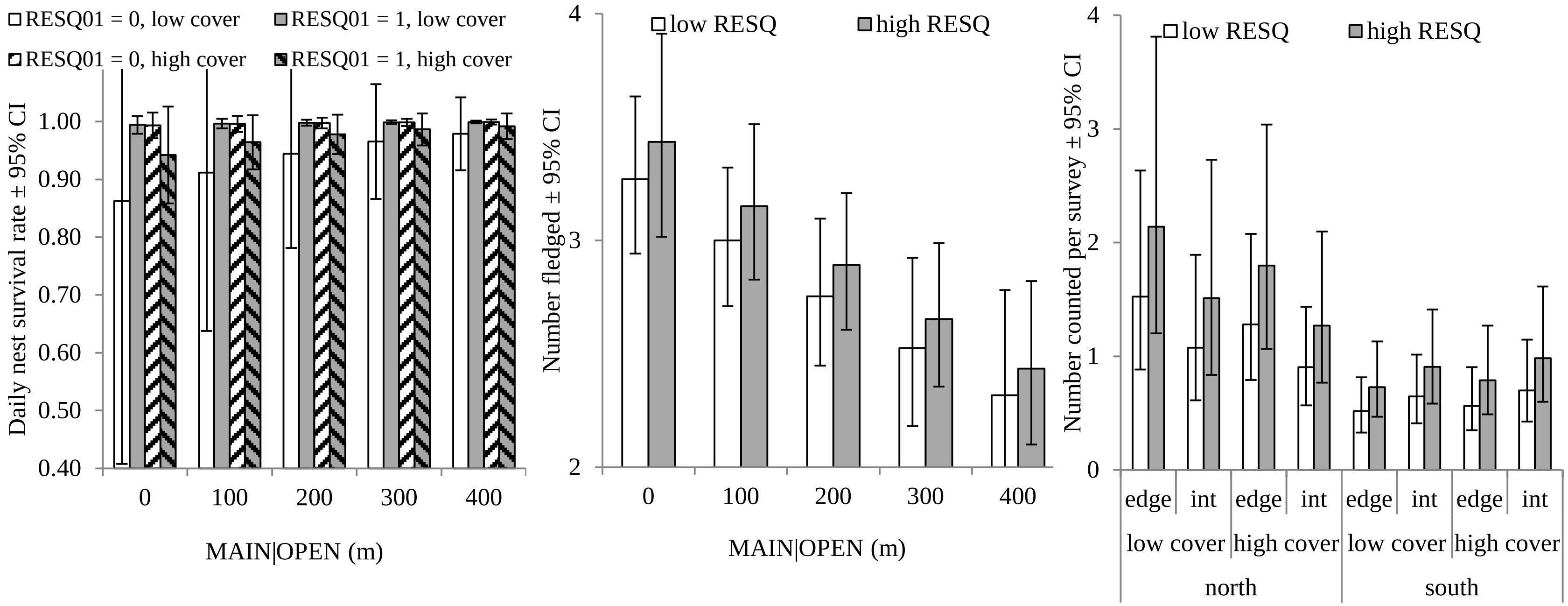

Figure 4.3. Predicted daily survival rate of canopy nests (left panel; maximum value on y-axis = 1.32), predicted number of young fledged from successful canopy nests (middle panel), and predicted number of canopy-nesting individuals counted per 10-minute point count survey (right panel) as a function of edge proximity, red squirrel presence (fate) or abundance (productivity and abundance; white and gray bars represent low and high predation risk, respectively), study site (abundance), and cover (fate [open and hashed bars represent low and high cover, respectively] and abundance). All predicted values (± 95% CI) are based on the top supported model that included edge and predator covariates. Variance estimates account for the lack of independence within plots and for multiple visits to each point count station.

model that considered the additive effect of predation risk and cover (Tables 4.1, 4.2). The top supported canopy nest fate model included both the effects of edge proximity (MAIN|OPEN) and the interaction between predation risk and cover. When squirrels were absent the predicted probability of nest survival increased >230% when tree density was increased from the 10th to the 90th percentile. When squirrels were present the probability of canopy nest survival decreased 90% (23.6 × 0.004) with the same increase in tree density (Fig. 4.3). All OR included 1.0 in their estimated CI.

The alternate nest site hypothesis was not supported (Table 4.2). We also found no support for any hypothesis, either alone or in combination, for explaining variation in nest productivity (Table 4.2, Appendix 4.7). Four hypotheses for nest productivity did not contain 1.0 in the CI of their estimated ORs despite receiving less support compared to the NULL. These ORs do include 1.0 in their estimated CIs when robust SEs clustered on study plot are excluded from the models however. We believe the smaller robust SEs result from a negative correlation within clusters rather than a meaningful effect of each hypothesis so we do not view these as robust models with strong biological support (Scribney 1998).

4.3.2. Abundance

We recorded 1685 songbirds during 216 point count surveys in the northern site and 1481 songbirds during 254 surveys in the southern site (Appendix 4.5). Shrub-nesting species made up nearly half of all individuals detected in both sites whereas ground and canopy-nesting species comprised approximately 34% and 15% of individuals, respectively. EDR was marginally higher in the forest interior compared to the forest edge for most guilds and species although no difference was statistically significant (all $P > 0.1$; Fig. 4.4). Average guild-level EDR (± 95% CI) at edge and interior stations was 47.1 m (46.4 – 47.8 m) and 48.6 m (46.0 – 51.3 m), respectively. Average species-level EDR at edge and interior stations was 49.8 m (44.8 – 55.2 m) and 54.1 m (47.2 – 62.0 m). The EDR for squirrels also did not differ between edge and interior stations ($P = 0.286$; Fig. 4.4). The difference in detection probability based on singing rate was not significantly affected by squirrel presence for any species (all $P > 0.2$) and did not vary consistently across species (Fig. 4.5). The mean (± 95% CI) detection probability at stations where squirrels were absent was 0.95 ± 0.07 and at stations where squirrels were present was 0.92 ± 0.07. Together these results indicate that variation in abundance can be attributed to the independent variables of interest and not to differences in detectability.

All hypotheses we considered received some support for explaining variation in the numbers of individuals detected during our surveys. Edge proximity and predation risk appeared in the best overall models for all nesting guilds (Table 4.3, Appendix 4.8). Considered independently, an edge effect was the top supported hypothesis for ground and shrub nesting species whereas edge was the second-best supported hypothesis for canopy nesters (Table 4.2). We also found support for an interaction between SITE and edge for ground and canopy nesters. In the north, all nesting guilds were more abundant at the forest edge compared to stations >100 m from the edge (Figs. 4.1 – 4.3). However, the ORs

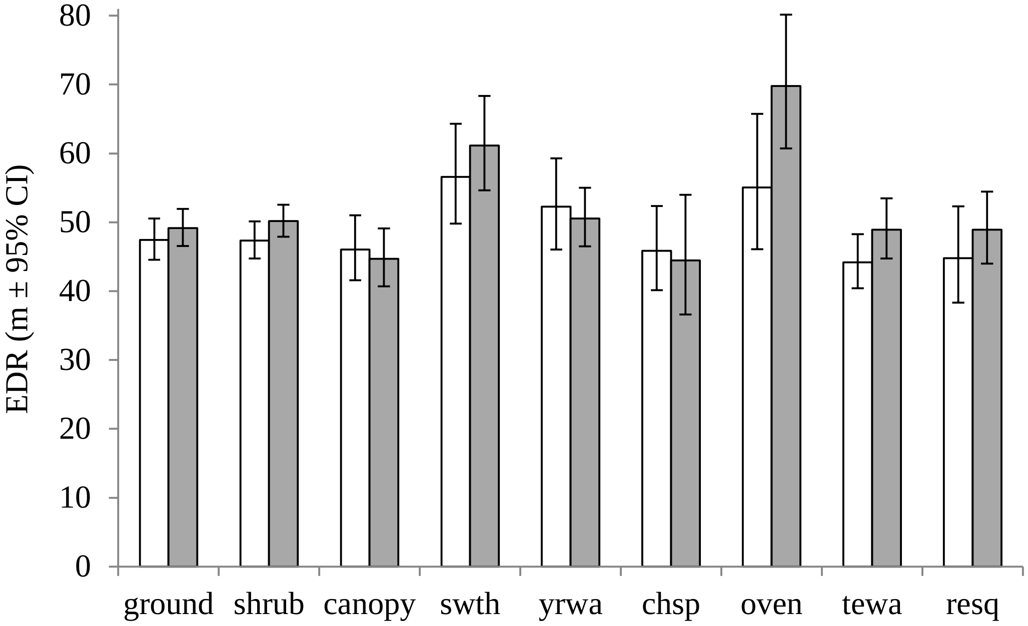

Figure 4.4. Average effective detection radius (EDR) at edge (white bars) and interior (gray bars) point count stations by nesting guild and species.

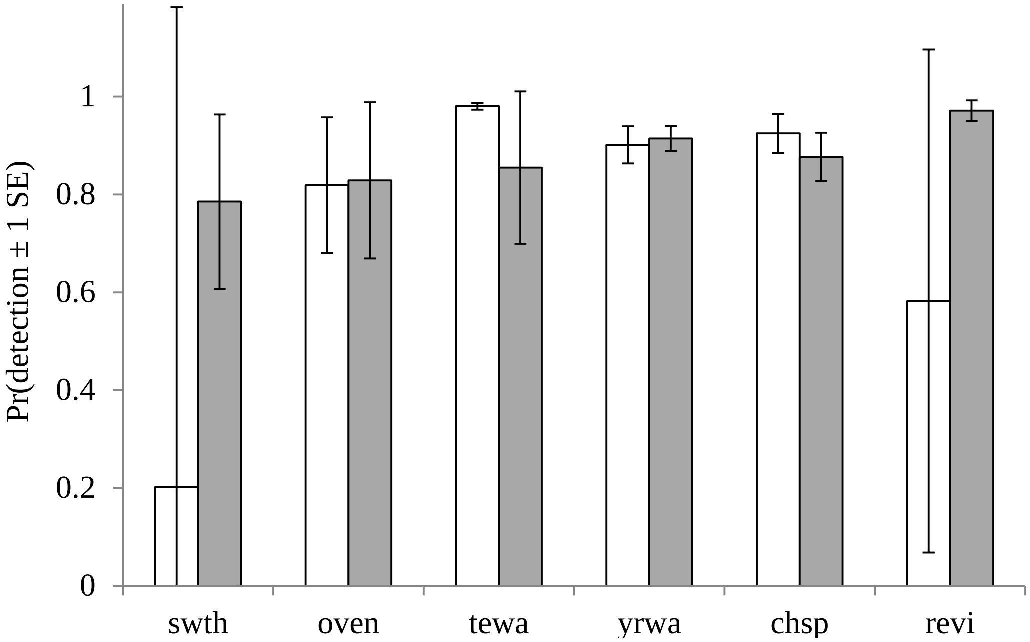

Figure 4.5. Predicted probability (± 1SE) of detecting a member of each species during a 100 m radius 10-minute point count survey when red squirrels are absent (white bars) and present (gray bars).

indicate that only canopy nesters were strongly attracted to edges in this site. In the south, ground nesters were more strongly attracted to edges and declined by a factor of 0.74 (CI: 0.57 – 0.96) at interior stations. In contrast, canopy nesters tended to be more abundant at interior stations (OR: 1.22 [0.68 – 2.12]). We did not find support for a site interaction with predation risk indicating each nesting guild responded similarly to squirrels in both sites. Shrub nesters and ground nesters in particular were less abundant at stations with a greater abundance of squirrels (Table 4.2, Figs. 4.1 – 4.3). In contrast, canopy nesters were significantly more abundant at stations that had more squirrels. For ground nesters, the top supported model overall, which considered both an interaction between SITE and edge plus the additive effects of predation risk, was strongly supported compared to the NULL (Table 4.2).

We also found strong support for the cover hypothesis with a SITE interaction for explaining variation in the abundance of shrub and canopy nesters. Cover was unsupported for ground nesters. We did not find strong support for an interaction between cover and predation risk, which indicates that birds were not selecting areas with more cover when risk of predation was high (Table 4.3). Cover was included in the top supported model overall for shrub and canopy nesters along with the effects of edge and predation risk and these models were strongly supported compared to the NULL and compared to any one hypothesis (Table 4.2). The response to cover was strongest in the north for both nesting guilds. Shrub nesters were 1.18 (1.05 – 1.32) times more abundant in areas of high shrub cover in the north but they did not respond to shrub cover in the south

Table 4.3. Top models ($\sum w \geq 0.90$) for explaining variation in abundance of (A) ground-nesting, (B) shrub-nesting, and (C) canopy-nesting songbirds. Data represent 216 surveys at 54 stations in Fort Simpson, NT (northern site), and 254 surveys at 82 stations in Chinchaga, AB (southern site). Independent variables are described in the Glossary. k is the number of model parameters. w_i is the Akaike weight of model i.

Model	Log likelihood	k	AIC_c	ΔAIC_c	w_i
A. Ground nesters [a]					
+ SITE × M100 + RESQ	-783.44	10	1587.36	0.00	0.42
+ SITE × M100 + RESQ × SHBCOVP	-781.85	12	1588.38	1.02	0.25
+ SITE × M100 + RESQ + SHBCOVP	-783.17	11	1588.92	1.56	0.19
+ SITE × M100	-787.26	9	1592.91	5.55	0.03
+ RESQ	-788.63	8	1593.56	6.20	0.02
B. Shrub nesters [a, b]					
+ MO100 + RESQ + SITE × SHBCOVP	-932.18	11	1886.94	0.00	0.34
+ MO100 + SITE × SHBCOVP	-933.96	10	1888.40	1.46	0.17
+ RESQ + SITE × SHBCOVP	-933.99	10	1888.46	1.52	0.16
+ SITE × SHBCOVP	-935.73	9	1889.85	2.91	0.08
+ MO100 + RESQ	-936.45	9	1891.30	4.36	0.04
+ MO100 + RESQ × SITE × SHBCOVP	-931.22	14	1891.37	4.43	0.04
+ SHBCOVP	-937.85	8	1892.02	5.08	0.03
+ RESQ × SITE × SHBCOVP	-932.98	13	1892.75	5.81	0.02
+ MO100	-938.30	8	1892.92	5.98	0.02
+ MAIN|OPEN	-938.35	8	1893.01	6.07	0.02
C. Canopy nesters [a, c]					
+ SITE × MO100 + RESQ + SITE × TREE	-580.36	12	1185.40	0.00	0.50
+ SITE × MO100 + RESQ	-583.24	10	1186.97	1.56	0.23
+ SITE × MO100 + RESQ × SITE × TREE	-578.70	15	1188.45	3.05	0.11
+ RESQ + SITE × TREE	-584.10	10	1188.69	3.29	0.10

[a] Null: SITE + DAY + DAY^2 + WIND + PTREE; Null AIC_c = 1599.99.

[b] Null AIC_c = 1895.17.

[c] Null AIC_c = 1203.72.

(OR: 0.96 [0.69 – 1.33]; Table 4.2, Fig. 4.2). Canopy nesters were 0.84 (0.68 – 1.04) times less abundant in areas of high tree density in the north but they did not respond to tree density in the south (1.08 [0.55 – 2.18]; Table 3.2, Fig. 3.3). SHBCOVP and TREE were not significantly correlated with MO100 in either site (Pearson's pairwise correlation with a Bonferroni correction, all $P > 0.63$).

4.4. Discussion

Those variables deemed important to nest fate were congruent with those deemed important for explaining variation in abundance for ground and shrub nesting species in our study sites (Table 4.2, Figs. 4.1, 4.2). This congruence supports the use of point count surveys as an effective means of assessing variation in habitat quality and prioritizing habitats for conservation for ground and shrub-nesting guilds in boreal regions similar to our sites. We cannot make a similar recommendation for canopy-nesting species without further study. Nest fate and abundance of canopy nesters responded similarly to predation risk by red squirrels. However, we did not find evidence that canopy nesters were less abundant near forest edges in the north despite weak support for a positive effect of edge distance on nest fate (Table 4.2, Fig. 4.3). We also did not find evidence that the abundance of canopy nesters was negatively associated with lower tree density in the south, which was identified as marginally important to fate when squirrels were present. We did not have sufficient numbers of canopy nests to include SITE in our fate models so we are unable to conclude whether there were site-specific differences in factors affecting fate. Although the direction of the response to edge and tree density differed between fate and abundance of canopy nesters and that these models were better supported than a null model, the CI did include 1.0 in their OR estimates indicating these models were not strongly supported.

There are several potential explanations for the apparent lack of congruence between dependent variables for canopy nests (see Chalfoun and

Schmidt 2012 for a thorough review of this topic). However, we suggest the most parsimonious explanation is that our sample of canopy nests is strongly biased towards Least Flycatchers (*Empidonax minimus*; 63% of nests; Appendix 4.2) compared to their proportional representation in the canopy-nesting guild (26% of individuals counted; Appendix 4.4). Least flycatchers also comprised a substantial proportion of the canopy nesting guild in the north (41%) whereas they were relatively uncommon in the south (6%). Therefore, our models for canopy nest fate and productivity may not accurately define habitat quality for all canopy nesting species and canopy nesting species in the south in particular. In addition, habitat selection by Least Flycatchers is strongly influenced by social factors (Sherry and Holmes 1985), which may further limit our ability to find congruence between factors accounting for variation in fecundity and abundance among canopy nests.

We did not find strong support that increasing edge proximity negatively affected nest fate. On the contrary, nest fate of ground nesting birds is marginally higher near edges. Our findings are consistent with those of other researchers that have concluded that negative edge effects on nest fate are uncommon in western North America (Tewksbury et al. 1998, Cavitt and Martin 2002, George and Dobkin 2002). We also found strong support that ground and shrub-nesting birds were more abundant near edges, which suggests habitats near edges might be of higher quality in terms of reproductive potential and that birds are capable of assessing this potential and are choosing to settle near edges. This finding is also consistent with several studies of abundance that suggest few boreal birds avoid linear feature edges (Bayne et al. 2005a, b, Machtans 2006).

Our abundance results cannot be explained by a higher detection probability at edge stations because the distance at which observers were recording birds they heard (EDR) was marginally higher at interior stations and because our counts are not adjusted estimates (i.e., we detected more birds on average in a smaller radius at the edge compared to the number of birds detected in a larger radius in the interior). Bayne et al. (unpublished manuscript) demonstrated experimentally that song transmission was not higher along the edge of linear features compared to through the forest interior. The forest canopy may provide a reflective surface and a stable microclimate that improves sound transmission rather than impedes it (Morton 1975, Marten and Marler 1977). Alternatively, the higher EDR in the forest may reflect a bias in distance estimation. Observers tend to overestimate distance in the 50-m range (Alldredge et al. 2007), which is the distance limit used to calculate EDR. Linear features may provide a visual benchmark that improves distance estimates at edge points, which would result in comparatively higher EDRs at interior points.

Negative edge effects on nesting songbirds commonly result from increased rates of nest predation and brood parasitism in edge habitats (Batáry and Báldi 2003). We did not find support for a positive effect of increasing edge proximity on the edge-related distribution of most nest predators (Chapter 3). As a result, the predicted probability of daily nest predation was highest at intermediate distance from a forest edge. Therefore, edges can in some circumstances represent higher quality habitat due to lower risk of nest predation. Nest fate and abundance of ground and shrub nesting birds were both higher in areas where red squirrels were less abundant, which supports this conclusion. However, contrary to our expectation, both nest fate and abundance of canopy nesters responded positively to red squirrel abundance. Emmering and Schmidt (2011) report a similar discrepancy in the abundance response between ground and canopy nesters to an experimental increase risk of chipmunk predation; ground nesters were less active near risky areas whereas canopy nesters showed no response. We have assumed that red squirrels were the dominant predator of canopy nests based on our video data from ground and shrub nests (Chapter 2). However, canopy nests had a high probability of survival compared to ground and shrub nests and avoiding predation risk by squirrels may be less important for canopy nesters. Instead, canopy nesters that nest and/or forage in conifers (e.g., Bay-breasted Warbler, Golden-crowned Kinglet) may gain additional benefits by selecting habitats preferred by squirrels where nest and foraging sites are more abundant (see below).

The hypothesis that ground and shrub nesters are choosing to settle in habitats where their dominant predator is less abundant, while attractive, is not the only explanation that could explain our result. This difference could represent a discrepancy in habitat preference between birds and squirrels. Alternatively, birds may have been less vocal in habitats where squirrels were abundant or pairs whose nests failed may have stopped singing and/or left the area. Squirrels are strongly associated with conifers, which supply their primary food source of cones, and they are less abundant in aspen dominated stands (Rusch and Reeder 1978). Using the same analyses applied to each nesting guild, we determined that squirrel abundance more than doubled (IRR ± 95% CI: 2.20 ± 1.49 – 3.27) when the proportion of conifer in the canopy (PTREE) increased from the 10th to the 90th percentile. However, we controlled for PTREE in our analyses of nesting guilds to control for the effects of canopy composition on bird abundance. We also established our study plots in mixed wood stands, which support the greatest numbers and diversity of boreal birds (Hobson and Bayne 2000). The proportion of conifer in the canopy was comparable between point count stations (Appendix 4.4), which indicates that conifers were roughly distributed evenly across our plots as individual trees or small patches rather than being clumped in extensive stands. We also found no evidence that detection probability was higher in the absence of squirrels. This is in contrast to Fontaine and Martin (2006a) who found that several bird species increased their singing frequency ~200% during a 1-min sampling window in areas where predators were eradicated. We did not account for the presence of red squirrels beyond our EDR or the presence of other potential nest predators, which could explain why we found no difference in singing frequency.

We are unable to refute the hypothesis that failed breeders may have stopped singing or left the area. Our abundance analyses controlled for sampling date but we did not consider an interaction between sampling date and red squirrel abundance to determine whether counts were more likely to decline with date at stations where squirrel were more prevalent. We performed a post-hoc analysis that added an interaction between squirrel abundance and the quadratic form of sampling date to the top supported predation risk model. Compared to the top supported risk model the interaction model received similar support (ER = 1.03) for ground nesters but received 24 times the support for shrub nesters. The number of shrub nesters recorded at stations where red squirrels were infrequently detected increased by 1.30 (CI: 0.99 – 1.65) between early and late sampling dates whereas abundance declined by 0.83 (0.64 – 1.09) over the same period where squirrels were abundant (10th and 90th percentiles used to represent magnitude of change in sampling date and squirrel abundance). This result is consistent with the hypothesis that failed nesters were no longer present or stopped singing. However, failed breeders typically renest at least once, particularly if they fail early in the nesting cycle whereas successful individuals may have dispersed to safer habitats to raise their broods. For example, Streby and Andersen (2013a, b) found that 58% of Ovenbirds depart their natal territory 24 h post-fledge for habitats that offer a lower risk of predation on dependent young. This may include selecting post-fledge habitats with fewer predators, which would account for the observed increase in abundance at stations where squirrels were less abundant. Shrub nests in our study fledged as early as 8 June and 26% of successful nests fledged before our point count surveys were completed (29 and 30 June in the north and south, respectively). We did not record settlement patterns and therefore we have no metric of habitat preference. Further study is required to determine whether ground and shrub nesting birds are preferentially selecting habitats with lower predation risk or if they are settling in available habitats and dispersing to safer areas to raise their dependent young.

We did not find strong support for an effect of nest concealment for explaining variation in nest fate with the exception of canopy nests that, contrary to prediction, had a lower probability of nest survival when tree density increased. Tree density may not accurately represent concealment at a canopy nest and higher tree densities may have facilitated the movement and subsequent discovery of canopy nests by arboreal predators (e.g., red squirrels and northern flying squirrels [*Glaucomys sabrinus*]). Martin and Joron (2003) also found that cover was ineffective at reducing nest predation by squirrels. In our study, average shrub cover (SHBCOVP ± 95% CI) at ground and shrub nests (18.3 ± 0.8%) was marginally higher than at point count stations (14.9 ± 1.2%), which suggests that nest cover in our study does not reflect an evolutionary 'adaptive peak' (Latif et al. 2012). Rather, cover may be more effective at reducing nest predation by visually-oriented avian predators compared to mammals (Weidinger 2002, Martin and Joron 2003, Eggers et al. 2005, 2006). Foraging mode by red squirrels could also explain the lack of support for the alternate nest site hypothesis. Pelech et al. (2009) found that nest predation by red squirrels was learned but they found no evidence that predation events subsequent to the initial predation were based on area-restricted or microhabitat search patterns. Therefore, swamping predators with an abundance of potential-yet-vacant alternate nests sites may be an ineffective strategy to reduce predation by red squirrels. Predation as a learned behaviour would also explain why we found more support for squirrel presence, rather that squirrel abundance, for explaining variation in nest fate. Faced with such an adept predator, high quality habitats may be best defined as ‘enemy-free space’ (Schmidt 2004).

We did not find support for any of our hypotheses for explaining variation in nest productivity. Our measure of productivity, number of young fledged from successful nests, may be too coarse to respond to the range of habitat qualities in our system. For example, parents may increase their investment in egg and nesting quality in response to differences in habitat quality as opposed to increasing egg or nestling quantity (Fontaine and Martin 2006b, Kaiser and Lindell 2007, Chalfoun and Martin 2007; but see Eggers et al. 2006, Monkkonen et al. 2009). Eggs and nestlings that receive more resources are more likely to survive post-fledge (Perrins 1965, Krementz et al. 1989). Nesting in higher quality habitats with lower predation risk also may have fewer negative physiological consequences for adults, which could increase lifetime productivity (Thomson et al. 2010). Further study into egg and nestling investment and physiological stressors would further refine our definition of quality habitat in the boreal forest.

Land managers and conservationists require efficient yet reliable tools to prioritize habitats for preservation or restoration. Our results demonstrate that abundance accurately captures local variation in reproductive potential for ground and shrub nesters and can serve to identify high quality habitats. We join Perot and Villard (2009) in calling for a reinstatement of abundance estimates in the practitioner’s toolbox. This recommendation comes with the caveat that our results may not apply to systems with a different forest composition, nest predator community, and/or higher levels of fragmentation. For example, less predator-free space may be available to ground and shrub nesting species with a strong conifer association (e.g., Magnolia Warbler). These species may be forced to trade-off predator avoidance with nest site availability and abundance may not reflect reproductive potential (Kristans 2007). The effectiveness of abundance for identifying high quality habitat should be evaluated before being applied in different regions and vegetation types (Rittenhouse et al. 2010, Griesser and Lagerberg 2012).

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Appendix 4.1. Models used to assess variation in the dependent variables nest fate (F), nest productivity (P), and abundance of ground (GND), shrub (SHB), and canopy (CAN) nests and species. Models without a specified substrate were applied to all nesting substrates. Descriptions of variables are provided in the Glossary. Interactions between risk and cover and between risk and alternate nest were generated from the top supported model containing a parameter of interest in the respective subset of models. The combined model set considered all additive permutations of the top supported models from each model subset plus the risk × cover and risk × alternate interactions. In addition to the independent variables of interest all fate and productivity models included SITE, linear and quadratic forms of DAYINIT (standardized to 1 = 16 May), CAM (reference level = no), RSHAVEDATA (ground and shrub nests only), and ALTHAVEDATA (shrub nests only) as nuisance variables. Fate models also included nest stage (INC, NESTL; reference level = lay), and productivity models included MAXCLUTCH. SITE , INC, CAM were excluded from canopy nest models due to limited sample size. All abundance models included SITE, linear and quadratic forms of DAY (standardized to the earliest day of sampling per site: north = 5 June, south = 30 May), WIND, and PTREE as nuisance variables. These nuisance variables were the only independent variables considered in the NULL models.

Model sets	Model	Dependent variables
1. Edge proximity	NULL	F, P, A
	+ MAIN	F, P, A
	+ MAIN2	F, P
	+ MAIN|OPEN	F, P, A
	+ MAIN|OPEN2	F, P
	+ M100	A
	+ MO100	A
	+ 3MAIN	A
	+ SITE × MAIN	F, P, A
	+ SITE × MAIN2	F, P
	+ SITE × MAIN|OPEN	F, P, A
	+ SITE × MAIN|OPEN2	F, P
	+ SITE × M100	A
	+ SITE × MO100	A
	+ SITE × 3MAIN	A
2. Predation risk	NULL	F, P, A
	+ RESQ	F, P, A
	+ RESQ01	F, P, A
	+ SITE × RESQ	F, P, A
	+ SITE × RESQ01	F, P, A
3. Cover	NULL	F, P, A
	+ GNDCOVN	F, P (GND)
	+ GNDCOVP	F, P, A (GND)
	+ SHBCOVN	F, P (GND, SHB)
	+ SHBCOVP	F, P, A (GND, SHB)
	+ TREE	F, P, A (CAN)
	+ CANOPY	F, P, A (CAN)
	+ SITE × GNDCOVN	F, P (GND)
	+ SITE × GNDCOVP	F, P, A (GND)
	+ SITE × SHBCOVN	F, P (GND, SHB)
	+ SITE × SHBCOVP	F, P, A (GND, SHB)

Model sets	Model	Dependent variables
	+ SITE × TREE	F, P, A (CAN)
	+ SITE × CANOPY	F, P, A (CAN)
	+ risk × cover	F, P, A
4. Alternate nest	NULL	F, P (SHB)
	+ ALTNEST	F, P (SHB)
	+ SITE × ALTNEST	F, P (SHB)
	+ risk × alternate	F, P (SHB)
5. Combined models	+ edge + risk + cover + alternate + risk × cover + risk × alternate	F, P, A (alternate for SHB only)

Appendix 4.2. Demonstration on how to incorporate records with missing data into your analyses using an indicator variable HAVEDATA and an interaction between HAVEDATA and the variable of interest.

The simulated dataset has 1000 records. The dependent variable *y* and the independent variable *z* each have 1000 observations. The dependent variable *x* has 750 observations. I demonstrate how an indicator and an interaction term can be used to incorporate the missing data without affecting the value of the coefficients.

An Ordinary Least Squares regression model is run to predict *y* as a function of *x*. Note, the number of observations is 750.

```
. regress y x

      Source |       SS       df       MS              Number of obs =     750
-------------+------------------------------           F(  1,   748) =    0.16
       Model |  1.46734754     1  1.46734754           Prob > F      =  0.6897
    Residual |   6880.4137   748  9.19841404           R-squared     =  0.0002
-------------+------------------------------           Adj R-squared = -0.0011
       Total |  6881.88105   749  9.18809219           Root MSE      =  3.0329

------------------------------------------------------------------------------
           y |      Coef.   Std. Err.      t    P>|t|     [95% Conf. Interval]
-------------+----------------------------------------------------------------
           x |  -.0087868       .022    -0.40   0.690    -.0519758    .0344022
       _cons |   .0277497   .1188559     0.23   0.815    -.2055813    .2610806
------------------------------------------------------------------------------
```

Now I predict y as a function of z (1000 observations)

```
. regress y z

      Source |       SS       df       MS              Number of obs =    1000
-------------+------------------------------           F(  1,   998) =    1.47
       Model |  13.4392129     1  13.4392129           Prob > F      =  0.2255
    Residual |  9118.08313   998  9.13635584           R-squared     =  0.0015
-------------+------------------------------           Adj R-squared =  0.0005
       Total |  9131.52234   999    9.140663           Root MSE      =  3.0226

------------------------------------------------------------------------------
           y |      Coef.   Std. Err.      t    P>|t|     [95% Conf. Interval]
-------------+----------------------------------------------------------------
           z |   -.065619    .054104    -1.21   0.225    -.1717896    .0405516
       _cons |   .2231531   .1903737     1.17   0.241    -.1504255    .5967318
------------------------------------------------------------------------------
```

Now predict y as a function of x + z. The program automatically drops the 250 records with missing observations. (I generated predicted values *a* to compare to a second model output below.)

```
. regress y x z

      Source |       SS       df       MS              Number of obs =     750
-------------+------------------------------           F(  2,   747) =    1.14
       Model |   20.992387     2  10.4961935           Prob > F      =  0.3195
    Residual |  6860.88866   747  9.18458991           R-squared     =  0.0031
-------------+------------------------------           Adj R-squared =  0.0004
       Total |  6881.88105   749  9.18809219           Root MSE      =  3.0306

------------------------------------------------------------------------------
           y |      Coef.   Std. Err.      t    P>|t|     [95% Conf. Interval]
-------------+----------------------------------------------------------------
           x |  -.0095268   .0219893    -0.43   0.665    -.0526949    .0336413
           z |  -.0908488   .0623093    -1.46   0.145     -.213171    .0314734
       _cons |   .3075618   .2256888     1.36   0.173     -.135498    .7506216
------------------------------------------------------------------------------

. predict a
(option xb assumed; fitted values)
(250 missing values generated)
```

To be able to consider the effects of *x* and *z* on *y* in a model selection framework the sample size must be equal across all models. One solution is to drop the *z* records with corresponding missing values of *x*.

```
. regress y z if x!=.

      Source |       SS       df       MS              Number of obs =    1000
-------------+------------------------------           F(  1,   998) =    2.11
       Model |  19.3045884     1  19.3045884           Prob > F      =  0.1462
    Residual |  9112.21775   998  9.13047871           R-squared     =  0.0021
-------------+------------------------------           Adj R-squared =  0.0011
       Total |  9131.52234   999    9.140663           Root MSE      =  3.0217

------------------------------------------------------------------------------
           y |      Coef.   Std. Err.      t    P>|t|     [95% Conf. Interval]
-------------+----------------------------------------------------------------
           z |  -.0903088   .0621079    -1.45   0.146    -.2121858    .0315682
       _cons |   .2997067     .21265     1.41   0.159    -.1175857     .716999
------------------------------------------------------------------------------
```

However, the coefficient for *z* has changed compared to *regress y z*.

An alternate solution is to replace the missing values with the mean value of *x*. This is a simple solution that will have little effect on your coefficients if only a few records are missing or your data are normally distributed, which these simulated data are. However, any deviation from normality will affect your coefficient estimates.

A third solution is to create a dummy variable *HAVEDATA* and an interaction term *INTERACT*.

```
. gen havedata=1 if x!=.
(250 missing values generated)

. replace havedata=0 if x==.
(250 real changes made)

. gen interact=havedata*x
(250 missing values generated)

. replace interact=0 if x==.
(250 real changes made)
```

For the purpose of this demonstration I replaced the values of *z* with their mean value for those records that have corresponding values of *x* that are missing. I did this for demonstration purposes only to control for the effect of 'new information' on *x* when these previously excluded data are incorporated into the model.

```
. summarize z

    Variable |       Obs        Mean    Std. Dev.       Min        Max
-------------+--------------------------------------------------------
           z |      1000       3.043    1.767562          0         11

. replace z=r(mean) if x==.
z was byte now float
(250 real changes made)
```

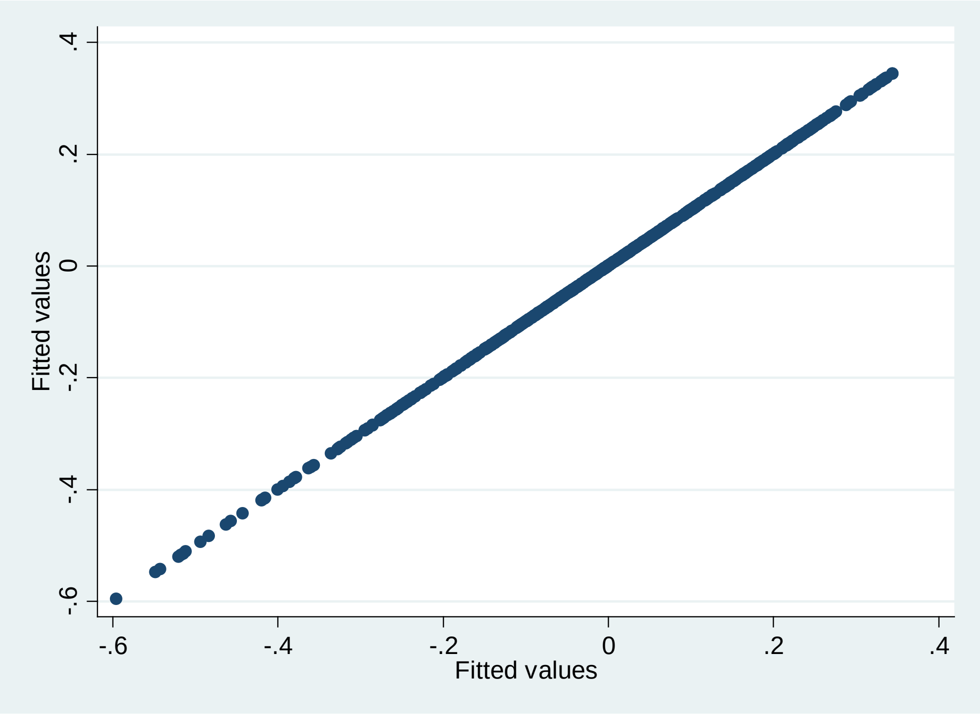
Now rerun the regression with *HAVEDATA* and *INTERACT* in place of *x*.

```
. regress y  havedata interact z

      Source |       SS       df       MS              Number of obs =    1000
-------------+------------------------------           F(  3,   996) =    0.78
       Model |  21.4962944     3  7.16543145           Prob > F      =  0.5033
    Residual |  9110.02604   996  9.14661249           R-squared     =  0.0024
-------------+------------------------------           Adj R-squared = -0.0007
       Total |  9131.52234   999    9.140663           Root MSE      =  3.0243

------------------------------------------------------------------------------
           y |      Coef.   Std. Err.      t    P>|t|     [95% Conf. Interval]
-------------+----------------------------------------------------------------
    havedata |  -.0312465   .2250309    -0.14   0.890    -.4728356    .4103426
    interact |  -.0095268   .0219438    -0.43   0.664    -.0525881    .0335345
           z |  -.0908488   .0621804    -1.46   0.144    -.2128684    .0311708
       _cons |   .3388083   .2690515     1.26   0.208    -.1891646    .8667812
------------------------------------------------------------------------------

. predict b
(option xb assumed; fitted values)
```

Compare the results of this model to *regress y x z*. The values for *INTERACT* and *x* are the same as are the values for *z*. The constant in the previous model is the combination of the constant in the current model and the coefficient for HAVEDATA (0.3388083 – 0.0312465 = 0.3075618).

A scatter plot of the predicted values from each model coincide.

```
. scatter a b
```



Appendix 4.3. Numbers of nests, average day of nest initiation (standardized to 1 = 16 May; ± 1 SD), and average maximum clutch size by nesting substrate and species that were included in analyses of nest fate analyses.

Code	Common name	Species name	Nest substrate	Nests (n)	Day initiation	Maximum clutch
CAN	**Canopy nester**		**Canopy**	**40**	**27.6 ± 7.1**	**4.33 ± 0.47**
GND	**Ground nester**		**Ground**	**167**	**19.5 ± 9.4**	**5.72 ± 0.48**
SHB	**Shrub nester**		**Shrub**	**364**	**25.4 ± 8.8**	**5.01 ± 0.39**
ALFL	Alder Flycatcher	*Empidonax alnorum*	Shrub	3	34.0 ± 3.0	4
AMRE	American Redstart	*Setophaga ruticilla*	Shrub	9	29.2 ± 3.1	5
AMRO	American Robin	*Turdus migratorius*	Shrub [a]	22	17.6 ± 13.6	4
BAWW	Black-and-white Warbler	*Mniotilta varia*	Ground	6	16.0 ± 3.6	5
BHVI	Blue-headed Vireo	*Vireo solitarius*	Canopy	2	16.0 ± 4.2	5
CEDW	Cedar Waxwing	*Bombycilla cedrorum*	Canopy	2	46.0 ± 1.4	4
CHSP	Chipping Sparrow	*Spizella passerina*	Shrub	101	24.2 ± 9.5	5
CONW	Connecticut Warbler	*Oporornis agilis*	Ground	1	31.0	5
DEJU	Dark-eyed Junco	*Junco hyemalis*	Ground	25	15.9 ± 13.7	6
HETH	Hermit Thrush	*Catharus guttatus*	Ground	15	18.2 ± 15.9	5
LEFL	Least Flycatcher	*Empidonax minimus*	Canopy	25	27.6 ± 4.7	4
LISP	Lincoln Sparrow	*Melospiza lincolnii*	Ground	3	20.0 ± 4.4	5
MAWA	Magnolia Warbler	*Setophaga magnolia*	Shrub	11	26.2 ± 9.6	5
NOWA	Northern Waterthrush	*Parkesia noveboracensis*	Shrub	2	20.0 ± 4.2	4
OVEN	Ovenbird	*Seiurus aurocapilla*	Ground	29	22.1 ± 8.1	6
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	Canopy	8	26.4 ± 6.8	5
REVI	Red-eyed Vireo	*Vireo olivaceus*	Shrub	10	28.6 ± 5.4	5
SWTH	Swainson's Thrush	*Catharus ustulatus*	Shrub	178	27.0 ± 7.0	5
TEWA	Tennessee Warbler	*Oreothlypis peregrina*	Ground	68	19.2 ± 4.1	6
WAVI	Warbling Vireo	*Vireo gilvus*	Canopy	1	27.0	5
WETA	Western Tanager	*Piranga ludoviciana*	Canopy	2	26.0 ± 12.7	5
WTSP	White-throated Sparrow	*Zonotrichia albicollis*	Ground	18	24.4 ± 10.3	5
YRWA	Yellow-rumped Warbler	*Setophaga coronata*	Shrub	30	21.0 ± 10.3	6
Total				**571**	**23.8 ± 9.3**	**5.17 ± 0.58**

[a] Includes two ground nests.

Appendix 4.4. Numbers of nests, numbers of nests with cameras, numbers of successful nests, average (± 1 SD) numbers of young fledged from successful nests, average edge proximity (MAIN), average predation risk (RESQ), average cover, and average numbers of alternate nest sites (ALTNEST) by nesting substrate and species in Fort Simpson, NT (North) and Chinchaga, AB (South).

	North								South							
Species Code	Nests (n)	Camera nests (n)	Fledged nests (n)^a	No. fledge	MAIN	RESQ	COVER^c	ALTNEST	Nests (n)	Camera nests (n)	Fledged nests (n)^b	No. fledged	MAIN	RESQ	COVER^c	ALTNEST
CAN	**30**	**2**	**24**	**2.9 ± 0.7**	**219.5 ± 162.6**	**0.35 ± 0.51**	**0.51 ± 0.21**	-	**10**	**1**	**7**	**3.6 ± 0.8**	**81.0 ± 104.3**	**3.06 ± 4.82**	**0.35 ± 0.33**	-
GND	**92**	**22**	**57**	**4.1 ± 1.0**	**193.1 ± 158.1**	**0.36 ± 0.67**	**14.9 ± 7.0**	-	**75**	**29**	**55**	**4.4 ± 1.1**	**100.0 ± 127.9**	**2.12 ± 4.71**	11.2 ± 5.7	-
SHB	**212**	**45**	**126**	**3.4 ± 0.9**	**197.3 ± 156.5**	**0.37 ± 0.73**	**22.5 ± 9.1**	**4.7 ± 10.7**	**152**	**53**	**83**	**3.6 ± 0.8**	**127.0 ± 162.1**	**2.02 ± 3.07**	18.1 ± 7.5	**18.4 ± 24.6**
ALFL	3	0	1	4.0	20.0 ± 34.6	0.00 ± 0.00	34.0 ± 7.1	-	0	-	-	-	-	-	-	-
AMRE	7	3	5	3.2 ± 1.3	201.0 ± 186.5	0.49 ± 0.84	24.7 ± 6.2	13.0 ± 29.4	2	1	2	4.5 ± 0.7	35.7 ± 30.7	0.44 ± 0.44	15.3 ± 0.3	41.5 ± 36.1
AMRO	11	2	8	2.6 ± 1.0	67.4 ± 72.1	0.06 ± 0.07	16.5 ± 7.1	7.3 ± 6.9	11	2	4	2.5 ± 1.0	91.2 ± 110.5	0.49 ± 0.6	18.7 ± 6.8	6.1 ± 4.9
BAWW	5	1	3	4.0 ± 1.7	317.4 ± 166.7	0.56 ± 0.74	19.4 ± 4.6	-	1	0	0	0.0	2.5	0.5	12.7	-
BHVI	0	-	-	-	-	-	-	-	2	0	2	4.0 ± 0.0	62.2 ± 19.5	10.08 ± 1.03	0.24 ± 0.01	-
CEDW	0	-	-	-	-	-	-	-	2	0	1	4.0	194.1 ± 251.8	0.16 ± 0.22	0.09 ± 0.12	-
CHSP	15	1	10	3.4 ± 0.8	46.4 ± 120.2	0.33 ± 0.58	18.6 ± 6.4	18.0 ± 27.9	86	24	44	3.7 ± 0.8	114.8 ± 167.1	1.93 ± 2.72	17.7 ± 6.7	20.1 ± 24.8
CONW	0	-	-	-	-	-	-	-	1	0	1	4.0	30.6	-	11.5	-
DEJU	7	0	5	3.6 ± 1.1	92.0 ± 160.6	0.45 ± 0.38	14.0 ± 5.2	-	18	7	13	3.9 ± 1.2	91.8 ± 136.2	1.85 ± 2.08	10.0 ± 5.9	-
HETH	14	10	7	3.6 ± 0.8	221.3 ± 143.2	0.75 ± 1.37	11.8 ± 8.0	-	1	0	1	4.0	104.0	1.99	8.8	-
LEFL	22	2	20	3.0 ± 0.7	213.6 ± 149.9	0.17 ± 0.25	0.52 ± 0.18	-	3	1	3	3.0 ± 1.0	52.2 ± 20.1	0.7	0.25 ± 0.03	-
LISP	0	-	-	-	-	-	-	-	3	0	3	3.7 ± 1.5	22.4 ± 19.5	0.32 ± 0.55	14.4 ± 6.4	-
MAWA	10	1	5	3.4 ± 0.6	290.9 ± 126.6	0.25 ± 0.27	25.3 ± 8.0	6.5 ± 8.1	1	1	1	3.0	102.2	3.43	15.8	-

	North								South							
Species Code	Nests (n)	Camera nests (n)	Fledged nests (n)[a]	No. fledge	MAIN	RESQ	COVER[c]	ALTNEST	Nests (n)	Camera nests (n)	Fledged nests (n)[b]	No. fledged	MAIN	RESQ	COVER[c]	ALTNEST
NOWA	2	1	1	4.0	86.2 ± 11.8	0.08 ± 0.11	15.1 ± 0.4	-	0	-	-	-	-	-	-	-
OVEN	13	1	10	4.6 ± 0.7	200.5 ± 131.2	0.38 ± 0.45	15.3 ± 6.2	-	16	12	14	4.6 ± 0.7	143.4 ± 150.2	3.54 ± 8.76	10.4 ± 5.8	-
RBGR	5	0	1	4.0	194.9 ± 180.4	1.14 ± 0.71	0.62 ± 0.30	-	3	0	1	4.0	47 ± 22.6	0.12 ± 0.16	0.70 ± 0.46	-
REVI	8	0	6	3.6 ± 1.1	203.4 ± 159.6	0.56 ± 0.92	23.4 ± 7.7	11.2 ± 6.0	2	0	2	3.5 ± 0.7	212.1 ± 51.3	3.09 ± 3.13	16.8 ± 0.4	23.0 ± 26.9
SWTH	135	38	77	3.3 ± 0.8	218.9 ± 148.6	0.43 ± 0.82	22.5 ± 9.6	2.9 ± 4.9	43	24	26	3.5 ± 0.7	157 ± 161	2.75 ± 4.04	17.6 ± 7.2	12.8 ± 18.3
TEWA	43	7	23	4.5 ± 0.7	199.6 ± 161.9	0.23 ± 0.38	15.2 ± 6.9	-	25	8	18	5.1 ± 1.1	113.8 ± 122.7	2.23 ± 3.22	10.6 ± 5.1	-
WAVI	1	0	1	2.0	484.1	0.00	0.49	-	0	-	-	-	-	-	-	-
WETA	2	0	2	3.0	213.4 ± 301.9	0.49 ± 0.27	0.19 ± 0.00	-	0	-	-	-	-	-	-	-
WTSP	8	2	7	3.6 ± 1.3	154.5 ± 165.0	0.22 ± 0.35	16.9 ± 8.7	-	10	2	5	3.8 ± 0.5	50.2 ± 106.7	0.74 ± 0.61	15.2 ± 6.1	-
YRWA	23	0	15	4.1 ± 1.0	202.7 ± 177.5	0.21 ± 0.41	23.3 ± 9.5	2.3 ± 3.1	7	1	4	4.3 ± 0.5	154.1 ± 214.1	0.69 ± 0.71	26.4 ± 15.2	37.3 ± 47.4
Total	**334**	**69**	**207**[a]	**3.6 ± 1.0**	**198.1 ± 157.1**	**0.37 ± 0.69**	**20.5 ± 9.4**	**4.7 ± 10.7**	**237**	**83**	**145**[b]	**3.9 ± 1.0**	**116.5 ± 150.2**	**2.08 ± 3.71**	**16.1 ± 7.9**	**18.4 ± 24.6**

[a] Four successful nests (2 CAN, 2 SHB; AMRO, RBGR, REVI, WETA) fledged an unknown number of young.

[b] One successful nest (SHB; SWTH) fledged an unknown number of young.

[c] Canopy nest cover = canopy tree density (m^{-2}; TREE). Shrub, ground, and total nest cover = average concealment between 0 - 3 m above ground within 7 m of nest (%; SHBCOVP)

Appendix 4.5. Average (± 1 SD) numbers of individuals by nesting substrate and species recorded per survey at 0 m, 200 m, and 400 m from the MAIN plot edge in Fort Simpson, NT (North), and Chinchaga, AB (South). Data represent 72 surveys (18 stations) per distance category in the north and 86 surveys at 0 m (28 stations) and 84 surveys at 200 and 400 m (27 stations per distance category) in the south. Average values of each independent variable included in the analyses of abundance analysis along with their description are provided below.

Dependent variables				North				South			
Code	Common name	Species name	Nest substrate	Total	0	200	400	Total	0	200	400
TOT [a]	**Total songbirds**			**1685**	**8.61 ± 4.62**	**7.25 ± 3.92**	**7.54 ± 4.01**	**1481**	**6.37 ± 2.66**	**5.54 ± 2.48**	**5.57 ± 2.49**
GND	**Ground nester**		**Ground**	**565**	**2.76 ± 1.76**	**2.65 ± 1.79**	**2.43 ± 1.55**	**524**	**2.49 ± 1.82**	**1.90 ± 1.35**	**1.79 ± 1.45**
SHB	**Shrub nester**		**Shrub**	**802**	**4.01 ± 2.78**	**3.69 ± 2.86**	**3.43 ± 2.62**	**662**	**2.69 ± 1.47**	**2.50 ± 1.49**	**2.63 ± 1.57**
CAN [a]	**Canopy nester**		**Canopy**	**256**	**1.50 ± 1.81**	**0.61 ± 0.83**	**1.44 ± 1.71**	**193**	**0.77 ± 0.98**	**0.73 ± 0.78**	**0.79 ± 0.84**
CAV	**Cavity nester**		**Cavity**	**62**	**0.33 ± 0.71**	**0.29 ± 0.62**	**0.24 ± 0.66**	**102**	**0.43 ± 0.76**	**0.40 ± 0.75**	**0.37 ± 0.65**
ALFL	Alder Flycatcher	*Empidonax alnorum*	Shrub	1	0.01 ± 0.12	0.00 ± 0.00	0.00 ± 0.00	2	0.02 ± 0.15	0.00 ± 0.00	0.00 ± 0.00
AMRE	American Redstart	*Setophaga ruticilla*	Shrub	30	0.06 ± 0.23	0.26 ± 0.71	0.10 ± 0.30	4	0.02 ± 0.22	0.01 ± 0.11	0.01 ± 0.11
AMRO	American Robin	*Turdus migratorius*	Shrub	25	0.28 ± 0.72	0.04 ± 0.20	0.03 ± 0.17	19	0.14 ± 0.38	0.06 ± 0.24	0.02 ± 0.15
ATTW	American Three-toed Woodpecker	*Picoides dorsalis*	Cavity	0				1	0.00 ± 0.00	0.01 ± 0.11	0.00 ± 0.00
BAWW	Black-and-white Warbler	*Mniotilta varia*	Ground	64	0.44 ± 0.63	0.28 ± 0.59	0.17 ± 0.50	5	0.03 ± 0.18	0.02 ± 0.15	0.00 ± 0.00
BBWA	Bay-breasted Warbler	*Setophaga castanea*	Shrub	24	0.08 ± 0.33	0.18 ± 0.59	0.07 ± 0.31	16	0.01 ± 0.11	0.08 ± 0.28	0.10 ± 0.30
BCCH	Black-capped Chickadee	*Poecile atricapillus*	Cavity	0				16	0.08 ± 0.38	0.11 ± 0.52	0.00 ± 0.00
BHVI	Blue-headed Vireo	*Vireo solitarius*	Shrub	6	0.04 ± 0.20	0.03 ± 0.17	0.01 ± 0.12	23	0.07 ± 0.30	0.10 ± 0.30	0.11 ± 0.35
BOCH	Boreal Chickadee	*Poecile hudsonicus*	Cavity	3	0.00 ± 0.00	0.01 ± 0.12	0.03 ± 0.24	20	0.03 ± 0.18	0.06 ± 0.24	0.14 ± 0.35
BOWA	Bohemian Waxwing	*Bombycilla garrulus*	Canopy	1	0.00 ± 0.00	0.01 ± 0.12	0.00 ± 0.00	0			
BRCR	Brown Creeper	*Certhia americana*	Cavity	0				9	0.02 ± 0.15	0.02 ± 0.15	0.06 ± 0.28
BTGN	Black-throated Green Warbler	*Polioptila melanura*	Shrub	0				39	0.17 ± 0.41	0.14 ± 0.35	0.14 ± 0.35
CAWA	Canada Warbler	*Cardellina canadensis*	Ground	0				3	0.01 ± 0.11	0.00 ± 0.00	0.02 ± 0.15

Dependent variables				North				South			
Code	Common name	Species name	Nest substrate	Total	0	200	400	Total	0	200	400
CCSP	Clay-colored Sparrow	*Spizella pallida*	Ground	3	0.03 ± 0.17	0.01 ± 0.12	0.00 ± 0.00	0			
CEDW	Cedar Waxwing	*Bombycilla cedrorum*	Canopy	1	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.12	7	0.01 ± 0.11	0.04 ± 0.19	0.04 ± 0.19
CHSP	Chipping Sparrow	*Spizella passerina*	Shrub	59	0.44 ± 0.79	0.25 ± 0.50	0.13 ± 0.33	128	0.81 ± 0.74	0.33 ± 0.57	0.36 ± 0.57
CMWA	Cape May Warbler	*Setophaga tigrina*	Canopy	0				4	0.00 ± 0.00	0.02 ± 0.15	0.02 ± 0.15
CONW	Connecticut Warbler	*Oporornis agilis*	Ground	0				10	0.07 ± 0.37	0.05 ± 0.21	0.00 ± 0.00
COYE	Common Yellowthroat	*Geothlypis trichas*	Ground	0				1	0.01 ± 0.11	0.00 ± 0.00	0.00 ± 0.00
DEJU	Dark-eyed Junco	*Junco hyemalis*	Ground	10	0.08 ± 0.33	0.00 ± 0.00	0.06 ± 0.23	72	0.27 ± 0.45	0.25 ± 0.56	0.33 ± 0.55
EAPH	Eastern Phoebe	*Sayornis phoebe*	Cavity	1	0.00 ± 0.00	0.01 ± 0.12	0.00 ± 0.00	0			
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	Canopy	0				49	0.13 ± 0.37	0.20 ± 0.43	0.25 ± 0.46
GRAJ	Gray Jay	*Perisoreus canadensis*	Shrub	22	0.18 ± 0.61	0.06 ± 0.23	0.07 ± 0.48	54	0.29 ± 0.68	0.19 ± 0.42	0.15 ± 0.53
HAWO	Hairy Woodpecker	*Picoides villosus*	Cavity	1	0.01 ± 0.12	0.00 ± 0.00	0.00 ± 0.00	0			
HETH	Hermit Thrush	*Catharus guttatus*	Ground	20	0.11 ± 0.43	0.10 ± 0.42	0.07 ± 0.48	8	0.00 ± 0.00	0.04 ± 0.19	0.06 ± 0.24
LEFL	Least Flycatcher	*Empidonax minimus*	Canopy	106	0.58 ± 1.37	0.14 ± 0.39	0.75 ± 1.38	11	0.05 ± 0.21	0.05 ± 0.21	0.04 ± 0.19
LISP	Lincoln's Sparrow	*Melospiza lincolnii*	Ground	3	0.04 ± 0.26	0.00 ± 0.00	0.00 ± 0.00	24	0.26 ± 0.51	0.00 ± 0.00	0.02 ± 0.15
MAWA	Magnolia Warbler	*Setophaga magnolia*	Shrub	81	0.24 ± 0.52	0.42 ± 1.03	0.47 ± 1.01	5	0.01 ± 0.11	0.01 ± 0.11	0.04 ± 0.19
MOWA	Mourning Warbler	*Geothlypis philadelphia*	Ground	0				1	0.01 ± 0.11	0.00 ± 0.00	0.00 ± 0.00
NOFL	Northern Flicker	*Colaptes auratus*	Cavity	3	0.03 ± 0.17	0.00 ± 0.00	0.01 ± 0.12	3	0.02 ± 0.15	0.00 ± 0.00	0.01 ± 0.11
NOWA	Northern Waterthrush	*Parkesia noveboracensis*	Shrub	24	0.06 ± 0.29	0.03 ± 0.17	0.25 ± 0.69	1	0.00 ± 0.00	0.01 ± 0.11	0.00 ± 0.00
OVEN	Ovenbird	*Seiurus aurocapilla*	Ground	206	0.51 ± 0.84	1.25 ± 1.02	1.10 ± 1.02	189	0.64 ± 0.68	0.95 ± 0.92	0.64 ± 0.85
PHVI	Philadelphia Vireo	*Vireo philadelphicus*	Canopy	0				10	0.08 ± 0.28	0.04 ± 0.19	0.00 ± 0.00
PISI	Pine Siskin	*Spinus pinus*	Canopy	2	0.01 ± 0.12	0.01 ± 0.12	0.00 ± 0.00	6	0.02 ± 0.15	0.02 ± 0.15	0.02 ± 0.15
PUFI	Purple Finch	*Carpodacus purpureus*	Canopy	1	0.01 ± 0.12	0.00 ± 0.00	0.00 ± 0.00	0			
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	Canopy	34	0.24 ± 0.54	0.13 ± 0.37	0.11 ± 0.32	18	0.12 ± 0.32	0.05 ± 0.21	0.05 ± 0.21

Dependent variables				North				South			
Code	Common name	Species name	Nest substrate	Total	0	200	400	Total	0	200	400
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	Cavity	1	0.00 ± 0.00	0.01 ± 0.12	0.00 ± 0.00	23	0.08 ± 0.31	0.07 ± 0.26	0.12 ± 0.36
RCKI	Ruby-crowned Kinglet	*Regulus calendula*	Canopy	27	0.13 ± 0.37	0.10 ± 0.38	0.15 ± 0.43	35	0.12 ± 0.32	0.10 ± 0.33	0.20 ± 0.49
REVI	Red-eyed Vireo	*Vireo olivaceus*	Shrub	148	0.53 ± 0.75	0.68 ± 0.84	0.85 ± 0.97	26	0.13 ± 0.34	0.10 ± 0.30	0.08 ± 0.32
SWTH	Swainson's Thrush	*Catharus ustulatus*	Shrub	285	1.63 ± 1.68	1.22 ± 1.55	1.11 ± 1.33	176	0.64 ± 0.77	0.63 ± 0.65	0.81 ± 0.83
TEWA	Tennesee Warbler	*Oreothlypis peregrina*	Ground	234	1.28 ± 1.20	1.00 ± 0.99	0.97 ± 0.95	159	0.86 ± 0.92	0.46 ± 0.61	0.55 ± 0.78
THSP	Unknown thrush	Catharus spp.	Shrub	1	0.01 ± 0.12	0.00 ± 0.00	0.00 ± 0.00	0			
VATH	Varied Thrush	*Ixoreus naevius*	Shrub	7	0.01 ± 0.12	0.00 ± 0.00	0.08 ± 0.44	0			
WAVI	Warbling Vireo	*Vireo gilvus*	Canopy	21	0.17 ± 0.41	0.01 ± 0.12	0.11 ± 0.36	20	0.14 ± 0.35	0.07 ± 0.26	0.02 ± 0.15
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*	Ground	1	0.01 ± 0.12	0.00 ± 0.00	0.00 ± 0.00	0			
WETA	Western Tanager	*Piranga ludoviciana*	Canopy	31	0.14 ± 0.42	0.10 ± 0.34	0.19 ± 0.43	15	0.02 ± 0.15	0.10 ± 0.30	0.06 ± 0.24
WIWA	Wilson's Warbler	*Cardellina pusilla*	Ground	1	0.01 ± 0.12	0.00 ± 0.00	0.00 ± 0.00	0			
WIWR	Winter Wren	*Troglodytes hiemalis*	Ground	0				8	0.00 ± 0.00	0.04 ± 0.19	0.06 ± 0.24
WOSP	Unknown woodpecker	*Spizella wortheni*	Cavity	12	0.08 ± 0.28	0.06 ± 0.23	0.03 ± 0.17	0			
WTSP	White-throated Sparrow	*Zonotrichia albicollis*	Ground	23	0.24 ± 0.52	0.01 ± 0.12	0.07 ± 0.26	40	0.33 ± 0.58	0.07 ± 0.26	0.07 ± 0.26
WWCR [a]	White-winged Crossbill	*Loxia leucoptera*	Canopy	30	0.19 ± 0.40	0.11 ± 0.32	0.11 ± 0.32	18	0.08 ± 0.28	0.05 ± 0.21	0.08 ± 0.28
WWPE	Western Wood-Pewee	Picoides spp.	Canopy	2	0.03 ± 0.17	0.00 ± 0.00	0.00 ± 0.00	0			
YBFL	Yellow-bellied Flycatcher	*Empidonax flaviventris*	Ground	0				4	0.00 ± 0.00	0.02 ± 0.15	0.02 ± 0.15
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*	Cavity	41	0.21 ± 0.58	0.19 ± 0.52	0.17 ± 0.53	30	0.19 ± 0.42	0.13 ± 0.40	0.04 ± 0.19
YRWA	Yellow-rumped Warbler	*Setophaga coronata*	Shrub	111	0.63 ± 0.86	0.58 ± 0.75	0.33 ± 0.71	222	0.65 ± 0.75	1.02 ± 0.85	0.95 ± 0.79
YWAR	Yellow Warbler	*Setophaga petechia*	Shrub	0				1	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.11
Independent variables											
DAY	Day of survey standardized to earliest survey day per site.				10.92 ± 7.64	10.92 ± 7.64	10.9 ± 7.6		13.8 ± 10.0	13.8 ± 10.1	13.8 ± 10.1
WIND	Beaufort ordinal wind value (0 - ≥5).				1.68 ± 1.69	1.64 ± 1.56	1.53 ± 1.56		0.36 ± 0.59	0.45 ± 0.68	0.45 ± 0.75

Dependent variables				North				South			
Code	Common name	Species name	Nest substrate	Total	0	200	400	Total	0	200	400
PTREE	Proportion of coniferous canopy trees within 11.3 m of station.				0.19 ± 0.17	0.24 ± 0.19	0.25 ± 0.23		0.21 ± 0.23	0.28 ± 0.24	0.42 ± 0.30
RESQ	Maximum number of red squirrels per station per year.				0.33 ± 0.68	0.33 ± 0.53	0.53 ± 0.70		1.19 ± 0.96	1.17 ± 0.99	1.60 ± 1.27
GNDCOVP	Percent ground cover (0 - 0.5 m above ground) within 5 m of station.				37.1 ± 12.2	28.0 ± 11.2	28.5 ± 9.1		24.0 ± 10.2	21.1 ± 7.7	19.3 ± 7.8
SHBCOVP	Percent shrub cover (0 - 3 m above ground) within 5 m of station.				19.3 ± 7.6	16.7 ± 7.2	19.1 ± 6.8		14.3 ± 7.2	12.5 ± 4.4	11.0 ± 5.0
TREE	Canopy tree density (-m^2) within 11.3 m of station.				0.39 ± 0.15	0.55 ± 0.35	0.47 ± 0.20		0.24 ± 0.18	0.16 ± 0.07	0.19 ± 0.09
CANOPY	Categorical canopy closure (1 – 4 in 25% increments).				1.00 ± 0.00	1.44 ± 0.62	1.50 ± 0.62		1.11 ± 0.31	1.59 ± 0.64	1.41 ± 0.57

[a] WWCR were frequently recorded in large flocks and are included here as occurrence.

[b] Day 1 = 29 May in Southern site and 4 June in Northern site.

Appendix 4.6. Candidate set of models used to explain variation in daily nest survival rate of ground, shrub, and canopy nests. Independent variables are described in the Glossary. *k* is the number of model parameters. w_i is the Akaike weight of model *i*.

A. Ground nests (n = 167 nests)

Models	Log likelihood	k	AIC_c	ΔAIC_c	w_i
+ MAIN + RESQ01	-191.12	10	402.339	0.00	0.15
+ MAIN	-192.61	9	403.31	0.97	0.09
+ RESQ01	-192.78	9	403.64	1.30	0.08
+ MAIN|OPEN	-192.78	9	403.65	1.31	0.08
+ MAIN + RESQ01 + GNDCOVP	-190.84	11	403.8	1.46	0.07
NULL [a]	-194.01	8	404.08	1.74	0.06
+ MAIN + GNDCOVP	-192.23	10	404.565	2.23	0.05
+ SITE × MAIN|OPEN	-192.42	10	404.95	2.61	0.04
+ SITE × MAIN|OPEN^2	-190.51	12	405.15	2.81	0.04
+ RESQ01 + GNDCOVP	-192.53	10	405.162	2.82	0.04
+ SITE × MAIN	-192.54	10	405.17	2.83	0.04
+ MAIN|OPEN^2	-192.57	10	405.25	2.91	0.03
+ GNDCOVP	-193.60	9	405.28	2.94	0.03
+ MAIN^2	-192.59	10	405.29	2.95	0.03
+ RESQ	-193.86	9	405.80	3.46	0.03
+ SHBCOVP	-193.97	9	406.01	3.68	0.02
+ GNDCOVN	-193.97	9	406.03	3.69	0.02
+ SHBCOVN	-193.99	9	406.07	3.73	0.02
+ MAIN + RESQ × GNDCOVP	-190.17	13	406.496	4.16	0.02
+ RESQ × GNDCOVP	-191.47	12	407.083	4.74	0.01
+ SITE × RESQ01	-192.50	11	407.12	4.78	0.01
+ SITE × GNDCOVP	-193.57	10	407.25	4.91	0.01
+ SITE × MAIN^2	-191.86	12	407.87	5.53	0.01
+ SITE × SHBCOVN	-193.93	10	407.95	5.61	0.01
+ SITE × SHBCOVP	-193.97	10	408.03	5.69	0.01
+ SITE × GNDCOVN	-193.97	10	408.04	5.70	0.01
+ SITE × RESQ	-193.63	11	409.38	7.05	0.00

[a] SITE + DAYINIT + DAYINIT^2 + INC + NESTL + CAM + RSHAVEDATA

B. Shrub nests (n = 364 nests)

Models	Log likelihood	*k*	AIC_c	ΔAIC_c	w_i
+ RESQ01	-496.82	10	1013.67	0.00	0.12
+ SITE × RESQ01	-495.21	12	1014.49	0.82	0.08
+ RESQ01 + SITE × SHBCOVP	-495.30	12	1014.66	0.99	0.07
NULL	-498.37	9	1014.78	1.11	0.07
+ SITE × RESQ	-495.67	12	1015.40	1.73	0.05
+ MAIN + RESQ01	-496.70	11	1015.45	1.78	0.05
+ RESQ01 + ALTNEST	-496.72	11	1015.49	1.82	0.05
+ SITE × SHBCOVP	-497.02	11	1016.08	2.41	0.04
+ MAIN + RESQ01 + SITE × SHBCOVP	-495.10	13	1016.26	2.59	0.03
+ SHBCOVP	-498.14	10	1016.32	2.65	0.03
+ MAIN	-498.21	10	1016.45	2.78	0.03
+ SITE × MAIN	-497.22	11	1016.50	2.83	0.03
+ SHBCOVN	-498.24	10	1016.51	2.84	0.03
+ MAIN|OPEN	-498.24	10	1016.52	2.85	0.03
+ ALTNEST	-498.29	10	1016.63	2.96	0.03
+ SITE × ALTNEST	-498.29	10	1016.63	2.96	0.03
+ RESQ01 + SITE × SHBCOVP + ALTNEST	-495.29	13	1016.65	2.98	0.03
+ RESQ	-498.37	10	1016.79	3.12	0.03
+ MAIN + RESQ01 + ALTNEST	-496.54	12	1017.14	3.47	0.02
+ SITE × SHBCOVN	-497.56	11	1017.17	3.50	0.02
+ MAIN + SITE × SHBCOVP	-496.76	12	1017.58	3.91	0.02
+ MAIN|$OPEN^2$	-497.98	11	1018.02	4.35	0.01
+ SITE × SHBCOVP + ALTNEST	-497.01	12	1018.07	4.40	0.01
+ MAIN + ALTNEST	-498.06	11	1018.18	4.51	0.01
+ MAIN + RESQ01 + SITE × SHBCOVP + ALTNEST	-495.06	14	1018.20	4.53	0.01
+ $MAIN^2$	-498.13	11	1018.31	4.64	0.01
+ RESQ01 × ALTNEST	-495.18	14	1018.43	4.76	0.01
+ SITE × MAIN|OPEN	-498.24	11	1018.53	4.86	0.01
+ SITE × SHBCOVP + RESQ01 × ALTNEST	-493.56	16	1019.22	5.55	0.01
+ MAIN + SITE × SHBCOVP + ALTNEST	-496.72	13	1019.51	5.84	0.01
+ SITE × $MAIN^2$	-496.92	13	1019.91	6.24	0.01
+ MAIN + RESQ01 × ALTNEST	-495.00	15	1020.10	6.43	0.00
+ MAIN + SITE × SHBCOVP + RESQ01 × ALTNEST	-493.32	17	1020.77	7.10	0.00
+ SITE × MAIN|$OPEN^2$	-497.92	13	1021.91	8.24	0.00
+ SITE × RESQ01 × SHBCOVP	-493.18	18	1022.49	8.82	0.00
+ MAIN + SITE × RESQ01 × SHBCOVP	-492.98	19	1024.12	10.45	0.00
+ SITE × RESQ01 × SHBCOVP + ALTNEST	-493.16	19	1024.47	10.80	0.00
+ MAIN + SITE × RESQ01 × SHBCOVP + ALTNEST	-492.93	20	1026.03	12.36	0.00

Models	Log likelihood	k	AIC_c	ΔAIC_c	w_i
+ SITE × RESQ01 × SHBCOVP + RESQ01 × ALTNEST	-491.52	22	1027.23	13.56	0.00
+ MAIN + SITE × RESQ01 × SHBCOVP + RESQ01 × ALTNEST	-491.27	23	1028.77	15.10	0.00

[a] SITE + DAYINIT + DAYINIT^2 + INC + NESTL + CAM + RSHAVEDATA + ALTHAVEDATA

C. Canopy nests (n = 40 nests)

Models	Log likelihood	k	AIC_c	ΔAIC_c	w_i
+ MAIN|OPEN + RESQ01 × TREE	-31.14	8	78.48	0.00	0.23
+ RESQ01 × TREE	-32.39	7	78.94	0.46	0.19
+ TREE	-34.83	5	79.74	1.26	0.12
+ MAIN|OPEN	-35.28	5	80.65	2.17	0.08
+ MAIN|OPEN + TREE	-34.34	6	80.80	2.32	0.07
+ RESQ01 + TREE	-34.58	6	81.29	2.81	0.06
+ MAIN	-35.85	5	81.78	3.30	0.04
NULL [a]	-36.90	4	81.85	3.37	0.04
+ MAIN|OPEN + RESQ01	-35.16	6	82.43	3.95	0.03
+ MAIN|OPEN + RESQ01 + TREE	-34.18	7	82.52	4.04	0.03
+ MAIN|OPEN^2	-35.27	6	82.65	4.17	0.03
+ RESQ01	-36.67	5	83.43	4.95	0.02
+ MAIN^2	-35.79	6	83.69	5.21	0.02
+ CANOPY	-36.87	5	83.83	5.35	0.02
+ RESQ	-36.89	5	83.86	5.38	0.02

[a] DAYINIT + DAYINIT^2 + NESTL

Appendix 4.7. Candidate set of models used to explain variation in the number of young fledged from successful ground, shrub, and canopy nests. Independent variables are described in the Glossary. *k* is the number of model parameters. w_i is the Akaike weight of model *i*.

A. Ground nests (n = 112 nests)

Models	Log likelihood	*k*	AIC$_c$	ΔAIC$_c$	w_i
NULL [a]	-193.69	7	402.46	0.00	0.20
+ GNDCOVN	-193.56	8	404.51	2.05	0.07
+ MAIN	-193.58	8	404.56	2.09	0.07
+ MAIN|OPEN	-193.60	8	404.61	2.14	0.07
+ SHBCOVP	-193.61	8	404.63	2.16	0.07
+ RESQ01	-193.65	8	404.69	2.23	0.06
+ SHBCOVN	-193.67	8	404.73	2.27	0.06
+ RESQ	-193.67	8	404.74	2.27	0.06
+ GNDCOVP	-193.68	8	404.77	2.30	0.06
+ MAIN + GNDCOVN	-193.44	9	406.65	4.19	0.02
+ MAIN^2	-193.46	9	406.69	4.22	0.02
+ SITE × GNDCOVN	-193.49	9	406.75	4.29	0.02
+ MAIN|OPEN^2	-193.49	9	406.75	4.29	0.02
+ MAIN + RESQ01	-193.50	9	406.77	4.31	0.02
+ RESQ01 + GNDCOVN	-193.51	9	406.79	4.33	0.02
+ SITE × MAIN	-193.57	9	406.91	4.45	0.02
+ SITE × MAIN|OPEN	-193.60	9	406.97	4.50	0.02
+ SITE × SHBCOVP	-193.61	9	406.98	4.52	0.02
+ SITE × SHBCOVN	-193.63	9	407.03	4.57	0.02
+ SITE × GNDCOVP	-193.65	9	407.07	4.61	0.02
+ MAIN + RESQ01 + GNDCOVN	-193.37	10	408.92	6.46	0.01
+ SITE × RESQ01	-193.38	10	408.94	6.48	0.01
+ SITE × RESQ	-193.65	10	409.48	7.02	0.01
+ SITE × MAIN|OPEN^2	-193.29	11	411.22	8.76	0.00
+ SITE × MAIN^2	-193.33	11	411.30	8.84	0.00
+ RESQ01 × GNDCOVN	-193.50	11	411.64	9.18	0.00
+ MAIN + RESQ01 × GNDCOVN	-193.35	12	413.86	11.40	0.00

[a] SITE + DAYINIT + DAYINIT^2 + CAM + MAXCLUTCH + RSHAVEDATA

B. Shrub nests (n = 206 nests)

Models	Log likelihood	*k*	AIC$_c$	ΔAIC$_c$	w_i
NULL	-332.09	8	680.91	0.00	0.14
+ RESQ01	-331.15	9	681.22	0.31	0.12

Models	Log likelihood	*k*	AIC$_c$	ΔAIC$_c$	w_i
+ ALTNEST	-331.89	9	682.71	1.80	0.06
+ SHBCOVP	-331.92	9	682.76	1.86	0.06
+ RESQ	-331.98	9	682.89	1.98	0.05
+ RESQ01 + ALTNEST	-330.95	10	683.03	2.12	0.05
+ SHBCOVN	-332.08	9	683.08	2.18	0.05
+ MAIN	-332.09	9	683.09	2.19	0.05
+ MAIN|OPEN	-332.09	9	683.09	2.19	0.05
+ RESQ01 + SHBCOVP	-331.08	10	683.28	2.37	0.04
+ MAIN + RESQ01	-331.14	10	683.40	2.49	0.04
+ SHBCOVP + ALTNEST	-331.70	10	684.52	3.62	0.02
+ MAIN + ALTNEST	-331.89	10	684.91	4.01	0.02
+ MAIN + SHBCOVP	-331.92	10	684.96	4.05	0.02
+ SITE × SHBCOVP	-331.92	10	684.96	4.05	0.02
+ MAIN^2	-331.95	10	685.04	4.13	0.02
+ RESQ01 + SHBCOVP + ALTNEST	-330.85	11	685.07	4.16	0.02
+ SITE × SHBCOVN	-332.00	10	685.13	4.23	0.02
+ MAIN|OPEN^2	-332.04	10	685.20	4.29	0.02
+ MAIN + RESQ01 + ALTNEST	-330.95	11	685.25	4.35	0.02
+ SITE × MAIN|OPEN	-332.07	10	685.27	4.36	0.02
+ SITE × MAIN	-332.08	10	685.29	4.38	0.02
+ SITE × RESQ01	-330.97	11	685.30	4.39	0.02
+ MAIN + RESQ01 + SHBCOVP	-331.05	11	685.46	4.55	0.01
+ SITE × RESQ	-331.17	11	685.69	4.78	0.01
+ MAIN + SHBCOVP + ALTNEST	-331.70	11	686.76	5.85	0.01
+ SITE × ALTNEST	-331.88	11	687.12	6.21	0.01
+ RESQ01 × SHBCOVP	-330.82	12	687.25	6.35	0.01
+ MAIN + RESQ01 + SHBCOVP + ALTNEST	-330.84	12	687.30	6.39	0.01
+ MAIN + RESQ01 × SHBCOVP × ALTNEST	-329.80	13	687.50	6.59	0.01
+ RESQ01 × SHBCOVP × ALTNEST	-329.83	13	687.55	6.64	0.01
+ MAIN + RESQ01 × ALTNEST + SHBCOVP	-330.30	13	688.49	7.58	0.00
+ SHBCOVP + RESQ01 × ALTNEST	-330.34	13	688.57	7.66	0.00
+ MAIN + RESQ01 × ALTNEST	-330.40	13	688.69	7.78	0.00
+ RESQ01 × ALTNEST	-330.42	13	688.74	7.83	0.00
+ MAIN + REQ01 × SHBCOVP + ALTNEST	-330.53	13	688.96	8.05	0.00
+ RESQ01 × SHBCOVP + ALTNEST	-330.53	13	688.96	8.05	0.00
+ SITE × MAIN|OPEN^2	-331.85	12	689.31	8.40	0.00
+ SITE × MAIN^2	-331.93	12	689.47	8.57	0.00
+ MAIN + RESQ01 × SHBCOVP	-330.80	13	689.50	8.59	0.00

[a] SITE + DAYINIT + DAYINIT^2 + CAM + MAXCLUTCH + RSHAVEDATA + ALTHAVEDATA

C. Canopy nests (n = 29 nests)

Models	Log likelihood	k	AIC_c	ΔAIC_c	w_i
NULL [a]	-43.99	4	97.64	0.00	0.29
+ MAIN|OPEN	-43.38	5	99.37	1.72	0.12
+ MAIN	-43.41	5	99.43	1.79	0.12
+ TREE	-43.63	5	99.86	2.22	0.10
+ CANOPY	-43.70	5	100.02	2.37	0.09
+ RESQ	-43.96	5	100.52	2.88	0.07
+ RESQ01	-43.98	5	100.58	2.93	0.07
+ $MAIN^2$	-43.24	6	102.30	4.66	0.03
+ MAIN|OPEN + TREE	-43.25	6	102.32	4.68	0.03
+ $MAIN\|OPEN^2$	-43.25	6	102.33	4.68	0.03
+ RESQ + TREE	-43.32	6	102.45	4.81	0.03
+ MAIN|OPEN + RESQ	-43.36	6	102.54	4.89	0.03
+ MAIN|OPEN + RESQ + TREE	-43.08	7	105.49	7.84	0.01
+ RESQ × TREE	-43.31	7	105.96	8.32	0.00
+ MAIN|OPEN + RESQ × TREE	-42.92	8	109.03	11.39	0.00

[a] DAYINIT + $DAYINIT^2$ + MAXCLUTCH

Appendix 4.8. Candidate set of models used to explain variation in the numbers ground, shrub, and canopy nesting species recorded during point count surveys. Independent variables are described in the Glossary. Data represent 216 surveys at 54 stations in Fort Simpson, NT (northern site), and 254 surveys at 82 stations in Chinchaga, AB (southern site). *k* is the number of model parameters. w_i is the Akaike weight of model *i*.

A. Ground nesters

Model	Log likelihood	*k*	AIC_c	ΔAIC_c	w_i
+ SITE × M100 + RESQ	-783.44	10	1587.36	0.00	0.42
+ SITE × M100 + RESQ × SHBCOVP	-781.85	12	1588.38	1.02	0.25
+ SITE × M100 + RESQ + SHBCOVP	-783.17	11	1588.92	1.56	0.19
+ SITE × M100	-787.26	9	1592.91	5.55	0.03
+ RESQ	-788.63	8	1593.56	6.20	0.02
+ RESQ01	-788.88	8	1594.07	6.71	0.01
+ SITE × M100 + SHBCOVP	-786.95	10	1594.38	7.02	0.01
+ M100	-789.04	8	1594.39	7.03	0.01
+ SHBCOVP + RESQ	-788.18	9	1594.75	7.39	0.01
+ SHBCOVP ×RESQ	-787.20	10	1594.88	7.52	0.01
+ SITE × RESQ	-788.58	9	1595.54	8.18	0.01
+ MAIN	-789.65	8	1595.62	8.26	0.01
+ SITE × RESQ01	-788.86	9	1596.11	8.75	0.01
+ SITE × MAIN	-789.01	9	1596.40	9.04	0.00
+ 3MAIN	-790.58	8	1597.48	10.12	0.00
+ SITE × 3MAIN	-790.37	9	1599.14	11.78	0.00
+ MO100	-791.54	8	1599.40	12.04	0.00
+ MAIN|OPEN	-791.72	8	1599.74	12.38	0.00
NULL [a]	-792.87	7	1599.99	12.63	0.00
+ SHBCOVP	-792.27	8	1600.86	13.50	0.00
+ SITE × MO100	-791.30	9	1601.00	13.64	0.00
+ GNDCOVP	-792.50	8	1601.31	13.94	0.00
+ SITE × MAIN|OPEN	-791.68	9	1601.75	14.39	0.00
+ SITE × SHBCOVP	-792.06	9	1602.51	15.15	0.00
+ SITE × GNDCOVP	-792.39	9	1603.18	15.82	0.00

[a] SITE + DAY + DAY^2 + WIND + PTREE

B. Shrub nesters

Model	Log likelihood	*k*	AIC_c	ΔAIC_c	w_i
+ MO100 + RESQ + SITE × SHBCOVP	-932.18	11	1886.94	0.00	0.34
+ MO100 + SITE × SHBCOVP	-933.96	10	1888.40	1.46	0.17

Model	Log likelihood	k	AIC$_c$	ΔAIC$_c$	w_i
+ RESQ + SITE × SHBCOVP	-933.99	10	1888.46	1.52	0.16
+ SITE × SHBCOVP	-935.73	9	1889.85	2.91	0.08
+ MO100 + RESQ	-936.45	9	1891.30	4.36	0.04
+ MO100 + RESQ × SITE × SHBCOVP	-931.22	14	1891.37	4.43	0.04
+ SHBCOVP	-937.85	8	1892.02	5.08	0.03
+ RESQ × SITE × SHBCOVP	-932.98	13	1892.75	5.81	0.02
+ MO100	-938.30	8	1892.92	5.98	0.02
+ MAIN|OPEN	-938.35	8	1893.01	6.07	0.02
+ MAIN	-938.54	8	1893.39	6.45	0.01
+ RESQ	-938.61	8	1893.53	6.59	0.01
+ M100	-938.70	8	1893.71	6.77	0.01
+ SITE × RESQ	-937.81	9	1894.01	7.07	0.01
+ SITE ×MAIN	-938.09	9	1894.57	7.63	0.01
+ SITE ×MAIN|OPEN	-938.11	9	1894.62	7.68	0.01
+ SITE ×MO100	-938.28	9	1894.94	8.00	0.01
+ 3MAIN	-939.38	8	1895.07	8.13	0.01
NULL [a]	-940.46	7	1895.17	8.23	0.01
+ SITE × 3MAIN	-938.47	9	1895.33	8.39	0.01
+ SITE × M100	-938.59	9	1895.57	8.63	0.00
+ SITE × RESQ01	-939.08	9	1896.55	9.61	0.00
+ RESQ01	-940.23	8	1896.76	9.82	0.00

[a] SITE + DAY + DAY^2 + WIND + PTREE

C. Canopy nesters – wwcr recorded as present

Model	Log likelihood	k	AIC$_c$	ΔAIC$_c$	w_i
+ SITE × MO100 + RESQ + SITE × TREE	-580.36	12	1185.40	0.00	0.50
+ SITE × MO100 + RESQ	-583.24	10	1186.97	1.56	0.23
+ SITE × MO100 + RESQ × SITE × TREE	-578.70	15	1188.45	3.05	0.11
+ RESQ + SITE × TREE	-584.10	10	1188.69	3.29	0.10
+ RESQ × SITE × TREE	-582.03	13	1190.86	5.46	0.03
+ SITE × MO100 + SITE × TREE	-585.64	11	1193.86	8.46	0.01
+ RESQ	-589.18	8	1194.67	9.26	0.00
+ SITE × RESQ	-588.20	9	1194.79	9.38	0.00
+ SITE × MO100	-588.87	9	1196.13	10.72	0.00
+ SITE × TREE	-589.09	9	1196.57	11.17	0.00
+ SITE × M100	-589.31	9	1197.01	11.61	0.00
+ M100	-591.14	8	1198.60	13.20	0.00
+ RESQ01	-591.91	8	1200.13	14.73	0.00
+ SITE × RESQ01	-590.96	9	1200.31	14.91	0.00

Model	Log likelihood	*k*	AIC$_c$	ΔAIC$_c$	w_i
+ CANOPY	-592.84	8	1201.99	16.59	0.00
+ MO100	-592.92	8	1202.14	16.74	0.00
+ TREE	-593.39	8	1203.10	17.70	0.00
+ SITE × CANOPY	-592.61	9	1203.62	18.22	0.00
NULL [a]	-594.74	7	1203.72	18.32	0.00
+ 3MAIN	-594.51	8	1205.33	19.93	0.00
+ MAIN	-594.60	8	1205.52	20.11	0.00
+ MAIN|OPEN	-594.73	8	1205.77	20.36	0.00
+ SITE × MAIN|OPEN	-594.05	9	1206.49	21.09	0.00
+ SITE × MAIN	-594.45	9	1207.29	21.89	0.00
+ SITE × 3MAIN	-594.51	9	1207.40	22.00	0.00

[a] SITE + DAY + DAY^2 + WIND + PTREE

Chapter 5. Using video monitoring to assess the accuracy of nest fate and nest productivity estimates by field observation.[4]

5.1. Introduction

Nest fate and nest productivity are key demographic parameters for understanding songbird population dynamics. Considerable effort has been made to improve statistical models of nest survival (reviewed by Jones and Geupel 2007), whereas little consideration has been paid to assessing and improving the accuracy of nest-fate and nest-productivity estimates based on field observations. Observation error in determining nest fate and estimating the number of young produced from each nest should be a major concern, particularly if estimates are biased by one or more factors that may vary among habitats or studies being compared. Here, we consider magnitude and sources of error in field-based estimates of nest fate and nest productivity, the implications of this error for population growth models, and the utility of cues commonly used to assess fate.

Nest fate and nest productivity are parameters that are measured with error because the final nest visit often is to an empty, undisturbed nest with no sign of adults or young in the immediate vicinity. Fate and productivity are generally determined on the basis of nest age, which itself is often an estimate, and the cues available at the nest on the last visit (Martin and Geupel 1993). Standard protocols deem a nest successful if the median age between the last active visit and the first

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[4] Ball, J. R., and E. M. Bayne. 2012. Using video monitoring to assess the accuracy of nest fate and nest productivity estimates by field observation. Auk 129:438-448.

inactive visit is within 2 days of the predicted age when fledging should have occurred, unless there is evidence to the contrary (Martin et al. 1997). The number of young fledged is typically estimated as the number of nestlings present on the last active nest visit (Martin et al. 1997).

The default conclusion that a nest was successful on the basis of these criteria has the potential to overestimate fecundity if late-stage nest predators leave no evidence of their visits. The prevalence of late-stage predation, partial predation, and force fledging by predators are poorly understood in most systems, but we should not expect these to be negligible. Several studies have reported increased rates of predation and incidences of force fledging at late-stage nests (Thompson et al. 1999, Pietz and Granfors 2000, McCallum and Hannon 2001, Williams and Bohall Wood 2002, Stake et al. 2005, Weidinger 2006). Late-stage nests should experience elevated predation rates if increased nestling begging and parental activity attracts predators (Skutch 1949, Martin et al. 2000, Haff and Magrath 2011). Nestlings deemed old enough to fledge by the above fate-assessment rules are also capable of fleeing the nest when approached by a predator. Finally, late-stage nestlings have a developed stress response (Sims and Holberton 2000, Suorsa et al. 2003), which may increase their likelihood of force fledging. The survival probability of force-fledged nestlings is unknown but is likely lower than that of fledged nestlings if force-fledged nestlings are younger and less developed (Perrins 1965, Krementz et al. 1989, Monrós et al. 2002, Vitz and Rodewald 2011) or are actively pursued by the predator. Depending on predation pressure near the end of nesting and the fate of force-fledged young, field estimates of nest fate and nest productivity may be strongly biased.

We used video data for a suite of cup-nesting songbirds in the boreal forest to examine how frequently nest fate and nest productivity were misidentified in the field. We examined whether error was attributable to the observer, factors specific to the nest (nestling age, nest substrate, nest fate), and the type of predator that visited the nest. Previous researchers have suggested that predators can be identified from nest remains (Rearden 1951, Sargeant et al. 1998; but see Larivière 1999, Liebezeit and George 2003), particularly when predators have dissimilar feeding behaviors (Anthony et al. 2004). The nest predators known to be in our system (Ball et al. 2009) differ in body size and nest predation behavior, and we expected nest fate and nest productivity to be more frequently misidentified for some types of predators. Inaccuracies in identification of nest fate and nest productivity in the field could have important consequences for models of population dynamics, particularly if differential biases exist within variables of interest. We considered the implications of observation error for estimates of daily and cumulative nest survival and for per capita annual productivity. Finally, we evaluated the efficacy of several cues commonly used to determine nest fate, with the goal of improving observer accuracy in future studies.

5.2. Methods

5.2.1. Study areas and field procedures.

We studied nesting success of songbirds in mature mixedwood boreal forest in two regions of western Canada. We established six 42-ha plots near Fort Simpson, Northwest Territories (61°52′N, 121°20′W), in 2005 and 2006, and nine 24-ha plots in the Chinchaga forestry region northwest of Manning, Alberta (57°18′N, 118°23′W), in 2006 and 2007. Both sites had similar songbird (J. Ball unpubl. data) and nest predator communities (Ball et al. 2009).

We visited each study plot every 3 days between late May and mid-July to search for and monitor nests. Infrared digital video cameras were preferentially placed at randomly selected Swainson’s Thrush (*Catharus ustulatus*) and Chipping Sparrow (*Spizella passerina*) nests. We opportunistically placed cameras at nests of other altricial species when target nests were unavailable. We typically delayed camera installation until late incubation or early nestling stage to avoid abandonment. Cameras were left in place until the nest was successful or failed. Observer disturbance was limited to battery changes every 6 days, ~10 m from the nest, unless adults were absent, in which case nests were visited to check and count contents.

5.2.2. Nest-fate and nest-productivity assessment.

We assessed the fate of each video-monitored nest in the field before confirming its fate from video. Each nest was classified as “depredated” or “successful” by an experienced technician using the available cues at the nest. Depredated nests fledged zero young, whereas successful nests fledged ≥1 young.

Depredated and successful nests were both commonly empty on the final nest check. Cues used to identify a depredated nest were (a) a damaged or dislodged nest bowl, or (b) destroyed or missing nest contents when nestlings were too young to fledge (Martin and Geupel 1993, Martin et al. 1997). Egg or nestling loss from a still-active nest did not necessarily indicate predation. Cues used to identify a nest as successful included (c) a compressed or flattened nest cup, (d) droppings in or on the nest rim, (e) droppings on the surrounding nest substrate, or (f) disappearance of one or more nestlings whose estimated median age between the previous and current visit was ≤2 days younger than the species' predicted fledging age (i.e., partially or completely fledged; Martin and Geupel 1993, Martin et al. 1997). We used species-specific average age of fledge (Poole 2011) to predict fledge age. Successful nests could contain one or more living nestlings if partially fledged or one or more dead nestlings if partially depredated or partially abandoned. The presence of (g) fledglings or (h) adults calling, alarm calling, or carrying food in the vicinity of the nest were also used as cues of success (but see Martin and Geupel 1993). Individual birds were not marked, and observers did not search extensively for fledglings of completed nests. Not all cues were necessary to conclude whether a nest was successful or depredated, nor did the presence of any single cue determine fate when nestlings approached fledging age. Instead, we used the total weight of evidence in assessing fate. Nest productivity was estimated to be the maximum number of nestlings present on the last active visit (Martin et al. 1997) unless there was evidence to the contrary (e.g., a nest partially fledged on last active visit or dead nestlings found in or beneath the nest after fledge).

We also determined nest fate and nest productivity from video. We distinguished nestlings that fledged from those that were force fledged by an adult, sibling, or predator. We defined "fledge" as a nestling that departs the nest and the immediate nest area under its own power without direct provocation from an adult or predator. We arbitrarily restricted "force fledge" to within 10 min following a predator's visit to the nest (average ± 95% confidence interval [CI] = 1.1 ± 0.4 min; $n = 27$). Chicks that departed the nest >10 min following departure of a predator were classified as "fledged" (average ± 95% CI = 36.7 ± 18.4 h; $n = 7$). The probability of force-fledged nestlings surviving likely depends on nestling age. We classified each force-fledged nestling as "successful" or "failed" in each of three scenarios: none survived (FF0), those aged ≤2 days from their predicted fledge age survived (FF2), and those aged ≤4 days from their predicted fledge age survived (FF4). We assumed that all force-fledged nestlings >4 days younger than their predicted fledge age died.

5.2.3. Statistical analyses.

We assessed the accuracy of nest fate estimates by comparing the proportion of successful nests estimated in the field to those quantified from video (FF0, FF2, FF4) using two-tailed Fisher's exact tests. We assessed the accuracy of nest productivity estimates by determining whether the mean number of young fledged from all nests and from successful nests varied with estimate type (i.e., field-based, FF0, FF2, FF4) using Poisson and zero-truncated Poisson regression models, respectively. We used Wald tests to determine whether the field estimate of mean productivity differed from each mean video estimate. We excluded nests from our productivity analyses when the fate of one or more nestlings could not be determined from video.

We used single-variable logistic regression models to determine whether correct identification of nest fate and nest productivity varied with observer (*n* = 3), nest fate (successful or depredated determined from video for FF0, FF2, FF4), nest substrate (ground or shrub–subcanopy), or nestling age. Nestling age (rounded to the nearest day) was calculated at the midpoint between the last active visit and the final visit. We quantified the dependent variables, correct identification of fate (1/0) and productivity (1/0), by comparing field estimates with each video-based estimate (FF0, FF2, FF4). The effects of observer, nest fate, and substrate on correctly identifying fate and productivity were considered individually as categorical independent variables. We considered three potential relationships between nestling age and the correct identification of fate and productivity. We considered nestling age as a continuous independent variable in both a linear model and a quadratic model that represents a nonlinear effect of age on accuracy. We also considered nestling age as a binary variable that was either > or ≤2 days younger than the predicted age of fledge. We standardized nestling age (StdAge = nestling age/average fledge age) to allow age-related comparisons across species with different lengths of nestling stage. We calculated Akaike weights and evidence ratios (ER; Burnham and Anderson 2002, Anderson 2008) to compare support among models, including a null model that did not include any covariates. Akaike weights indicate the weight of evidence for a given model in relation to the set of models considered, whereas the ER is the weight of evidence for a given model in relation to another model and is calculated as the ratio of model Akaike weights. We repeated our model selection procedure for nest fate and nest productivity under each category of video fate (FF0, FF2, and FF4).

We also examined whether correct identification of nest fate and nest productivity was influenced by predator type. We categorized predators on the basis of body size and general predatory behavior on nestlings that we observed on video. Large mammals (American Black Bear [*Ursus americanus*] and American Marten [*Martes americana*]; *n* = 9) commonly removed all nest contents during a single visit and often disturbed the nest or nest substrate. Avian predators (Sharp-shinned Hawk [*Accipiter striatus*], Common Raven [*Corvus corax*], and Great Gray Owl [*Strix nebulosa*]; *n* = 17) rarely disturbed the nest. Sharp-shinned hawks were the most common avian predator and they depredated one nestling per visit over a period of minutes to several hours whereas ravens and Great Gray Owls depredated all nestlings on the first visit (mean lapse between first and last predation ± SD = 0.45 ± 0.71 days) . Small mammals (Least Chipmunk [*Eutamias minimus*], Deer Mouse [*Peromyscus maniculatus*], Northern Flying Squirrel [*Glaucomys sabrinus*], Red-backed Vole [*Clethrionomys gapperi*], and Short-tailed Weasel [*Mustela erminea*]; *n* = 11) rarely removed more than one nestling per visit, and smaller members of this group frequently left wounded or dead and partially consumed nestlings in the nest bowl. Most visits occurred within minutes to hours (0.17 ± 0.32 days). The amount of nest disturbance varied and, when present, often resulted from a prolonged struggle between adults and the predator. Red Squirrels (*Tamiasciurus hudsonicus*; *n* = 52) usually removed nestlings individually over a period of minutes to hours (0.13 ± 0.28 days) and rarely disturbed the nest while doing so. Nests that were force fledged by a parent or siblings were excluded because of small sample size (*n* = 2). We also excluded first predators to nests visited by two predators (*n* = 3).

Predator type was included as an independent categorical variable in a single-variable logistic regression model for each category of fate and productivity (FF0, FF2, FF4). We included "fledge" as the predator type for successful nests that were not visited by a predator (i.e., not partially depredated or force fledged; *n* = 9) for a total of six predator types. Fledge served as the baseline for assessing whether predator type affected the accuracy of fate and productivity estimates. We used odds ratios and Wald tests to determine whether nests depredated by each predator type had a different likelihood of having their fate or productivity estimated correctly, compared with a nest that was successful and compared with nests depredated by other predators. A predator with an odds ratio of 1.0 (or a 95% CI that overlaps 1.0) indicates a nest whose fate is equally likely to be assessed correctly as a nest that was successful. Predators with odds ratios and 95% CI > 1.0 are more likely to be assessed correctly than successful nests, whereas predators with odds ratios and 95% CI < 1.0 are less likely to be assessed correctly than successful nests. The magnitude of the odds ratio in relation to 1.0 indicates the strength of the association.

We used logistic exposure models in SAS, version 9.1.3 (PROC GENMOD; SAS Institute, Cary, North Carolina; Shaffer 2004) to calculate age-related changes in daily nest survival rate on the basis of field and video estimates of nest fate (FF0, FF2, FF4). This procedure models the probability of a nest surviving the interval between nest checks on the basis of a binomial response distribution. The probability of surviving an interval depends on interval length, which is equal to the number of days between nest checks for successful intervals and equal to 1 for failed intervals (Rotella et al. 2004). We did not use video to correct the length of the terminal exposure interval, but we expect this source of error to be minimal because of the short interval duration (Stanley 2000). We used Akaike's information criterion corrected for small sample size (AIC_c) and ER to identify the age model that best described variation in daily survival rate for each fate type. We considered StdAge as a continuous independent variable in linear, quadratic, and cubic models. We also considered age as a categorical variable by converting StdAge to a 12-day nestling period for all species and binning observations into 2-day increments. We pooled the first two age categories (>0 to ≤4 days old) because no nests failed during the first interval. We also pooled nests >10 days old. Nests containing eggs were binned into age class zero. This resulted in a total of six age categories. Finally, we considered a model with age as a binary variable based on whether nestlings were > or ≤2 days younger than their predicted age of fledge. We used the best-supported daily survival rate model to calculate the probability of nest success for each fate type using a 12-day egg and 12-day nestling exposure period, which we chose for illustrative purposes. We estimated mean nest survival probability ± 95% CI using a Monte Carlo simulation with 10,000 replicates. Each replicate of nest survival was the product of the back-transformed period-specific estimates of daily survival exponentiated by their respective period lengths. Survival probabilities for each period were randomly drawn from a distribution described by their respective logit estimates (± SE) of survival, assuming a normal distribution of errors.

We quantified the implications of error in fate and productivity estimates on population growth by calculating the finite rate of growth as $\lambda = S_a + F \times S_j$ (Flaspohler et al. 2001), where S_a and S_j are annual adult and juvenile survival, respectively, and F is the mean per capita annual productivity of females per pair. We used adult and juvenile survival probabilities of 0.6 and 0.3, respectively (*sensu* Flaspohler et al. 2001), for illustrative purposes. We calculated mean productivity of females per pair as $F = [p \times y(2 - p)]/2$, where p is probability of nest success and y is mean number of young raised per successful nest. We assumed that all failed pairs renested once with an equal probability of success and that all broods had an equal sex ratio (Flaspohler et al. 2001). Successful pairs in our study did not renest. We used a Monte Carlo simulation with 10,000 replicates to estimate mean λ ± 95% CI. Values for p and y for each replicate were randomly drawn from their respective distributions (determined above), whereas values for S_a and S_j were fixed.

We used single-variable logistic regression models to evaluate the utility of each field cue for identifying actual nest fate. Nest fate was a binary dependent variable determined from video (FF0, FF2, FF4; success = 1, depredated = 0).

Each field cue was a binary independent variable coded as present (1) or absent (0) at the final nest visit when fate was assessed. We hypothesized that successful nests would be associated with nestlings whose median age was ≤2 days younger than the predicted age of fledge, a flattened nest bowl, fecal droppings in or around the nest, and the presence of adults or fledglings. We also hypothesized that successful nests would not be associated with damaged nest bowls and missing nest contents. Not all cues were consistently recorded for all nests, so we were unable to use AIC_c to compare models because of unequal sample sizes. Therefore, field-cue utility was assessed on the basis of odds ratios and *P* values ($\alpha = 0.05$). Odds ratios indicate the likelihood that the presence of a cue is associated with a successful nest compared with the nests where that cue was absent. All values are presented ± 95% CI unless stated otherwise.

5.3. Results

5.3.1. Observation accuracy

We recorded the fate of 42 ground and 85 shrub–subcanopy nests representing 13 species (Appendix 5.1). We also recorded the fate of all nestlings in 117 nests. One or more nestlings disappeared from 10 broods prior to camera placement or during camera battery failure, and their fates are unknown. On the basis of field cues, we estimated that 78 nests were successful and 49 nests were depredated (Table 5.1). Video revealed that 21 nests estimated to be successful were partially (14 nests) or entirely (7 nests) depredated, and 5 nests classified as depredated actually fledged 1 or more young. Successful nests fledged their first young at StdAge = 0.97 ± 0.04, and the average lapse between first and last fledge was 0.18 ± 0.11 days. Nests that were depredated were first visited by a predator at StdAge = 0.54 ± 0.08 and were last visited by a predator 0.23 ± 0.11 days later. Video also identified 20 nests in which one or more nestlings were force fledged by a predator (18 nests), a sibling (1 nests), or an adult (1 nest). StdAge of force-fledged nestlings was 0.81 ± 0.08.

Table 5.1. Estimated and actual nest fates of 42 ground and 85 shrub–subcanopy songbird nests.

	Fate estimated in the field		
Actual fate	Fledge	Depredated	Total
Fledge [a]	52	3	55
Fledge + force fledge [b]	4	0	4
Fledge + depredated	5	2	7
Depredated + force fledge	9	5	14
Force fledge	1	1	2
Depredated	7	38	45
Total	78	49	127

[a] Camera battery failed at one nest immediately following fate of first two nestlings. Fate of remaining two nestlings unknown but presumed similar to that of siblings.

[b] One nest partially force fledged by an adult and another nest partially force fledged by a sibling.

Assuming that all force-fledged nestlings failed (FF0), the fate of 105 nests (83%) were correctly identified in the field. The proportion of nests that were successful was similar between field and video (FF0) estimates (z = 1.52, P = 0.13; Table 5.2). Overall nest productivity was overestimated in the field (χ^2 = 11.32, df = 1, P < 0.001), whereas productivity of successful nests was similar (χ^2 = 1.07, df = 1, P = 0.30). If force-fledged young within 2 days of fledge were assumed successful (FF2), the fate of 108 nests (85%) were accurately identified in the field. The proportion of nests that were successful was similar between field and video (FF2) estimates ($z = 0.38$, $P = 0.70$). Overall nest productivity was overestimated in the field ($\chi^2 = 4.47$, df = 1, $P = 0.03$), whereas productivity of successful nests was similar ($\chi^2 = 1.87$, df = 1, $P = 0.17$). Finally, if force-fledged young within 4 days of fledge were assumed successful (FF4), field estimates accurately identified the fate of 111 nests (87%). Field and video (FF4) estimates were similar for the proportion of successful nests ($z = 0.26$, $P = 0.80$), overall nest productivity ($\chi^2 = 1.76$, df = 1, $P = 0.18$), and productivity of successful nests ($\chi^2 = 1.97$, df = 1, $P = 0.16$; Table 5.2).

Table 5.2. Proportion of nests that were successful, average nest productivity (number fledged per nest), estimated cumulative probability of nest survival, and estimated population growth rate (λ) of boreal forest songbirds as determined by field observations and video. Video-based estimates differ depending on assumed fate of force-fledged young (FF0 = none survive; FF2, FF4 = nestlings ≤2 days and ≤4 days, respectively, from their predicted fledge date survive). All values are presented with 95% confidence intervals in parentheses.

	Field	FF0	FF2	FF4
Successful nests [a]	0.61 (0.53–0.70)	0.52 (0.43–0.61)	0.59 (0.51–0.68)	0.63 (0.55–0.71)
Productivity (overall) [b]	2.3 (2.0–2.6)	1.7 (1.5–1.9)	1.9 (1.7–2.2)	2.1 (1.8–2.3)
Productivity (successful only) [c]	3.9 (3.4–4.3)	3.5 (3.0–4.0)	3.4 (3.0–3.9)	3.4 (3.0–3.9)
Nest survival [d]	0.60 (0.50–0.69)	0.56 (0.47–0.64)	0.60 (0.50–0.69)	0.62 (0.52–0.71)
Population growth (λ)	1.09 (1.01–1.16)	1.02 (0.95–1.10)	1.03 (0.96–1.10)	1.04 (0.97–1.11)

[a] Number of nests with known fate = 127.

[b] Number of nests with known fate of all nestlings = 117.

[c] Number of successful nests with known fate of all nestlings: Field = 70, FF0 = 56, FF2 = 65, FF4 = 70.

[d] 12-day egg and 12-day nestling stages were used for illustrative purposes.

5.3.2. Factors affecting the accuracy of nest-fate and nest-productivity estimates

We found strong support for a fate model explaining variation in the correct identification of nest fate based on FF0 criteria (Table 5.3A). The ER indicates that a fate model was 40.8× (≈ 0.73/0.02) more likely to be the best model than the null model and 3.2× more likely to be the best model than the next-best-fitting quadratic age model. The odds (± 95% CI) of a successful nest being classified correctly are 12.2 (4.9–30.4) to 1. A depredated nest was 0.21× (0.07–0.62) less likely to be classified correctly than a successful nest. Support for a fate-model declined for FF2 and FF4 fates (ER = 1.3 and 0.42 compared with the null model, respectively). Depredated nests were 0.45× (0.17–1.2, FF2) and 0.72× (0.25–2.1, FF4) less likely to be classified correctly than successful nests. We also found moderate support for a quadratic age model explaining variation in the correct identification of nest fate. The ER indicates that a quadratic age model was 12.7× more likely to be the best model compared with the null model based on FF0 criteria (Table 5.3A). The quadratic age model also received moderate support compared with the null model for FF2 fates (ER = 17.7), but support declined for FF4 fates (ER = 3.4). Field estimates were more likely to correctly identify nest fate when nestlings were several days younger than their average age of fledge or when nestlings were older than their average age of fledge. Field estimates were less accurate at identifying nest fate when nestling age was just prior to the predicted fledging age (Fig. 5.1). Observer, nest substrate, and the

Table 5.3. Model set explaining variation in field-based estimates correctly identifying (A) nest fate (*n* = 127 nests) and (B) nest productivity (*n* = 117 nests). The dependent variables, correct identification of fate (1/0) and productivity (1/0), were quantified by comparing field and video-based (FF0) estimates. Observer (*n* = 3), nest fate (successful or depredated), and nest substrate (ground or shrub–subcanopy) were categorical independent variables. Standardized nestling age, which controls for differences in length of nestling stages and allows age-related calculations across species, was included as a continuous independent variable in both a linear (StdAge) and a quadratic (StdAge2) model. Nestling age also was included as a binary independent variable (Age) that was either > or ≤2 days younger than the predicted age of fledge. All force-fledged nestlings were presumed dead (FF0; *n* = 27 nests).

Model	Log likelihood	*n* parameters	AIC_c	ΔAIC_c	*L*(model|*x*) [a]	Akaike weight
(A) Fate	–53.80	2	111.70	0.00	1.00	0.73
StdAge2	–53.92	3	114.03	2.33	0.31	0.23
Null	–58.54	1	119.12	7.42	0.02	0.02
StdAge	–58.40	2	120.90	9.21	0.01	0.01
Age	–58.53	2	121.16	9.46	0.01	0.01
Nest substrate	–58.53	2	121.16	9.46	0.01	0.01
Observer	–58.08	3	122.35	10.65	0.00	0.00
(B) StdAge2	–55.56	3	117.34	0.00	1.00	0.98
StdAge	–61.70	2	127.50	10.16	0.01	0.01
Null	–63.20	1	128.44	11.10	0.00	0.00
Fate	–62.37	2	128.85	11.51	0.00	0.00
Age	–63.03	2	130.17	12.83	0.00	0.00
Nest substrate	–63.20	2	130.50	13.16	0.00	0.00
Observer	–62.39	3	131.00	13.66	0.00	0.00

[a] Model likelihood given data *x* = $\exp(-\frac{1}{2}\Delta AIC_c)$.

remaining age models received no support compared with the null model (all ER < 1.0; Table 5.3A).

The fate of nests depredated by Red Squirrels, avian predators, and large mammals were less likely to be classified correctly than nests that were successful based on FF0 criteria. The results for FF2 fates were similar to FF0 for all predator types and are not discussed in detail. Only large mammals were less likely to be classified correctly on the basis of FF4 criteria. Compared with

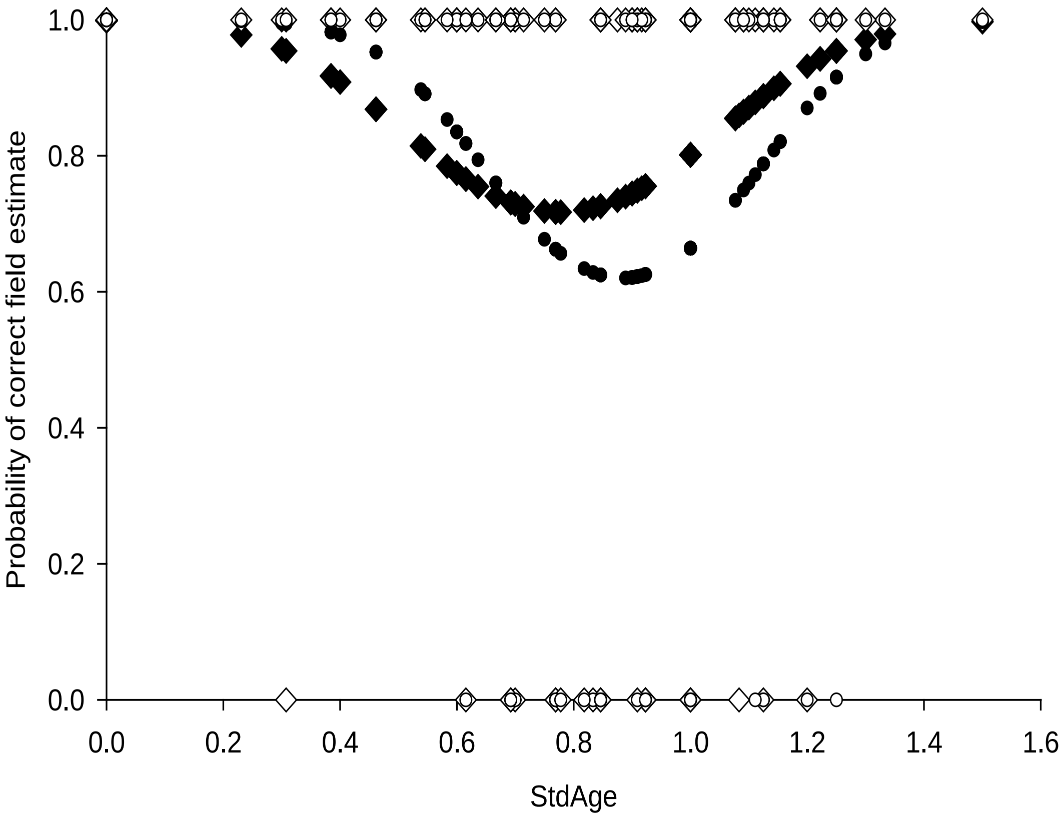

Figure 5.1. Modeled probability (filled symbols) of field observations correctly identifying nest fate (diamonds; open symbols: 0.0 = incorrect, 1.0 = correct) and nest productivity (circles) with increasing nestling age, assuming that no force-fledged nestlings survived (FF0). Nestling age was standardized (StdAge = nestling age/average fledging age) to allow age-related calculations across species with different lengths of nestling period.

nests that were successful, nests depredated by Red Squirrels were 0.15× (FF0: 0.04–0.57, $\chi^2 = 7.73$, df = 1, $P = 0.005$) to 0.26× (FF4: 0.06–1.1, $\chi^2 = 3.42$, df = 1, $P = 0.065$) less likely to be classified correctly, nests depredated by avian predators were 0.13× (FF0: 0.02–0.65, $\chi^2 = 6.06$, df = 1, $P = 0.001$) to 0.19× (FF4: 0.03–1.1, $\chi^2 = 3.62$, df = 1, $P = 0.057$) less likely to classified correctly, and nests depredated by large mammals were 0.11× (FF0 and FF4: 0.02–0.68, $\chi^2 = 5.67$, df = 1, $P = 0.017$) less likely to classified correctly. The odds of a nest depredated by small mammals being classified correctly did not differ from that of successful nests (FF0: 0.39 [0.04–4.3], $\chi^2 = 0.60$, df = 1, $P = 0.44$). No nests depredated by small mammals were misclassified on the basis of FF4 criteria. We did not find any difference between predators in the likelihood of correctly assessing nest fate (all $P \geq 0.30$).

We found strong support for a quadratic age model explaining variation in the correct identification of nest productivity (Table 5.3B). The ER indicates that the quadratic age model was 257× more likely to be the best model compared with the null model (FF0). Support for the quadratic age model remained strong under FF2 and FF4 criteria (ER = 317 and 176, respectively). Nest productivity was less likely to be estimated correctly in the field when nestling age was just prior to the predicted fledge age compared with nestlings that were younger or older (Fig. 5.1). No other model received significant support compared with the null (all ER < 1.7; Table 5.3B). The productivity estimates of nests depredated by Red Squirrels, avian predators, and large mammals were less likely to be correct than productivity estimates of nests that were successful for FF0 fates. Results for FF2 and FF4 fates are similar and are not presented. Productivity was 0.13× (0.03–0.48, $\chi^2 = 9.17$, df = 1, $P = 0.003$), 0.08× (0.02–0.39, $\chi^2 = 9.63$, df = 1, $P = 0.002$), and 0.14× (0.02–0.84, $\chi^2 = 4.64$, df = 1, $P = 0.031$) less likely to be estimated correctly for nests depredated by Red Squirrels, avian predators, and large mammals, respectively. The odds of productivity estimates being correct for nests depredated by small mammals did not differ from successful nest estimates (FF0: 0.48 [0.04–5.3], $\chi^2 = 0.37$, df = 1, $P = 0.55$). We did not find any difference between predators in the likelihood of correctly assessing nest productivity (all $P \geq 0.14$).

5.3.3. Daily nest survival rate and rate of population growth

Variation in daily nest survival rates based on field and video estimates of fate (FF0, FF2, FF4) were each best explained by a model that included StdAge as a six-category variable (Akaike weight range: 0.74–0.99). The only other model to receive moderate support was a cubic age model explaining variation in FF0 nest fate ($\Delta AIC_c = 2.88$). The ER in support of the categorical model was 4.2× the cubic model. All other models had $\Delta AIC_c > 4.0$. Daily survival rate did not differ between fate categories when nestlings were >2 days from their predicted fledging age (Fig. 5.2). Daily survival rate of FF0 fate was less than field-based estimates when nestlings were ≤2 days from their predicted fledging age. However, cumulative survival was similar between field and video-based estimates (Table 5.2) because of observation error at younger ages. The rate of population growth based on field estimates of nest fate and nest productivity was ~6% higher than video-based estimates (Table 5.2).

5.3.4. Utility of field cues for predicting actual nest fate

Nestling age was the field cue most strongly associated with successful nests (Table 5.4). A nest whose median nestling age based on the nest visitation schedule was ≤2 days younger than its predicted fledging age was 25.9× (FF0) to 63.2× (FF2) more likely to have been successful than a nest whose nestlings were considered too young to fledge. This relationship was strongest for FF2 fates because nestlings ≤2 days before fledging are old enough to flee from predators,

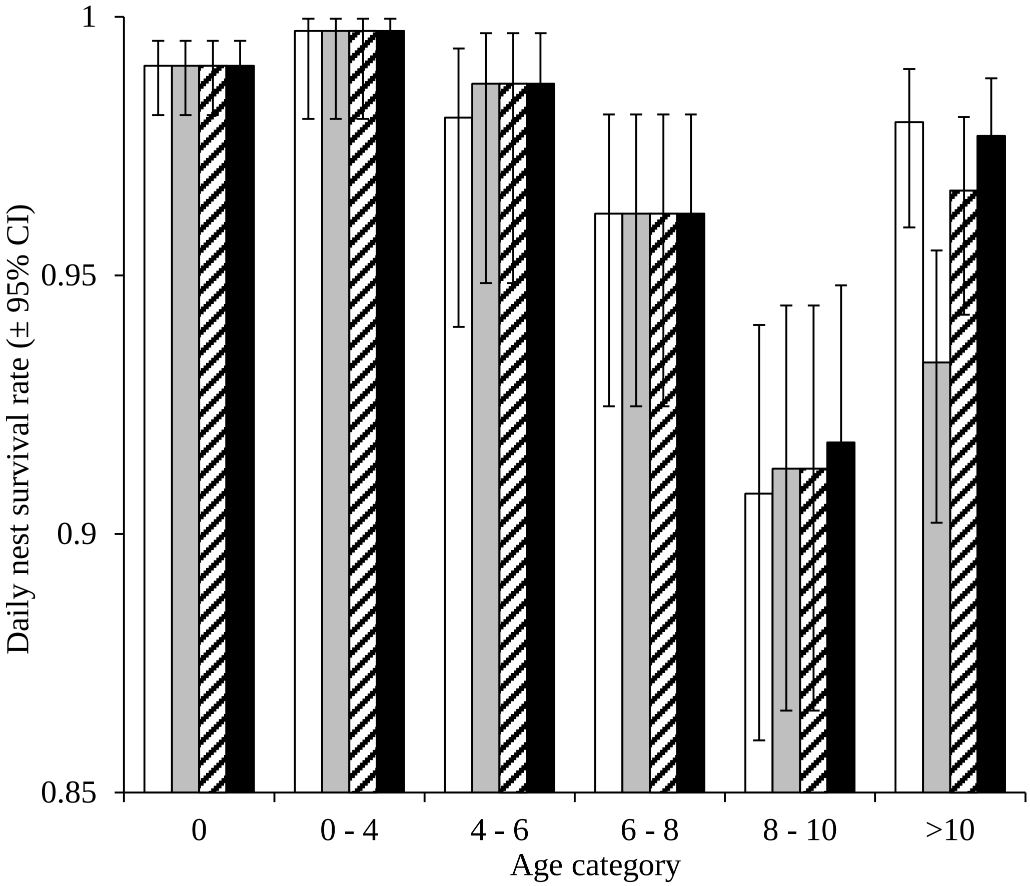

Figure 5.2. Field (white bars) and video-based estimates of daily nest survival rate with nestling age (six-category age model). Video-based estimates assume that no force-fledged nestlings survived (FF0; gray bars) and that force-fledged nestlings ≤2 days (FF2; hashed bars) and ≤4 days (FF4; black bars) from the predicted age of fledge survived. Nestling age was standardized to 12 days to allow age-related calculations across species with different lengths of nestling period. All nests containing eggs were categorized as age 0.

which in this case is equated to fledging. This result is not unexpected, given that nestlings are more likely to leave the nest after having achieved a certain level of development that partly comes with age. Of the 77 nests deemed old enough to fledge, video revealed that 9 (12%) were force fledged ≤2 days from their average age of fledge (FF2), 1 (1%) was force fledged >2 days and ≤4 days from their average age of fledge (FF4), and 7 (9%) were depredated. Six of 66 nests (9%)

that were successful (based on FF0 criteria) had a median age >2 days younger than their predicted fledging age.

Table 5.4. Field cues used by observers to identify nest fate. Odds ratios refer to the likelihood that the presence of each cue was associated with a successful nest. Nest fate was determined from video and varies depending on the presumed fate of force-fledged nestlings: none survived (FF0), or those ≤2 days (FF2) or ≤4 days (FF4) younger than their predicted fledge age survived.

		Odds ratio (± 95% CI)		
Cues predicting success	n[a]	FF0	FF2	FF4
Old enough	127	25.9 (9.4–71.0)	63.2 (20.6–194.6)	40.0 (14.1–113.3)
Nest flattened	50	18.3 (4.1–81.4)	25.3 (5.5–116.1)	26.1 (5.4–125.4)
Fecal droppings out of nest	116	7.5 (3.3–17.2)	8.3 (3.5–19.9)	10.9 (4.2–28.1)
Fecal droppings in nest	116	3.7 (1.6–8.6)	5.6 (2.1–15.0)	7.7 (2.5–23.7)
Adult observed or heard	119	4.6 (1.9–10.8)	3.0 (1.3–7.2)	2.3 (0.98–5.6)
Fledgling observed or heard	119	4.4 (0.50–39.0)	[b]	[b]
Loss of nest contents	118	0.21 (0.04–1.05)	0.15 (0.03–0.77)	0.12 (0.02–0.63)
Nest damaged	117	0.25 (0.09–0.66)	0.27 (0.11–0.69)	0.26 (0.10–0.67)

[a] Number of nests where presence or absence of cue was recorded.
[b] Not recorded in the field.

Nest condition also was a useful cue identifying nest fate (Table 5.4). Damaged nests had odds of approximately 1 in 4 of being successful compared with nests that were not damaged. Flattened nests were >18× more likely to have been successful than nests that were not flattened. Fecal droppings were a useful cue for identifying successful nests, particularly if the droppings were outside the nest (Table 5.4). In both cases the strength of this association increased as younger force-fledged nestlings were considered successful. It is not known whether fecal droppings served as a cue to predators or if fecal droppings were correlated with nestling development and propensity to flee the nest if approached by a predator. Adults were more likely to be detected at successful nests, but the strength of this association was weak and declined as increasingly younger force-fledged young were considered successful. Loss of nest contents or the presence of fledglings were not useful predictors of nest fate (Table 5.4), but observers did not search extensively for fledglings on the final nest visit.

5.4. Discussion

To our knowledge, this is the first study to consider how error in estimating nest success affects estimates of population growth. We found that field-based estimates of nest fate in our system were reasonably accurate, ranging from 83% to 87% correct, and that the probability of nest survival was similar between field and video estimates, particularly when force-fledged nestlings ≤2 days younger than their predicted fledge age were considered successful (FF0). Similar findings on the accuracy of nest-fate and nest-survival rates have been previously reported (Pietz and Granfors 2000, Williams and Bohall Wood 2002). Nest productivity was overestimated in the field by as much as 35% in our system because of error in fate estimation, partial predations, and force fledging. Together, error in our field estimates of nest fate and nest productivity resulted in population growth rate being overestimated by ~6%.

Our estimates of nest survival and population growth are meant to illustrate the effects of estimation error only and are not intended to describe our study population as a whole. First, our values of adult and juvenile survival have no empirical basis in our study and were chosen for illustrative purposes only. However, the 6% difference between field and video-based estimates of lambda are independent of survival, so long as the assumption of juvenile survival being half of adult survival (Ricklefs 1973) is maintained. Second, we focused on video-monitored nests. Because we did not place cameras at early-stage nests, all video nests had to have survived laying and early incubation, when predation rates can be high (Martin et al. 2000). For this reason, we assume that our estimates of population growth rate are likely higher than actual values, and we caution others against drawing inferences from them.

Virtually all nest survival studies define nest fate as “fledged” or “failed.” We have clearly demonstrated that nest fate is not binary or so easily defined. In our boreal forest system, 21% of nests experienced some other fate; predators partially depredated 6% of nests and partially or entirely force fledged the young from another 14% of nests. Predator-mediated force fledging has previously been documented by other nest video studies (Thompson et al. 1999, Pietz and Granfors 2000, Weidinger 2006), but the prevalence of force fledging is poorly understood in many systems. The survival probability of force-fledged young also is unknown, but we expect that it is lower than that of fledged young. More than one-third of all force-fledged nestlings were >2 days younger than their predicted fledge age. Several researchers have described positive relationships between juvenile survival and nestling condition (Perrins 1965, Krementz et al. 1989, Monrós et al. 2002, Vitz and Rodewald 2011). Nestlings forced from the nest earlier than intended may be less well developed than nestlings that fledge at a later age. The utility of adult presence as a field cue for identifying successful nests declined as increasingly younger force-fledged young were considered successful. This further suggests a positive effect of fledging age on juvenile survival probability. Predators also may pursue and kill force-fledged young.

Thompson et al. (1999) resighted 3 of 4 nestlings forced from the nest by a snake, which highlights that this threat is not applicable to all predators. Additional work is required to quantify the effects of nestling age and force fledging by predators on juvenile survival.

Final nest visits were frequently to an empty, undisturbed bowl. In the absence of cues indicating that the nest had failed, observers followed protocol and common practice and concluded that the nests were successful if their midpoint age was ≤2 days of the predicted fledge date. However, fate and productivity were most frequently misidentified when fating occurred immediately prior to the predicted fledge date and when nests were depredated because the default was to classify these nests as successful in the absence of any evidence to suggest otherwise. Estimates of nest fate and nest productivity were most accurate when nestlings were >2 days younger than the predicted age of fledge or when nestlings were older than the predicted age of fledge and when nests were successful. Being old enough is a precursor and an obvious cue that absent nestlings may have fledged. However, the midpoint between the final two visits should only be used as a guideline, particularly if the duration between nest visits is several days. A nest that was last active several days prior to the expected fledge date could have a midpoint age ≤2 days from fledge on the terminal visit even though nestlings were >2 days from fledge during a portion of that exposure period. The fate of these nests are more likely to be estimated incorrectly in the field than that of nests too young to fledge or nests whose entire exposure period between the last active and terminal visit is ≤2 days from fledge. Censoring all data after the earliest possible age of fledge (*sensu* Manolis et al. 2000, Stanley 2004, Weidinger 2007) would not be appropriate in the present study because daily survival rate is not constant in the late nestling stage and estimates of nest survival are therefore biased. In our current example, censoring the >10 days age category and exponentiating the daily survival rate estimate of nests aged 8–10 days for the remaining 4 days of the 24-day nesting period resulted in nest survival estimates between 0.52 and 0.55. The bias was largest for the field estimate, which was overestimated by 8% on average. Video-based estimates of nest survival were overestimated 2–7%, on average, for FF0 and FF4 fates, respectively. We suggest that reducing the duration between visits to late-stage nests would increase the applicability of midpoint age estimates to fledging propensity (Martin et al. 1997). Our video data also show that ~10% of nestlings fledged >2 days prior to their average age of fledge. Therefore, observers should use the midpoint age estimate as a cue, not a requirement, to be considered together with other available evidence.

Observers also should avoid concluding that an empty, undisturbed late-stage nest was successful. In the present study this resulted in nest survival and nest productivity being consistently overestimated, particularly when force-fledged young were assumed to have failed. Nest fate and productivity were most frequently misidentified at nests depredated by Red Squirrels, avian predators, and large mammals. Our video data show predators as large as martens and bears emptying a nest of its contents without disturbing the nest structure. Nests depredated by small mammals were less likely to be misidentified. Other studies have similarly documented predators taking nestlings without disturbing the nest (Thompson et al. 1999, Pietz and Granfors 2000, McCallum and Hannon 2001, Williams and Bohall Wood 2002, Liebezeit and George 2003). Because the presence of adults as a field cue was weakly associated with successful nests, we suggest that researchers spend additional time searching for young or adults when defaulting to a successful fate estimate.

Locating fledglings may be the most conservative means of assessing nest fate and nest productivity, but this can be time consuming and impractical, particularly if family groups disperse widely, the habitat is complex, and the local breeding population is synchronous and unmarked (see also Martin and Geupel 1993). Using failure as the default fate when fledglings are not found would result in nest survival and nest productivity being underestimated when family groups or individual fledglings are difficult to locate. Instead, we encourage researchers to focus on nestling age, nest condition, and the presence of fecal droppings outside of the nest bowl to improve accuracy in identifying successful nests in the field. Together these cues are indicative of nestlings that are sufficiently developed to leave the nest cup and capable of, and possibly prepared for, fledging.

Observer accuracy in estimating nest fate also could be improved by devoting increased attention to training field personnel to distinguish successful and damaged nests. We found that flattened nests were underreported compared with other cues, possibly because the term was too vague or subjective to be of any use or because it was inapplicable in our system. Written comments by observers suggested that damage and flattened nests were difficult to distinguish and that their interpretation often depended on other available cues. Observers were more likely to report that a nest deemed successful looked “used but intact” rather than flattened. In the context of the current study this typically indicated that the bowl appeared dirty in color and was compacted into a well formed cup. Nests of some species (e.g., Chipping Sparrow) often collapse just prior to fledging (J. R. Ball and E. M. Bayne pers. obs.), making nest integrity a problem. Only on rare occasions was the nest intact and the rim completely flattened. We suggest that researchers develop their own working definitions of used and damaged nests to assist field observers in distinguishing among these cues. Using video to link known fates to final nest condition would improve observer accuracy and should be used to evaluate whether nest success and nest productivity measures show differential biases in estimation error between variables of interest (i.e., habitat types).

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Appendix 5.1. Nest fate and nest productivity for a suite of boreal forest songbirds as estimated by field and video observation. Nest fate and productivity as determined by video vary depending on whether all force-fledged nestlings are presumed dead (FF0) or nestlings ≤2 days (FF2) and ≤4 days (FF4) from the predicted age of fledge are presumed to have survived.

		Nest fate									Nest productivity [a] (number fledged/nest ± SD; *n*)			
		Field		Video							Field	Video [b]		
Common name (Latin name)	*n*	Fledge	Depredated	Age fledge [a] (days ± SD)	Fledge	Depredated	Fledge + force-fledge	Fledge + depredated	Depredated + force-fledge	Force-fledge	Fledge	FF0	FF2	FF4
American Redstart (*Setophaga ruticilla*)	2	2	0	7	1	0	1	0	0	0	4.0 (–; 1)	4.0 (–; 1)	4.0 (–; 1)	4.0 (–; 1)
American Robin (*Turdus migratorius*)	5	3	2	14 (± 1.4)	1	3	0	1	0	0	2.0 (± 1.7; 3)	2.5 (± 2.1; 2)	2.5 (± 2.1; 2)	2.5 (± 2.1; 2)
Chipping Sparrow (*Spizella passerina*)	23	9	14	9.6 (± 1.4)	9	9	0	1	3	1	3.9 (± 0.7; 7)	3.5 (± 1.2; 8)	3.1 (± 1.3; 11)	3.1 (± 1.3; 11)
Dark-eyed Junco (*Junco hyemalis*)	7	3	4	12	1	5	0	0	1	0	4.3 (± 0.6; 3)	4 (–; 1)	4.0 (± 0.0; 2)	4.0 (± 0.0; 2)
Hermit Thrush (*Catharus guttatus*)	8	4	4	12.3 (± 0.6)	4 [c]	3	0	0	1	0	3.5 (± 1.0; 4)	3.3 (± 1.2; 3)	3.3 (± 1.2; 3)	3.5 (± 1.0; 4)
Least Flycatcher (*Empidonax minimus*)	3	2	1	13.5 (± 0.7)	2	1	0	0	0	0	4.0 (± 0.0; 2)	4.0 (± 0.0; 2)	4.0 (± 0.0; 2)	4.0 (± 0.0; 2)
Magnolia Warbler (*Setophaga magnolia*)	1	1	0	–	0	1	0	0	0	0	3.0 (–; 1)	0.0 (–; 0)	0.0 (–; 0)	0.0 (–; 0)
Northern Waterthrush (*Parkesia noveboracensis*)	1	0	1	-	0	1	0	0	0	0	0.0 (–; 0)	0.0 (–; 0)	0.0 (–; 0)	0.0 (–; 0)

Ovenbird (*Seiurus aurocapilla*)	11	10	1	8.9 (± 0.6)	7	2	0	2	0	0	4.4 (± 1.0; 9)	4.0 (± 1.4; 8)	4.0 (± 1.4; 8)	4.0 (± 1.4; 8)
Swainson's Thrush (*Catharus ustulatus*)	48	31	17	11.9 (± 1.5)	18	16	3	2	8	1	3.6 (± 0.6; 29)	3.0 (± 1.0; 20)	3.1 (± 0.9; 24)	3.1 (± 1.0; 28)
Tennesee Warbler (*Oreothlypis peregrina*)	12	8	4	9.5 (± 0.8)	8	3	0	0	1	0	5.5 (± 0.5; 6)	5.2 (± 1.2; 6)	4.6 (± 1.9; 7)	4.6 (± 1.9; 7)
White-throated Sparrow (*Zonotrichia albicollis*)	4	4	0	9.8 (± 0.5)	3	0	0	1	0	0	3.5 (± 1.7; 4)	2.8 (± 2.1; 4)	2.8 (± 2.1; 4)	2.8 (± 2.1; 4)
Yellow-rumped Warbler (*Setophaga coronata*)	2	1	1	10	1	1	0	0	0	0	4.0 (–; 1)	4.0 (–; 1)	4.0 (–; 1)	4.0 (–; 1)
Total	127	78	49		55	45	4	7	14	3	3.9 (± 1.0; 70)	3.5 (± 1.3; 56)	3.4 (± 1.3; 65)	3.4 (± 1.3; 70)

[a] Excludes nests where number fledged was <1 or fate of one or more nestlings is unknown

[b] FF0 excludes force-fledged young. FF2 and FF4 assume that force-fledged nestlings were successful if they were ≤2 days and ≤4 days, respectively, of their species' average age of fledge.

[c] Camera battery failed at one nest immediately following fate of first two nestlings. Fate of remaining two nestlings unknown but presumed similar to siblings.

Chapter 6. Nest predation and edge effects in the boreal forest

6.1. Summary of thesis

Results from this study suggest that edges created by oil and gas linear features do not have strong negative effects on the nesting success or the spatial distribution of boreal forest songbirds in western Canada. To assess the potential for negative edge effects required that I first identify which predators were chiefly responsible for depredating nests and determine whether they responded positively to edges (Thompson 2007, Lahti 2009). Prior to this study, our understanding of the boreal nest predator community was based largely on artificial nest studies (e.g., Bayne and Hobson 1997, Song 1998, Cotterill and Hannon 1999; but see McCallum and Hannon 2001, Hannon et al. 2009). I found that these studies overemphasized the importance of small mammals and corvids as nest predators and underemphasized the importance of raptors and of red squirrels in particular (Chapter 2). I documented 11 different species of nest predators, all of which were endemic to the boreal forest. Red squirrels were the dominant predator of both eggs and nestlings in both study sites. Sharp-shinned Hawks, American marten, and red-backed vole were also identified as important nest predators.

I also did not find strong support for a positive effect of increasing edge proximity on the spatial distribution of the majority of nest predators. Only American black bears and deer mice were more commonly found near edges but these species depredated few nests (< 4% each; Chapter 3). I also did not find support for a positive effect of increasing edge proximity on the probability of nest predation by each predator species. The apparent lack of a positive numerical or functional response by the majority of nest predators to linear feature edges suggests linear feature edges may not present a higher risk of nest predation for songbirds.

Concern has been raised that birds nesting in anthopogenically fragmented landscapes, particularly those in western North America, may not be capable of accurately assessing habitat quality (Bock and Jones 2004). This has important implications not only for individual fitness and population dynamics, but for researchers that commonly use measures of bird abundance to prioritize habitats for conservation. I used a common suite of habitat variables to assess variation in nesting success and local abundance to determine if birds were preferentially using habitats with similar qualities to those with higher reproductive success (Chapter 4). I found weak support that ground nest fate was higher near edges and strong support that both ground and shrub nesting birds were more abundant near edges compared to forest interiors. This suggests edge habitats are of higher quality compared to interiors, particularly for ground nesting species. None of the habitat variables I considered received support for explaining variation in nest productivity. My metric of productivity (number of young fledged) may have been too coarse to detect subtle differences in habitat quality that may be related to edges.

I found weak support that both ground and shrub nest success were marginally lower when red squirrels were present. However, I failed to find support for an effect of vegetation (shrub density or numbers of alternate nest sites) on nest fate for either guild and neither guild used areas with more vegetation when red squirrels were abundant. Squirrels are capable of learning where to find nests (Pelech et al. 2010) and microhabitat characteristics may be ineffective at reducing nest predation risk by squirrels. Instead, I found strong support for a negative effect of red squirrel abundance on the abundance of both guilds. Together, these results suggest ground and shrub nesters are capable of assessing spatial variation in habitat quality and are preferentially using habitats with higher reproductive potential. Researchers should feel confident using abundance as a metric for prioritizing habitats for their conservation in landscapes similar to this study. A similar recommendation cannot be made for canopy nesting species without further study (see below; Chapter 4).

Conservation programs aimed at birds should target high quality source habitats that are capable of sustaining populations (i.e., $\lambda \geq 1$). Nest fate and nest productivity are key demographic parameters for understanding songbird population dynamics yet little consideration has been paid to assessing the accuracy of these field-based estimates. I compared assessments of fate and productivity of video-monitored nests that were made in the field with those later determined in the lab to determine if field-based estimates were accurate (Chapter 5). Fate is typically defined as ≥ 1 nestling successfully fledged and I found that field-based estimates of fate were reasonably accurate. However, predators partially depredated 6% of nests and partially or entirely force-fledged the young from an additional 14% of nests. Field-based assessments overestimated nest fate by 17% if force-fledged young are assumed to have failed. Nest productivity was consistently overestimated by 10 - 35% regardless of the presumed fate of force-fledged young. Together, these errors resulted in population growth rate being overestimated by as much as 7%. The fate of these force-fledged young is unknown. Resolving this uncertainty would improve our assessments of habitat quality and our models of population dynamics

6.2. Discussion and areas for future research

I determined that nest fate responded, albeit weakly, to edge proximity and the presence of red squirrels (Chapter 4). Here I consider whether different combinations of these parameters create source ($\lambda > 1$) or sink ($\lambda < 1$) habitats in my study ($\lambda = S_a + S_j \times ([p \times y(2 - p)]/2)$; Chapter 5). I also consider whether source habitats are reclassified as sinks when I account for observer error in estimating nest fate and nest productivity. Daily nest survival rate for each nest guild responded similarly to increased distance from an edge and increased risk of predation; ground and shrub nests were negatively related to both parameters whereas canopy nests were positively related to both parameters. Therefore I estimated daily nest survival probability at edges in the absence of squirrels and at 400 m from an edge in the presence of squirrels. The remaining nest survival model parameters where held constant at average values. Probability of nest survival (p) was calculated by exponentiating daily probability values by the average stage duration for each guild. I applied estimates for the incubation stage to both the incubation and laying stages because I had little data for the latter stage and because my estimates for some parameter combinations were too low to be plausible. Because variation in nest productivity (*y*) was not explained by edges or squirrels, I used average values of the number of young fledged per successful nest for each nesting guild (ground = 4.28 ± 0.10 [1 SE], shrub = 3.48 ± 0.06, canopy = 3.07 ± 0.14). Adult (S_a) and juvenile (S_j) survival were held constant at 0.6 and 0.3, respectively. I divided my field-based estimate of λ by 1.07 to calculate λ’, which represents finite rate of growth assuming all force-fledged young fail to survive. CI were calculated from a Monte Carlo simulation with 2000 replicates using the method described in Chapter 5. According to field-based estimates of λ, the combinations of edge proximity and red squirrel presence that were associated with higher nest survival rates were source habitats for all nesting guilds (Table 6.1). However, when I accounted for potential observer error (λ’), those habitats identified as the highest quality for shrub and canopy nests were no longer identified as source habitats.

Table 6.1. Probability of nest survival, field-based estimates of finite rate of population growth (λ), and video-corrected estimates of finite rate of population growth (λ’) for each nest guild at different combinations of edge proximity and red squirrel presence.

Guild	Edge (m)	Squirrel	Nest survival	λ	λ'
Ground	0	absent	0.76 (0.59 - 0.87)	1.20 (1.13 - 1.25)	1.12 (1.05 - 1.16)
	400	present	0.37 (0.21 - 0.53)	0.98 (0.85 - 1.10)	0.92 (0.78 - 1.03)
Shrub	0	absent	0.59 (0.48 - 0.69)	1.03 (0.98 - 1.08)	0.97 (0.91 - 1.01)
	400	present	0.44 (0.34 - 0.54)	0.96 (0.90 - 1.01)	0.89 (0.83 - 0.95)
Canopy	0	absent	0.30 (0.01 - 0.71)	0.82 (0.61 - 1.02)	0.77 (0.57 - 0.96)
	400	present	0.90 (0.58 - 0.99)	1.05 (0.97 - 1.10)	0.98 (0.92 - 1.03)

These estimates of λ and λ’ highlight the importance of potential errors in field-based assessments of habitat quality. Perhaps more importantly, they highlight the importance of resolving uncertainties in other demographic parameters affecting population dynamics. For example, λ is highly sensitive to variation in adult and juvenile survival (Saether and Bakke 2000, Donovan and Thompson 2001, Flaspohler et al. 2001). These parameters are poorly studied and undocumented for most species of songbirds (Faaborg et al. 2010). Fecundity also is important to population dynamics, particularly for short-lived species (Saether and Bakke 2000, Donovan and Thompson 2001). Nest success is the most commonly studied demographic parameter for birds (Faaborg et al. 2010). I demonstrated that field-based estimates consistently overestimate productivity because of partial predations and force-fledging by predators. Whereas λ' assumed that all force-fledged young failed to survive, the fate of force-fledged young is not known. Older nestlings and those force-fledged by predators less likely to pursue chicks off the nest may have a higher probability of survival (Thompson et al. 1999, Streby et al. 2013). If I assumed all force-fledged young survived, high quality habitats for canopy nests are identified as being stable (λ = 1.00 [0.93 – 1.05]); the best habitats for shrub nests are still identified as sinks, however (λ = 0.98 [0.91 – 1.01]). I also did not have a reasonable sample size to estimate nest survival during laying and I assumed that nest survival during this period would be similar to that during incubation. However, adults that leave partial clutches unguarded against predators during laying may incur higher rates of nest predation (Latif et al. 2012). Further research aimed at clarifying these uncertainties is necessary to develop effective bird conservation programs.

This study focused on one type of edge in one type of forested habitat in two regions of the western boreal forest that were both relatively intact and far from alternate habitat-types. I did not find strong support for a negative effect of edge proximity on nest fate. Only the predicted fate of canopy nest fate was marginally lower nearer edges and only when squirrels were absent and tree density was low, or squirrels were present and tree density was high (Fig. 4.3). In contrast, the predicted fate of ground nests was marginally higher near the edge. When any study finds no effect, a concern is statistical power. While having one of the largest sample sizes of nests monitored in the boreal forest, it is possible I might have drawn different conclusions with larger sample sizes. However, I found that the average (weighted by 1/SE) daily survival rate of shrub and ground nests increased 0.2% to 1.0%, respectively, between the forest interior and the forest edge (daily survival rate of shrub nests increased from 0.963 in the forest interior to 0.965 at the forest edge; daily survival rate of ground nests increased from 0.970 in the forest interior to 0.980 at the forest edge). Assuming a nest period duration of 30-days and a constant daily nest survival rate, the probability of a shrub and ground nest surviving at an edge increased 6.4% to 36%, respectively, compared to a forest interior. Therefore, a larger sample size of nests would not have given me more power to detect a negative edge effect on the fate of shrub and ground nests because the pattern of nest survival is in the opposite direction.

Previous studies that have found strong evidence of a negative edge effect on nest fate and that have provided an estimate of effect size suggest edges had a larger effect on nest fate than what I found. For example, Driscoll and Donovan (2004) report that daily survival rate of Wood Thrush nest decreased 1.9% from 0.971 at interior nests (> 200 m from a forest-field edge; n = 25 nests) to 0.953 at edge nests (≤ 200 m from a forest-field edge; n = 110 nests). Assuming a nest period duration of 30-days and a constant daily nest survival rate, the probability of a Wood Thrush nest surviving at an edge decreased 43% compared to a forest interior. King et al. (1996) report a similar 50% reduction in nest period survival for Ovenbirds at forest-clearcut edges (n = 30 nests) compared to forest interiors (n = 24 nests) during one year of study. In this study the average daily survival rate of canopy nests decreased 0.6% from 0.998 in the interior to 0.992 at the forest edge, which resulted in a 17% reduction in nest period survival. The difference in the magnitude of the negative edge response between this study and those mentioned previously provides further evidence that edge proximity did not have strong negative effects on nest fate in this study. Although a 17% reduction in nest survival appears substantial, fecundity has a small effect on the population dynamics of songbirds compared to survival (Flaspohler et al. 2001). For example, a 17% reduction in nest fate had the same effect on λ as a 2.1% reduction in adult and juvenile survival.

I used a mensurative approach to test the edge effect hypothesis. An experimental study design would potentially have provided a more powerful test with a more direct test of causality (McGarigal and Cushman 2002). However, there are a number of significant restrictions that dissuade most researchers from using such experiments to test edge effects. These include the logistics associated with implementing a replicated design at a sufficiently large scale that is relevant to nest predator space use, time lags in the abiotic and biotic responses to edge creation, and the inherent variability among landscapes that can affect results. Mensurative experiments can be highly effective when design controls such as those used here are used to minimize variation in the dependent variable that is due to factors unrelated to the variables of interest (i.e. forest type). Mensurative experiments are well suited to an information theoretic approach to select among competing models (Burnham and Anderson 2002). My statistical models also included a number of dummy variables to control for additional variation unrelated to my parameters of interest. These dummy variables were present in all models, including the NULL models which did not contain a parameter of interest. Because variation in the dummy variables was largely minimized by study design, there was little variation available in some factors (i.e. tree species composition) to better explain variation in the dependent variable. This frequently resulted in small difference in log likelihood values within a model set. This is not indicative of poor model fit per se, but a lack of explanatory power by those variables of interest that did have a reasonable amount of variation (i.e. distance to edge). While I did not compare support between the NULL model and a model that did not contain any covariates (i.e., an intercept-only model) I suspect the NULL model would have been strongly supported.

Pooling species into nest substrate guilds may have masked important edge effects occurring at the species level. However, my primary interest was the effect of edges on the probability of nest predation and nests in different strata have inherent differences in nest predation risk (Martin 1993). I did not consider other ecological groupings such as edge vs. forest interior specialists because of the uncertainty associated with identifying species with forest interiors (Villard 1998). I also did not consider species-specific responses to edge because the sample sizes of nests across the distance to edge gradient was small for the majority of species and there was little reason to suspect that species would have inherently different rates of nest predation that were not largely explained by nesting substrate.

Several habitat and nest predator attributes commonly associated with negative edge effects were not present in this study, which may explain my results. First, negative edge effects commonly result from positive numerical or functional responses to edges by corvids or an influx of predators and brood parasites from adjacent habitat types (Chalfoun et al. 2002, Batary and Baldi 2004). Gray Jays were the most commonly detected corvid in this study (Chapter 3) and they are purported to be important nest predators based on anecdotal observations and artificial nest studies (Ouellet 1970, Strickland and Ouellet 2011). The results from this study indicate their role as a nest predator has been overestimated. We did observe jays depredating two nests not monitored by cameras (n = 665) but they were not recorded depredating camera-monitored nests (n = 145; Chapter 2).

I also recorded coyotes Coyotes (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), American Crows (*Corvus brachyrhynchos*), and Brown-headed Cowbirds (*Molothrus ater*) in the southern study site. These species, which are more commonly associated with agriculture, were either making forays into the forest from nearby agriculture (approximately 40 km away) or had taken up residence in the forest. I found no evidence that agriculture-associated species were depredating nests in this study (Chapter 2). These species were rarely detected compared to endemic nest predators, which suggest the southern site was located too far from agriculture for non-forest species to have a detectable effect on nest fate. There also is no evidence to suggest that increased proximity to agriculture would result in a shift in the nest predator community to agriculture-associated species and/or higher rates of predation near edges. For example, McCallum and Hannon (2001) and Hannon et al. (2009) found that American Redstart nests in the southern boreal forest with an extensive agriculture matrix were depredated by forest-associated predators and that predation was unrelated to forest edge proximity. They did, however, find that 12% of nests were parasitized by cowbirds. Cowbirds movements are closely tied to agriculture (Howell et al. 2007). However, the presence of cowbirds on my study plots indicates they are capable of travelling long distances into the forest, possibly by using linear features as travel corridors. Birds nesting near edges in forests more closely connected to agriculture by linear features may experience increased rates of brood parasitism near edges. Research on the movements of cowbirds in the boreal forest are needed to determine whether linear features connected to agriculture facilitate the movement of cowbirds into the forest.

Second, local edge effects tend to be stronger in more fragmented landscapes (Stephens et al. 2003, Driscoll and Donovan 2004, Lloyd et al. 2005). Linear features density differed between my northern and southern sites (1.05 ± 0.03 km/km^2 and 2.43 ± 0.13 km/km^2, respectively) but I failed to find support for site-related difference in nest fate. I did find support for site-related differences in abundance and in the edge response of some nest predators by some survey methods (Chapter 4). Most predators were more abundant in the south. Deer mice also were more common near edges in the south as were Gray Jays and red squirrels by one survey method. The remaining predators tended to be less common near edges or showed no evidence of an edge response. However, there is no clear explanation to suggest these differences were related to edge density rather than other differences between sites. Gray Jays and deer mice are expected to increase in abundance and be more prevalent near edges in fragmented habitats (Bayne and Hobson 1997, Chalfoun et al. 2002, Ibarzabal and Desrocher 2004, Thompson et al. 2008; but see Ibarzabal and Desrocher 2005) whereas squirrels, marten, and red-backed vole are all expected to show neutral or negative responses to loss of forest cover and increased edge density (Bayne and Hobson 1997, 1998, Chapin et al. 1998, Hargis et al. 1999, Tewksbury et al. 1998, Poole et al. 2004, Ibarzabal and Desrocher 2005, Hannon et al. 2009, Tigner 2012). The lack of support for a difference between sites and for a positive response by predators to edges may be due to the low level of fragmentation. Maximum plot-level line density in this study was 4.7 km/ km^2 whereas line densities can exceed 26 km/km^2 in some areas of the western boreal forest (Tigner 2012). However, as suggested above, many of the dominant nest predators are expected to decrease in abundance with increasing fragmentation. Therefore, higher densities of linear feature density are not predicted to result in increased rates of nest predation or negative edge effects.

The diversity of species in the nest predator community necessitated the use of several survey methods to quantify their edge-related distribution. Doing so resulted in conflicting edge responses between methods for some species surveyed by multiple methods. A consistent edge response across survey methods would provide strong evidence about the edge-related distribution of a species (e.g., black bear; Table 3.6). Conversely, an inconsistent response among methods increases the uncertainty in the edge response (e.g., Sharp-shinned Hawks and American marten; Table 3.6). Such inconsistencies highlight potential incompatibilities between some methods and some types of predator species. For example, both accipitrine hawks and marten are quiet, elusive species that may be more readily detected by observers on open linear features compared to within a closed forest during random walk surveys. Differences between methods may also explain inconsistencies among the results of different studies.

Finally, I focused on linear features edges in mixed wood forest. Several other edge types, both natural and anthropogenic, and other forest types were not considered. Linear features share one or more attributes with other types of edge. For example, they often lack woody vegetation and they create an abrupt transition from forest to clearing. However, linear features are also unique in many ways. Most obviously, they are linear corridors through the forest that often extend several kilometers in length to intersect other linear features in a network of clearings. They are also narrow compared to many other disturbances. In this study, some lines were sufficiently narrow that the canopy was closed. This undoubtedly limits the magnitude and depth of abiotic effects in the forest (Murcia 1995, Harper et al. 2005), which may mitigate the effect of edges on habitat quality and species distributions. Edge effects may also differ among forest types due to differences in abiotic responses and differences in the abundance and composition of the predator and prey communities. Further study is needed in multiple landscapes with different edge densities and edge types to determine if and under what conditions the results from this study can be generalized to other boreal regions.

6.3. Research contribution

Habitat fragmentation and degradation are considered to be among the primary threats to bird populations in North America, including those in the boreal forest (Johnson 2007, Wells 2011, North American Bird Conservation Initiative 2012). The potential for negative edge effects are of particular concern in the western boreal forest due to the proliferation of edge habitat associated with continued growth in the energy sector. Negative edge effects are commonly due to increased rates of nest predation near edges. This study makes an important contribution to the edge effect literature by focusing on the predators (Lahti

2009). To my knowledge, this is the first study to identify the predators of real songbird nests in the boreal forest and to document their numerical and functional response to edges. This is also the first study to assess the accuracy of field-based estimates of nest success (see Streby et al. 2013 for a more recent example). Finally, I assessed the effects of edges and predation risk on nesting success and confirmed that abundance is a reliable metric for assessing habitat quality for boreal songbirds (*sensu* van Horne 1983). The results from this study should prove useful for assessing the potential impacts of future development in the boreal forest, for designing efficient and effective conservation programs targeted at boreal birds (e.g. Thompson and Ribic 2012), and for researchers and practitioners whose work relies on field-based estimates of nesting success.

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