

ENERGY SECTOR EDGE EFFECTS ON SONGBIRD NEST FATE AND NEST PRODUCTIVITY IN THE BOREAL FOREST OF WESTERN CANADA: A PRELIMINARY ANALYSIS

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Abstract. Western Canada's boreal forest is becoming increasingly fragmented by pipelines, seismic lines, and service access roads. These linear features create edge habitat, which is assumed to negatively impact songbirds. However, the effect of edges on boreal forest songbirds is largely unknown. Abundance estimates, which are often used to assess habitat change for songbirds, assume that individuals selectively settle in high quality habitats, rather than choosing to settle in habitats that ultimately result in lower reproductive success. We considered the reproductive (nest survival and nest productivity) and abundance responses of songbirds to forest edges in two boreal landscapes with different linear feature densities. Contrary to our prediction, reproductive success was not lower in the more fragmented landscape, which may be too far from a non-forested system to experience a large influx of non-forest predators or Brown-headed Cowbirds (*Molothrus ater*). We also found that survival of ground nests improved, rather than declined as predicted, near the forest edge. Survival of above-ground nests and productivity of ground and above-ground nests were unaffected by edge proximity. Songbird abundance increased near the forest edge, which supports the use of abundance to measure habitat changes for songbirds in regions similar to our study sites. However, we caution that not all edges are equal and that our results for linear features in remote boreal regions may not have the same effect as other anthropogenic edges created elsewhere.

Key Words: nest success, nest predation, boreal forest songbirds, edge effects, energy sector.

EFFETS DES BORDURES PRODUITES PAR LE SECTEUR ENERGETIQUE SUR LE DESTIN ET LA PRODUCTIVITE DES NIDS DE PASSEREAUX DE LA FORET BOREAL DE L'OUEST CANADIEN : ANALYSES PRELIMINAIRES.

Résumé. La forêt boréale de l'Ouest canadien devient de plus en plus fragmentée par les pipelines, lignes d'exploration sismique et chemins d'accès. Ces structures linéaires créent un habitat de bordure qui est reconnu pour avoir des impacts négatifs sur les passereaux. Cependant, l'effet des bordures sur les passereaux de la forêt boréale demeure inconnu. Les estimations d'abondance, qui sont souvent utilisées pour évaluer des changements dans l'habitat de passereaux, assument que les individus sélectionnent les habitats de haute qualité plutôt que de choisir de s'établir dans des habitats qui résultent ultimement en un moins bon succès reproducteur. Nous avons considéré la reproduction (survie et productivité des nids) et l'abondance de passereaux aux bordures de forêts dans deux paysages boréaux avec différentes densités de structures linéaires. Contrairement à notre prédiction, le succès reproducteur n'était pas plus faible dans le paysage plus fragmenté, qui est peut-être trop éloigné d'un système non-forestier pour subir une importante venue de prédateurs non-forestiers ou du vacher à tête brune (*Molothrus ater*). Nous avons également trouvé que la survie des nids au sol augmente plutôt que de diminuer à proximité de la bordure de forêt comme nous l'avions prédit. La survie des nids au-dessus du sol et la productivité des nids au sol et de ceux au-dessus du sol n'étaient pas affectées par la proximité de la bordure. L'abondance de passereaux a également augmenté près de la bordure de forêt, ce qui supporte l'utilisation de l'abondance comme mesure des changements dans l'habitat des passereaux dans des régions similaires à nos sites d'étude. Cependant, il faut être prudent puisque les bordures ne sont pas toutes égales et que nos résultats pour les structures linéaires dans une région isolée de la forêt boréale peuvent ne pas avoir le même effet que d'autres bordures anthropiques créés ailleurs.

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INTRODUCTION

The boreal forest of North America represents one quarter of the world's remaining intact forests, and it is an important resource to nearly half of all North American birds (Blancher and Wells 2005). However, the growth in energy sector activity in Canada's western boreal forest is rapidly changing the face of this landscape. Of particular concern is the increasing numbers of seismic lines and pipelines fragmenting the forest (Schneider et al. 2003). These linear features have no natural disturbance analogue and, although they are expected to alter conditions in the adjacent forest edge, their ecological footprint in the boreal is largely unknown.

Abundance estimates of songbirds are a common method of assessing the effects of habitat alteration. However, an implicit assumption of using abundance to assess habitat quality is that individuals selectively settle in higher quality habitats, i.e., density is positively correlated with habitat quality. Several researchers have questioned this assumption (Gates and Gysel 1978, Van Horne 1983, Vickery et al. 1992), particularly when anthropogenic habitat alteration creates an ecological trap (Bock and Jones 2004). 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 2001). For this reason, reproductive success can be a more reliable indicator of local habitat quality than abundance (Temple and Wiens 1989). Therefore, many researchers have chosen to examine whether nest predation near the habitat edge changes the reproductive success of songbirds relative to forest interiors (Paton 1994, Hartley and Hunter 1998, Batary and Baldi 2004).

Here we consider edge-related changes in habitat quality for nesting boreal forest songbirds by monitoring nest fate and nest productivity with respect to proximity of an energy sector linear feature. Nest predators commonly destroy the entire nest and nest fate is a useful indicator of edge-related differences in predation probability. However, because nest fate does not consider partial success and therefore links weakly to annual reproductive success (Thompson et al. 2001), we also examined edge-related differences in nest productivity. This study was conducted in two boreal landscapes of differing linear feature density. The first was a northern site with a single linear feature in an otherwise contiguous forest. The second was a southern site with several linear features and a greater proximity to non-forest habitats. We

predicted stronger negative edge effects on nest fate and nest productivity in the southern landscape given the greater habitat fragmentation and the observed presence of human-associated predator species that are not native to the boreal forest and Brown-headed Cowbird (*Molothrus ater*) brood parasites in the south. We discuss our results with reference to the local predator communities and to a preliminary analysis of edge-related variation in songbird abundance in the northern study site.

METHODS

STUDY AREA

Our study plots were established in mature, closed stands of boreal 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 generally 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 mid-story canopy was typically absent.

We focused on forest edges associated with energy sector linear features (pipelines, seismic lines, and limited-use service roads). This was done to minimize confounding the effects associated with habitat edges with additional effects associated with habitat loss (e.g., isolation), adjacent habitat type (e.g., forestry cut blocks or agriculture), and additional effects from high-use roads (e.g., vehicle mortalities and vegetation dusting). In our study, all energy sector linear features can be generally characterized as open, straight corridors that often extend several kilometers in length. In regions of high energy sector activity, these linear features periodically intersect creating a network of open corridors. The linear features in our study varied in width and state of revegetation. Pipelines were typically 25 m wide, seismic lines were typically 8 m wide, and service roads ranged between 12 and 25 m. Most lines were kept free of extensive woody vegetation by periodic clearing and by occasional ATV use.

Data were collected from two regions with different levels of energy sector activity. We established six 42-ha plots at a northern site near Fort Simpson, NT (61°52'N, 121°20'W) in 2005 and 2006. Each plot in the northern site was adjacent to a single linear feature (hereafter low-impact site). We also established seven 24-ha plots at a southern site in the Chinchaga

Forestry Region, AB (57°18'N, 118°23'W) in 2006. We added two additional plots to the southern study site the following year for a total of nine plots in 2007. Each plot in the southern site (hereafter high-impact site) was bordered by one or two linear features and each was bisected by one or more additional linear features. Each plot was a minimum 1.2 km (high-impact) to 2 km (low-impact) from the other plots. Plot sizes and spatial configuration were chosen to minimize the likelihood that smaller predators would predate all nests on a single plot or that large predators would predate multiple plots (Donovan et al. 1997, Stephens et al. 2003).

NEST FATE AND NEST PRODUCTIVITY

Nest searching was performed on all six plots of the low-impact site during both 2005 and 2006. At the high-impact site we searched for nests on seven plots in 2006 and on an additional 2 plots (nine in total) in 2007. Each plot was visited every three days to search for and to monitor nests, resulting in roughly equal search effort amongst plots within each field season. Nest searchers were instructed to search each plot equally with respect to distance from the forest edge. Nest contents were recorded on each visit that the adults were absent or when inadvertently flushed from the nest. 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. Observers were instructed to visit and depart nests on different paths and to not use the same path on subsequent visits to avoid creating a visible path to the nest.

A nest was considered successful if a minimum of one nestling fledged. A nest was deemed successful when a) behavioral cues of the parent birds suggested one or more fledglings were in the immediate area, or 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). Observers did not have time to locate adults that were not in the immediate vicinity of the nest to determine if fledglings were present. 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.

Distance to the nearest anthropogenic edge was computed in ArcGIS (version 9.1) based on the GPS coordinates of each nest location (GPS positions were differentially corrected in 2006 (low-impact only) and 2007). We restricted our definition of anthropogenic edge to linear features with little-to-no vegetation regrowth in the understory based on the rationale that open linear features would more strongly influence the movement patterns of predators and habitat conditions in the adjacent forest compared to heavily overgrown linear features. The location and revegetation state of each linear feature was confirmed in the field. We also measured the width of each linear feature and used this as a buffer width in ArcGIS to determine the location of each linear feature edge when computing nest distance from the edge. Nests located on a linear feature have a distance of zero.

SONGBIRD ABUNDANCE

We conducted systematic point counts during 2005 and 2006 in the low-impact site only. Counts were conducted on all six plots used for nest searching. We used three transects per plot spaced 200 m apart and running into the forest perpendicular to the forest edge. Three survey stations were located on each transect, one centered on the pipeline edge, one centered 200 m from the forest edge, and one centered 400 m from the forest edge, for a total of nine stations per plot. We chose a distance of 200 m between plot centers to reduce the probability of double-counting the same individual.

Each count lasted 10 min during which all species heard or observed were recorded along with their estimated distance from the observer (all detections beyond 100 m were excluded from our analyses). Each survey station was visited twice annually during the breeding season (early-June and late-June) when activity levels were expected to be highest.

VEGETATION MEASUREMENTS

The vegetation structure and composition was surveyed at each point count station in the low-impact site in 2005 using a modified nest vegetation survey protocol (Martin et al. 1997). The variables used in our present analysis include tree density (counted in an 11.3-m radius from the station), percentage of trees that were deciduous, total downed woody material (number of pieces > 2 cm in diameter intersecting two perpendicular 22.6-m transects each centered on the station), percent litter cover, percent forb cover (percent cover was visually estimated), density of shrubs

(number of shrub stems were counted in five 1-m radius quadrats that were centered at the station and in four opposing directions 5 m from the station), and the percentage of shrubs that were coniferous.

STATISTICAL ANALYSES

Nest fate and nest productivity

Variation in nest fate was analyzed using a single logistic-exposure model (PROC GENMOD, SAS Institute 2002) that allowed us to consider the effects of nest-, stage-, and group-specific covariates on the daily survival probability of a nest (Shaffer 2004). Variation in nest productivity was analyzed using a single zero-truncated Poisson model (StataCorp 2007).

Both the nest fate and the nest productivity models considered three parameters of interest: study area (low-impact or high-impact), distance from the nearest anthropogenic edge (m), and nesting substrate (ground or above-ground; Martin 1993), and the interactions between distance and study area, and distance and substrate. The nest fate model also controlled for variation associated with study year (first or second season in each study area), date (standardized to the earliest date a nest was found: 22 May = 1), date \times date (values centered by subtracting the mean date from each value before multiplication to avoid collinearity with date), plot (one of 15 study plots), nesting stage (build, lay, incubation, nestling), and camera present (yes or no). The nest productivity model also controlled for variation associated with study year, date (standardized to the earliest date that fate was assessed: 8 June = 1), date \times date (values centered), plot, and clutch size (average maximum number of eggs by species and study area recorded in nests observed with a complete clutch).

We considered daily nest survival probability and nest productivity for all songbirds species combined. However, we did not include cavity nesting species because we were unable to view nest contents to count nestlings and there was insufficient time to search extensively for fledglings to assess fate. We also excluded eight nests that were abandoned due to video camera placement (see Ball et al. 2009).

Songbird abundance

We used a mixed-effects model to analyze the abundance response of songbirds to the forest edge. Data were analyzed for all songbirds, all ground-nesting songbirds, all shrub-nesting songbirds, all canopy-nesting songbirds, and for a series of relatively

common individual species. Each model included point count station as a random effect to account for the multiple visits to each station. Each model also included seven vegetation variables as continuous covariates (see above) and distance from edge as a categorical variable (edge, intermediate, or far).

A Poisson or negative binomial error distribution and log-link were used in the analyses. The decision to use a Poisson or negative binomial was based on a likelihood-ratio test that tested whether the additional term required by the negative binomial was significant or not. Our goal was not to identify the vegetation attributes that influence species but to control for potential sources of vegetation-related variability that may confound our ability to assess edge effects on songbird abundance. Therefore, we performed a backwards stepwise removal of vegetation variables (variables with $P > 0.2$ were removed) to maximize our power to detect distance from edge effects. Finally, the adjusted mean abundance of songbirds was calculated for each distance class by removing the effects of the vegetation covariates on songbird abundance.

RESULTS

We located a total of 463 nests representing 28 species in the low-impact study site and 347 nests representing 30 species in the high-impact study site. Together, this sample represents the largest number of nests ever found during a boreal songbird research project. Many of the nests in both study regions were found either on the linear feature or in close proximity to the forest edge. This edge-distribution of nests was much more skewed in the high-impact site compared to the low-impact site due to the higher density of linear features in the high-impact site (55% of the high-impact site nests were within 50 m of the forest edge compared to 24% of low-impact site nests and 10% of the high-impact site nests were beyond the maximum nest distance of 406 m from an edge that we recorded in the low-impact site).

NEST FATE AND NEST PRODUCTIVITY

The nest fate analysis models the probability of a nest surviving the interval between nest visits (Shaffer 2004) and is, therefore, restricted to nests with a minimum of two visits. Our data met this requirement for 652 songbird nests (96 ground and 275 above-ground nests in the low-impact site; 83 ground and 198 above-ground nests in the high-impact site). Daily nest survival probability did not differ between low- and

high-impact sites (0.971 v. 0.966, respectively; $P = 0.645$).

We found a significant effect of distance from the nearest forest edge on the daily survival rate of ground nests (distance \times substrate interaction) in both sites (Table 1). However, the relationship was opposite to that predicted. For every 100 m increase in distance from the forest edge the predicted daily nest survival rate of ground nests declined by a factor of 0.78 (95% CI = [0.64, 0.95], $P = 0.014$; Fig. 1). We did not detect an edge effect on above-ground nests. Other parameters explaining a significant amount of variation in daily nest survival probability include date, date \times date, build, lay and incubation nesting stages, and plot 2 in the low-impact site (Table 1). This indicates that, controlling for the other sources of variation, nest survival probability is higher early and late in the breeding season compared to the middle of the breeding season (i.e., date and date \times date), and that earlier nesting stages have a lower survival probability than the nestling stage.

The average number of young fledged (\pm 1SE) from successful songbird nests was similar between the low- and high-impact sites (3.5 ± 0.07 v. 3.7 ± 0.09 , respectively). Ground nests fledged one more chick on average than above-ground nests (4.1 ± 0.13 and 4.3 ± 0.15 chicks from 59 ground nests in both the low- and high-impact sites, respectively, compared to 3.3 ± 0.07 and 3.4 ± 0.10 chicks from 154 and 99 above-ground nests in the low- and high-impact sites, respectively).

Ground nesting species tend to have larger clutches than above-ground nesting species (Martin 1995) and when we controlled for the significant effect of average clutch size on nest productivity (odds ratio [95% CI]; 1.22 [1.05, 1.42], $P = 0.009$; Table 1) we did not detect any effect of study site, nesting substrate, or distance from the nearest forest edge on the number of young fledged (all $P > 0.4$). In most instances, the predicted relationship was in the opposite direction to that expected because nest productivity tended to decline with increasing distance from the forest edge (Fig. 2).

SONGBIRD ABUNDANCE

Overall, we detected 56 species of birds on our six low-impact plots during two years of study. Total songbird abundance was higher near the edge than in the forest interior (Table 2). This pattern was particularly pronounced for shrub-nesting species. Ground-nesting and canopy-nesting species showed no edge-related differences in total abundance ($\alpha = 0.05$). Individual species that showed significant increases in abundance close to the edge included American Robin (*Turdus migratorius*), Black-and-white Warbler (*Mniotilta varia*), Chipping Sparrow (*Spizella passerina*), Hermit Thrush (*Catharus guttatus*), and White-throated Sparrow (*Zonotrichia albicollis*). The only species that showed consistently lower abundance near the forest edge relative to the forest interior was the Ovenbird (*Seiurus aurocapilla*) (Table 2).

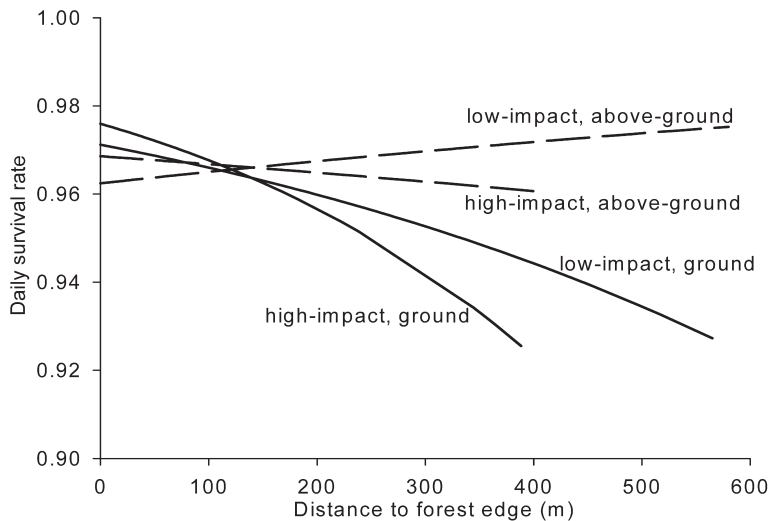


FIGURE 1. Modeled relationship between daily survival probability of ground and above-ground songbird nests with distance from a linear feature edge in two boreal landscapes that differed in energy sector activity, Fort Simpson, NT (low-impact) and the Chinchaga Forestry Region, AB (high-impact), Canada.

TABLE 1. PARAMETER ESTIMATES (β) AND 95% CONFIDENCE INTERVALS (CI) FOR A LOGISTIC-EXPOSURE MODEL OF DAILY NEST SURVIVAL PROBABILITY ($S = e^{(\text{MODEL})} / (1 + e^{(\text{MODEL})})$) AND FOR A ZERO-TRUNCATED POISSON MODEL OF THE NUMBER OF YOUNG FLEDGED FROM SONGBIRD NESTS IN FORT SIMPSON, NT (LOW-IMPACT), AND THE CHINCHAGA FORESTRY REGION, AB (HIGH-IMPACT), CANADA. COEFFICIENTS OF SIGNIFICANT PARAMETERS ($\alpha = 0.05$) ARE IN BOLD TYPE. CATEGORICAL PARAMETERS WITH A COEFFICIENT VALUE OF ZERO ARE THE REFERENCE PARAMETER AND COEFFICIENTS OF THE REMAINING CATEGORY LEVELS REFLECT THE EFFECT OF EACH PARAMETER RELATIVE TO THEIR PARTICULAR REFERENCE.

Parameter	Daily nest survival				Nest productivity			
	β	LCI	UCI	<i>P</i>	β	LCI	UCI	<i>P</i>
intercept	6.285	4.904	7.666	0.000	0.365	-0.272	1.003	0.261
date	-0.139	-0.204	-0.074	0.000	0.003	-0.006	0.012	0.458
date ²	0.002	0.001	0.002	0.001	-0.001	-0.001	0.000	0.043
low-impact study area	-0.185	-0.973	0.603	0.645	0.000	0.000	0.000	
high-impact study area	0.000	0.000	0.000		0.134	-0.261	0.530	0.505
low-impact (year 1)	0.082	-0.238	0.402	0.615	0.000	0.000	0.000	
low-impact (year 2)	0.000	0.000	0.000		0.095	-0.063	0.253	0.237
high-impact (year 1)	0.135	-0.341	0.610	0.579	0.000	0.000	0.000	
high-impact (year 2)	0.000	0.000	0.000		-0.005	-0.277	0.267	0.971
low-impact plot 1	0.100	-0.522	0.722	0.753	0.000	0.000	0.000	
low-impact plot 2	0.605	0.031	1.178	0.039	-0.007	-0.357	0.343	0.968
low-impact plot 3	0.306	-0.379	0.991	0.381	-0.518	-1.363	0.328	0.230
low-impact plot 4	0.345	-0.132	0.821	0.156	-0.001	-0.394	0.393	0.997
low-impact plot 5	0.361	-0.240	0.962	0.239	-0.028	-0.511	0.455	0.910
low-impact plot 6	0.000	0.000	0.000		0.069	-0.285	0.422	0.704
high-impact plot 1	0.326	-0.496	1.149	0.437	0.000	0.000	0.000	
high-impact plot 2	0.131	-0.614	0.8754	0.731	-0.055	-0.384	0.274	0.743
high-impact plot 3	-0.022	-0.846	0.802	0.958	0.024	-0.383	0.431	0.908
high-impact plot 4	0.207	-0.590	1.005	0.611	0.024	-0.339	0.387	0.896
high-impact plot 5	0.234	-0.584	1.053	0.575	0.146	-0.194	0.487	0.400
high-impact plot 6	-0.321	-1.342	0.700	0.538	0.057	-0.238	0.352	0.705
high-impact plot 7	0.535	-0.471	1.540	0.297	-0.074	-0.404	0.256	0.660
high-impact plot 8	0.147	-0.606	0.901	0.702	-0.029	-0.369	0.311	0.867
high-impact plot 9	0.000	0.000	0.000		0.009	-0.333	0.351	0.959
distance	-0.001	-0.003	0.001	0.571	-0.000	-0.001	0.000	0.523
distance × low-impact	0.001	-0.001	0.004	0.238	0.000	0.000	0.000	
distance × high-impact	0.000	0.000	0.000		-0.000	-0.002	0.001	0.746
camera (no)	0.124	-0.190	0.437	0.439	-	-	-	
camera (yes)	0.000	0.000	0.000		-	-	-	
substrate ground	0.275	-0.140	0.691	0.194	0.082	-0.115	0.280	0.413
substrate above-ground	0.000	0.000	0.000		0.000	0.000	0.000	
distance × ground	-0.003	-0.004	-0.001	0.014	0.000	-0.001	0.001	0.746
distance × above-ground	0.000	0.000	0.000		0.000	0.000	0.000	
stage (build)	-2.463	-3.056	-1.869	0.000	-	-	-	
stage (lay)	-1.747	-2.214	-1.280	0.000	-	-	-	
stage (incubation)	-0.427	-0.718	-0.136	0.004	-	-	-	
stage (nestling)	0.000	0.000	0.000		-	-	-	
clutch size	-	-	-		0.202	0.050	0.354	0.009

DISCUSSION

Contrary to our prediction, reproductive success was not lower in Alberta despite the higher levels of energy sector impact. This result is somewhat surprising given the density of linear features in this region. It was not possible to get much beyond 400 m from a forest edge in the high-impact site and greater than one third of nests found in the high-impact site were either on a linear feature or within 10 m of a linear feature edge.

The lack of difference in nesting success between sites is also surprising given the

increased proximity of the high-impact Alberta site to agricultural habitats and the observed presence of human-associated predators and brood parasites in this region. However, our data (Ball et al. 2009) demonstrate that only boreal forest-associated predators were responsible for destroying nests in both study sites. Because negative edge effects tend to be strongest along forest-field ecotones (Batary and Baldi 2004), our high-impact site may still be too far removed from a non-forested habitat for human-associated predators and brood parasites to be a major threat. For example, observers recorded one coyote (*Canis latrans*),

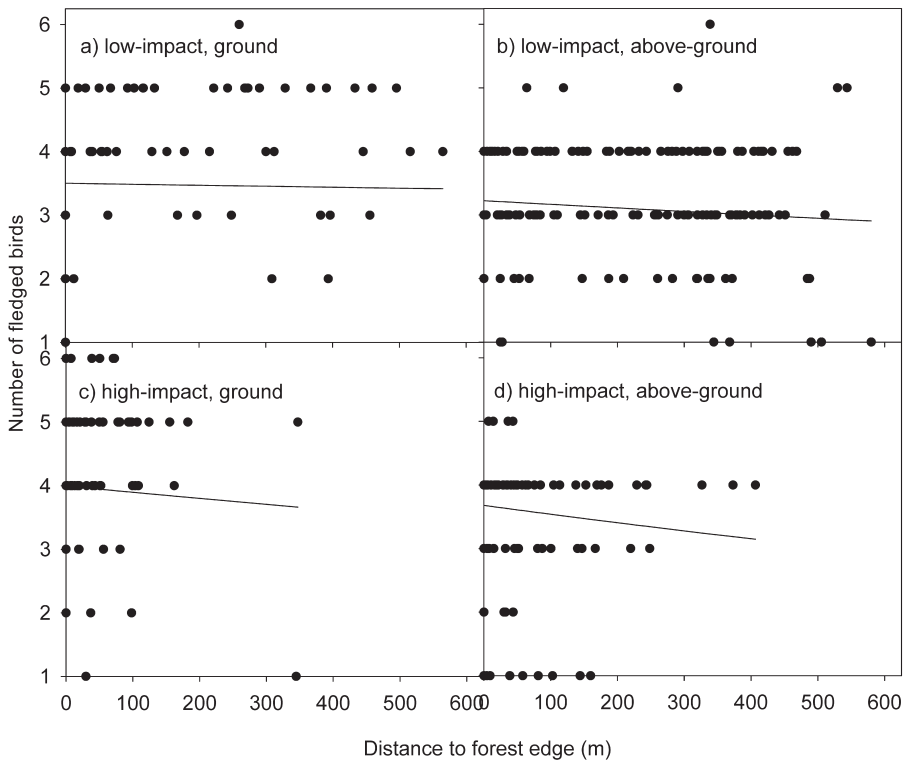


FIGURE 2. Observed number of young fledged from successful nests (circles) and the predicted relationship between number of young fledged from successful nests and distance from a linear feature edge (solid line) in ground and above-ground nests at the low-impact study site near Fort Simpson, NT, Canada (a and b, respectively) and from ground and above-ground nests at the high-impact site in the Chinchaga Forestry Region, AB, Canada (c and d, respectively).

two American Crows (*Corvus brachyrhynchos*), four Brown-headed Cowbirds, and nine white-tailed deer (*Odocoileus virginianus*) in >1700 h of predator surveys during two years in the high-impact site (J. Ball unpublished data). This is compared to >1400 red squirrels (*Tamiasciurus hudsonicus*) recorded during the same period. Observers at the low-impact site recorded one human-associated predator, a white-tailed deer, during nearly 4300 h of surveys (J. Ball unpublished data). Therefore, although human-associated predators were present at the high-impact southern site, they were rare compared to forest-associated predators and they did not negatively impact reproductive success.

We also did not detect a negative effect of edge proximity on nest fate or nest productivity. In contrast to our predictions, nesting near edges had a slightly positive effect on the daily survival rate of ground nests whereas no edge effect was found on the fate of above-ground nests or on nest productivity. We found a similar positive association between songbird

abundance and edge proximity in the low-impact site although this was for shrub-nesting birds. This suggests that abundance can serve as a relatively effective indicator of habitat quality for boreal forest songbirds in regions similar to our study sites. This is in contrast to the warnings described above for forest songbirds using human-modified habitats, particularly those adjacent to agricultural landscapes.

We do not have any evidence to suggest that the spatial distribution of the majority of songbird nest predators responds either positively or negatively to forest edge proximity (J. Ball, unpublished data). Therefore, the nests of edge songbirds are likely not being encountered more frequently than those nests of interior birds. Instead, we suggest that songbirds nesting adjacent to linear features may experience improved nest fate because they are able to take advantage of additional food resources that are available on the linear feature and in the immediate forest edge (Ries et al. 2004). This would allow adults to better coordinate their activities at the nest

TABLE 2. ADJUSTED MEAN ABUNDANCE OF SONGBIRDS (AND 95% CONFIDENCE INTERVALS) AT POINT COUNT STATIONS 0 M (EDGE), 200 M (INTERMEDIATE), AND 400 M (FAR) FROM THE FOREST EDGE IN THE LOW-IMPACT SITE NEAR FORT SIMPSON, NT, CANADA.

Songbird	Species name	Edge	Intermediate	Far	P
ALL		10.9 (6.4, 18.8)	8.0 (4.7, 13.7)	8.8 (5.1, 15.2)	0.02
CANOPY		1.4 (1.1, 1.9)	1.0 (0.8, 1.4)	1.7 (1.3, 2.3)	0.05
SHRUB		2.5 (2.1, 2.9)	1.8 (1.5, 2.1)	1.5 (1.2, 1.8)	0.001
GROUND		2.1 (1.8, 2.5)	1.8 (1.5, 2.1)	2.0 (1.7, 2.4)	0.42
American Redstart	<i>Setophaga ruticilla</i>	0.02 (0.002, 0.12)	0.07 (0.02, 0.29)	0.04 (0.01, 0.20)	0.42
American Robin	<i>Turdus migratorius</i>	0.16 (0.07, 0.35)	0.04 (0.01, 0.13)	0.03 (0.01, 0.12)	0.04
Bay-breasted Warbler	<i>Dendroica castanea</i>	0.65 (0.03, 0.16)	0.12 (0.07, 0.24)	0.04 (0.01, 0.10)	0.08
Black-and-White Warbler	<i>Mniotilta varia</i>	0.40 (0.28, 0.58)	0.19 (0.11, 0.31)	0.15 (0.08, 0.27)	0.004
Blue-headed Vireo	<i>Vireo solitarius</i>	0.01 (0.00, 0.09)	0.03 (0.01, 0.11)	0.01 (0.01, 0.07)	0.64
Chipping Sparrow	<i>Spizilla passerina</i>	0.39 (0.27, 0.56)	0.22 (0.14, 0.35)	0.11 (0.05, 0.21)	0.002
Dark-eyed Junco	<i>Junco hyemalis</i>	0.05 (0.02, 0.15)	0	0.02 (0.01, 0.1)	0.62
Gray Jay	<i>Perisoreus canadensis</i>	0.10 (0.04, 0.25)	0.04 (0.01, 0.13)	0.04 (0.01, 0.13)	0.29
Hermit Thrush	<i>Catharus guttatus</i>	0.05 (0.02, 0.14)	0.01 (0.02, 0.05)	0.01 (0.01, 0.04)	0.03
Least Flycatcher	<i>Empidonax minimus</i>	0.22 (0.09, 0.53)	0.06 (0.02, 0.19)	0.60 (0.26, 1.38)	0.01
Magnolia Warbler	<i>Dendroica magnolia</i>	0.21 (0.11, 0.42)	0.25 (0.13, 0.48)	0.29 (0.15, 0.54)	0.82
Ovenbird	<i>Seiurus aurocapilla</i>	0.35 (0.24, 0.52)	0.78 (0.59, 1.02)	0.76 (0.58, 0.99)	0.002
Rose-breasted Grosbeak	<i>Pheucitcus ludovicianus</i>	0.12 (0.04, 0.33)	0.08 (0.03, 0.22)	0.10 (0.04, 0.27)	0.65
Ruby-crowned Kinglet	<i>Regulus calendula</i>	0.11 (0.05, 0.22)	0.05 (0.02, 0.13)	0.06 (0.03, 0.13)	0.31
Red-eyed Vireo	<i>Vireo olivaceus</i>	0.44 (0.30, 0.65)	0.40 (0.28, 0.57)	0.57 (0.41, 0.79)	0.31
Swainson's Thrush	<i>Catharus ustulatus</i>	0.87 (0.69, 1.11)	0.66 (0.50, 0.87)	0.64 (0.49, 0.85)	0.17
Tennessee Warbler	<i>Vermivora peregrina</i>	0.85 (0.66, 1.10)	0.69 (0.53, 0.90)	0.79 (0.62, 1.01)	0.55
White-throated Sparrow	<i>Zonotrichia albicollis</i>	0.20 (0.09, 0.41)	0.01 (0.001, 0.10)	0.07 (0.02, 0.19)	0.02
Yellow-rumped Warbler	<i>Dendroica coronata</i>	0.42 (0.29, 0.61)	0.49 (0.35, 0.67)	0.24 (0.15, 0.39)	0.05

and reduce the probability of nest detection by predators (Martin and Ghalambor 1999, Conway and Martin 2000, Eggers et al 2005a).

The idea that edges offered improved access to food resources is supported by the increased abundance of individuals and the greater number of nests found near the forest edge, both of which would be predicted if food availability was an important component of habitat quality and individuals were capable of accurately assessing and selecting high quality habitats (i.e., an ecological trap is not present). The Ovenbird was the only species that was less abundant near the forest edge. The Ovenbird was also the only species in the low-impact site that nests and forages almost exclusively on the ground and that is exclusively insectivorous. Given that the microclimate is warmer near the edge and litter depth is shallower (J. Ball, unpublished data), soil invertebrates may be less available compared to the forest interior where the Ovenbird was more abundant (Burke and Nol 1998).

We do not believe that nests were more abundant near the forest edge because they were easier to find. If anything, the increased density of understory vegetation in the forest immediately adjacent to the edge (J. Ball, unpublished data) likely improved nest concealment. Instead, we suggest that more nests were found near the edge because there were more birds near the edge as our abundance data indicates. The increased edge skewness of nests in the high-impact site reflects the reduction in interior habitat with increasing linear feature density. We cannot refute that observers may have failed to devote equal effort across the plot. Many nests are found by flushing the adult by chance and observers continually cross the near distances as they enter and exit the plots. However, we contend that it is highly improbable that the edge-related distribution of effort was as skewed as the distribution of nests.

We collected data on insect prey abundance and on local predator abundance as part of our study and we will consider the effects of these covariates on parental nest attendance behavior and on nest fate and nest productivity in future analyses. Edge-related differences in vegetation structure and composition may also provide additional nest concealment and protection from nest predation (Eggers et al. 2005b) and we intend to incorporate nest vegetation characteristics in our future analyses.

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