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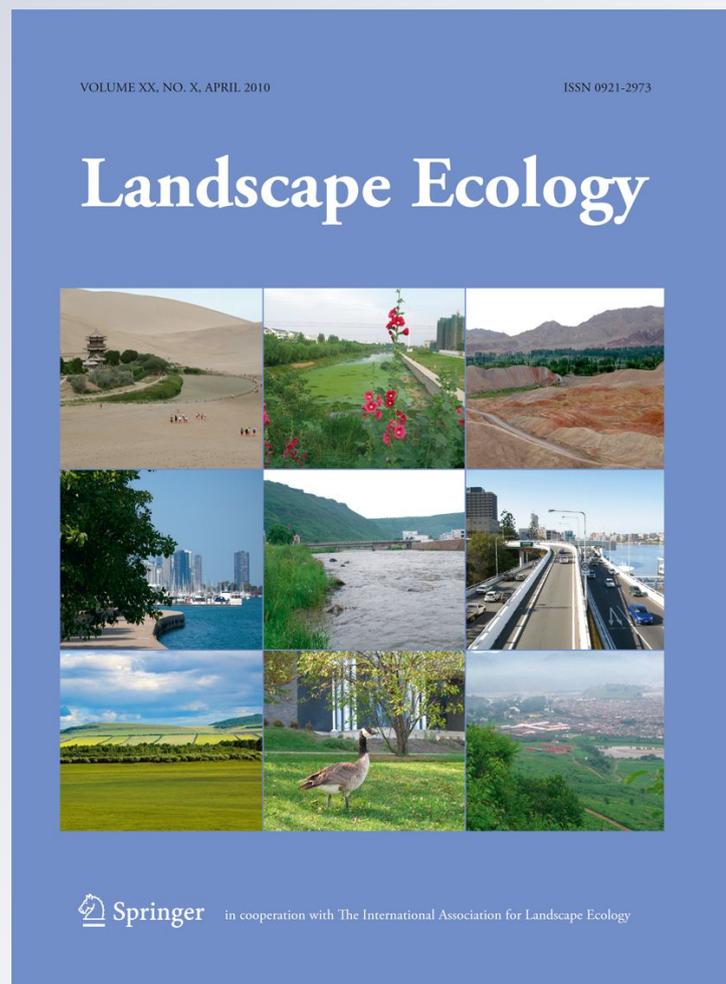
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Edge effect and matrix influence on the nest survival of an old forest specialist, the Brown Creeper (*Certhia americana*)

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Abstract Conservation strategies should be based on a solid understanding of processes underlying species response to landscape change. In forests fragmented by agriculture, elevated nest predation rates have been reported in many forest bird species, especially near edges. In intensively-managed forest landscapes, timber harvesting might also be associated with negative edge effects or broader “context” effects on some species when the matrix provides additional resources to their major nest predators. In this study, we hypothesized that proximity to a forest edge and proportion of cone-producing plantations will increase nest predation risk in fragments of relatively undisturbed forest. We focused on the Brown Creeper (*Certhia americana*), an indicator species of late-seral forests. We compared habitat configuration and composition at four spatial scales (0.14, 0.5, 1 and 2 km) around 54 nests and related daily nest survival rate to the distance to the nearest forest edge, mean patch size of late-seral forest ($r = 141$ m), proportion of non-forested lands ($r = 141$ m), density of maintained

roads ($r = 1$ km), proportion of cone-producing spruce plantations ($r = 2$ km), and year. The best model included distance to the nearest edge and proportion of cone-producing plantations. Distance of nests to the nearest edge was the best individual predictor of daily nest survival. A larger sample of nests showed a significant threshold in distance to the nearest forest edge; nests located at least 100 m away were more likely to fledge young. These results suggest that even in managed forest landscapes, matrix effects can be important and some bird species may exhibit negative edge effects.

Keywords Brown Creeper · Conifer plantations · Habitat fragmentation · Multi-scale analysis · Nest predation · Road density · Thresholds · New Brunswick · Managed forest landscapes

Introduction

Compared to agriculture, forest management is considered to have a moderate impact on species inhabiting habitat fragments (Andrén 1992; Mönkkönen and Reunanen 1999; Bayne and Hobson 2002). Intensive forest management generally reduces (a) stand age, (b) variation in stand composition through conversion of mixedwood stands into deciduous or coniferous-dominated stands (Etheridge et al. 2006; but see Amos-Binks et al. 2010), and (c) landscape heterogeneity (Rempel et al. 2007).

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Intensive timber harvesting is accompanied by silvicultural treatments (e.g. partial harvesting, plantation, thinning) which require the maintenance of an extensive road network. The potential effects of such forest road networks on forest biodiversity have rarely been examined, but the few studies that have been conducted suggest that these effects may be significant, either negatively (Ortega and Capen 2002; Courbin et al. 2009; Houle et al. 2009) or positively (Spellerberg 1998; Whitaker et al. 2007).

Songbirds are frequently used as indicators of ecological integrity because they respond to habitat alterations over multiple spatial scales (Rolstad 1991; Vander Haegen 2007). Nest predation is the most important cause of reproductive failure in songbirds (Ricklefs 1969; Martin 1995) and predation rates can be influenced by landscape composition and configuration (Robinson et al. 1995; Driscoll and Donovan 2004; Cornell and Donovan 2010).

Forest management simultaneously alters habitat at local and landscape scales, which poses both challenges and opportunities for ecologists and land managers. Silvicultural treatments modify stand structure, which may affect local habitat suitability (Griesser et al. 2007; Poulin et al. 2008, 2010; Roberge et al. 2008). Forest management can also modify patch attributes such as size and shape and create landscape mosaics that may increase nest predation risk (Malt and Lank 2009). Even-aged forest management is commonly applied to coniferous stands, which can create sharp habitat edges. Forest edges may be characterized by increased rates of predator movements (Cain et al. 2003) which, in turn, reduces avian reproductive success (Hartley and Hunter 1998; Batáry and Báldi 2004). However, edge effects on forest birds do not appear to be as severe in managed forest landscapes as they are in agricultural landscapes (Andrén 1992; Hartley and Hunter 1998; Bayne and Hobson 2002).

Lahti (2001) reviewed the literature to compare the relative effects of proximity to edges, edge type, and degree of habitat fragmentation on nest predation risk. He concluded that these predictors had no consistent effect. Degree of habitat fragmentation, however, tended to have a significant influence on nest predation risk, especially in forest landscapes. This may reflect the fact that in agricultural landscapes, forests are generally more fragmented than in managed forest landscapes and the agricultural

matrix often provides more food to potential nest predators. Additionally, forest management is not known to favour brood parasites such as the Brown-headed Cowbird (*Molothrus ater*) (Robinson et al. 1995; Schmiegelow et al. 1997). Patterns in nest predation may defy generalizations owing to the complex relationships between matrix habitat, potential nest predators, and generalist mesopredators controlling smaller nest predators (Lahti 2001).

We hypothesized that intensive, even-aged forest management followed by spruce plantation would cause a negative edge effect on the reproductive success of bird species associated with old forest fragments. When planted conifers start producing cones, nest predators such as the red squirrel may show a numerical response, increasing in turn nest predation risk in adjoining stands. In this study, we selected the Brown Creeper (*Certhia americana*) as a focal species owing to its strong association with late seral forest (Haney 1999; Hejl et al. 2002; Poulin et al. 2008) and because we could find and monitor its nests relatively easily. This species has a large territory relative to its body mass; it requires snags or declining trees for nesting, and high densities of large-diameter trees to meet its foraging requirements (Poulin et al. 2008; J.-F. Poulin unpubl. data). Its Palearctic counterpart, the Eurasian Treecreeper (*C. familiaris*), has been found to be sensitive to intensive forest management. The level of physiological stress of nestlings declined with increasing forest patch area (Suorsa et al. 2004) and nest predation rate increased with edge density and the proportion of young stands within a 500-m radius (Huhta et al. 2004). Because these studies were conducted using nestboxes, it is potentially risky to extrapolate their results to natural nests (Wesolowski 2007). In North America, effects of habitat context (neighbourhood, landscape) on Brown Creeper reproductive success are essentially unknown (Hejl et al. 2002). As forest management intensity increases across many regions of North America (Manolis et al. 2000; Betts et al. 2007), it is critical to investigate potential effects of this land use trend on species associated with relatively undisturbed stands.

This study aims to identify key factors influencing Brown Creeper nest survival at different spatial scales in an intensively managed forest. For this purpose, we compared habitat composition and configuration at four spatial scales (141 m, 500 m, 1 km, and 2 km)

around successful and unsuccessful nests. We also investigated the relationship between distance to the nearest hard edge and fledging success. We predict that proximity to hard edges (e.g. deciduous forest/clear-cut; deciduous forest/conifer plantation) will reduce Brown Creeper daily nest survival rate and that landscape composition and configuration will also have a significant influence. More specifically, we predict that daily nest survival rate will be higher in larger patches of deciduous forest, and in landscape contexts with lower proportions of cone-producing plantations. At finer spatial scales, we hypothesize that variables increasing the probability of a predator encountering a nest will be important, whereas at broader spatial scales, variables influencing predator abundance will be important to daily nest survival rate.

Methods

Study area

The study was conducted in north-western New Brunswick, Canada (47° 05'–47° 50' N; 67°00'–67°50' W) on two adjacent, intensively-managed forest districts (Black Brook and West Tobique). The study area covers ca. 5,000 km², 25% of which is represented by northern hardwood stands dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*) and American beech (*Fagus grandifolia*). Deciduous stands are managed through uneven-aged silvicultural systems (partial harvesting) whereas mixed and coniferous stands are mainly under even-aged management (clearcutting) followed by spruce plantation (see Poulin et al. 2008 for details). Most nests were located in patches of northern hardwoods that have not been treated for at least 30 years (Etheridge et al. 2006), or in 1–5 year old selection cuts (Fig. 1).

Nest searching and monitoring

We searched for nests in deciduous stands from early May to the end of July 2005–2007. The forest management regime created a landscape with hard edges (e.g. closed-canopy deciduous stands adjacent to clear-cuts or plantations). Nest searches were

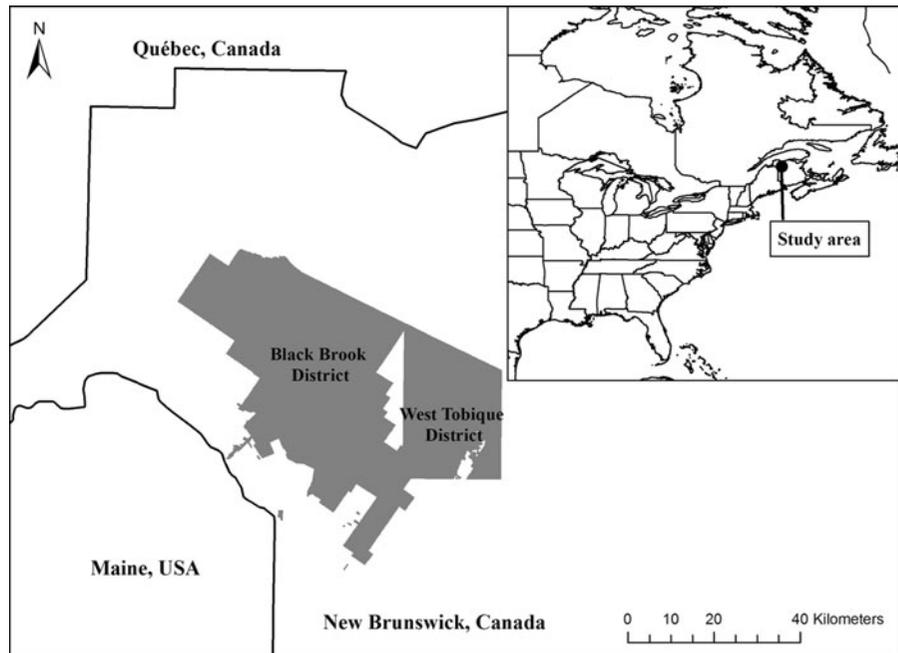
conducted in different forest stands from year to year. New areas searched were located at least 500 m away from nests monitored in previous years. All nests found were then monitored every 3 days until their fate could be determined (≥ 1 young fledged, predated, or abandoned). Nest abandonment was suspected in 7% of nesting attempts monitored (breeding activity was never recorded after nest construction was initiated) and those nests were excluded from the analysis. Renesting attempts were removed to avoid pseudo-replication. Brown Creeper densities are low enough that we can safely assume that nests built in the vicinity of a known nest shortly after it failed represented renesting attempts. This assumption was confirmed in another study where we had colour-banded adults (É. D'Astous and M.-A. Villard, unpubl. data). Of 81 nests whose fate was determined, 54 were retained for the analyses (19 in 2005, 18 in 2006 and 17 in 2007). We excluded renesting attempts, nests from the same location but on different years, and nests located at the edge of the study area and for whom we could not obtain GIS data.

Measurement of landscape metrics

We quantified habitat configuration and composition within four different radii centered on individual nests (141 m, 500 m, 1 km and 2 km). The 141 m radius represents the approximate size of a Brown Creeper territory (J.-F. Poulin and M.-A. Villard, unpubl. data). Because the landscape ecology of the Brown Creeper is essentially unknown, we quantified neighbourhood/landscape contexts over 0.5, 1, and 2 km radii to investigate their influence on nest fate. For example, the extent of red squirrel dispersal movements (see Larsen and Boutin 1994; Haughland and Larsen 2004) would make it possible for individuals to immigrate to the vicinity of creeper nests from a 300–600 m neighbourhood in a single year.

We distinguished four land cover types: untreated stands, harvested stands, spruce plantations and non-forested lands. Untreated stands included immature (<69 years old) and mature (>70 years old) stands of all types (coniferous, mixed, and deciduous) because the Brown Creeper does not exhibit clear preferences for stand type during the breeding season (Hejl et al. 2002; Guénette and Villard 2005). Harvested stands

Fig. 1 Geographic location of the study area



were divided according to their composition because management systems differed among them. Categories were partially harvested stands (deciduous, mixed, or coniferous) and clear-cuts. Non-forested lands corresponded to roads and road verges, gravel pits, and alder spp. stands. Spruce plantations were split into two age classes (0–10 year's vs >10 years) to roughly distinguish young vs cone-producing plantations (Blum 1990; Nienstaedt and Zasada 1990; Viereck and Johnston 1990). Finally, we measured the distances from nests to the nearest hard edge (i.e. spruce plantation, maintained road, or skid trail in partially harvested stands), to the nearest spruce plantation (regardless of age), and to the nearest cone-producing plantation. Finally, year was included as an independent variable because Brown Creeper fledging success varies from year to year in our study area (Poulin et al. 2010).

Habitat configuration was quantified using effective mesh size (Jaeger 2000). This landscape metric is the equivalent of the mean patch area, standardized for the number of patches. Effective mesh size was calculated for mature stands and cone-producing plantations because we hypothesized that they influence Brown Creeper nest survival and this metric appears to be a good predictor in Creepers' habitat selection (Poulin et al. 2008).

Statistical analyses

We used discriminant function analysis to screen variables influencing nest survival. Separate analyses were performed for habitat amount and habitat configuration variables at each of the four spatial scales considered. All variables were normally distributed and, variables with correlation coefficients >0.7 did not enter into the same model to reduce multicollinearity. The equality of variance–covariance matrix criterion of discriminant function analysis was met. Variables were selected using a forward stepwise approach. Variable screening led to the selection of 5 landscape variables that were used in model building (Table 1).

We modeled daily survival rate (DSR) of Brown Creeper nests using logistic regression in program MARK (White and Burnham 1999). Encounter histories were digitized as suggested by Dinsmore et al. (2002). For this purpose, 16 May was considered as day 1 and all nest visits were numbered sequentially. The five parameters required to model DSR were the day the nest was found (k), the last day the nest was found to be active (l), the last day the nest content was verified (m), the fate of the nest (f), and the proportion of nests with the same encounter history. Nests from different years (2005, 2006, and

Table 1 Variables selected by a discriminant function analysis for inclusion in logistic models predicting daily nest survival rate of Brown Creeper nests, with corresponding ranges in values

Variable	Description	Range
LSF	Mean patch size of late-seral forest within a 141-m radius	0–6.25 ha
NF	Proportion of non-forest land cover within a 141-m radius	0–25%
ED	Distance to the nearest (hard) forest edge	1–400 m
RD	Density of maintained roads within a 1-km radius	1.1–4.5 km/km ²
PL	Proportion of cone-producing spruce plantations within a 2-km radius	2.8–60%

Table 2 Models selected for the analyses

β_0	Null model
$\beta_0 + YR$	Univariate models
$\beta_0 + PL$	
$\beta_0 + ED$	
$\beta_0 + NF$	
$\beta_0 + LSF$	
$\beta_0 + RD$	Landscape models
$\beta_0 + PL + RD + T$	
$\beta_0 + PL + RD + TT$	
$\beta_0 + YR + PL + RD + T$	
$\beta_0 + YR + PL + RD + TT$	
$\beta_0 + ED + NF + LSF + T$	Local/neighbourhood habitat models
$\beta_0 + ED + NF + LSF + TT$	
$\beta_0 + YR + ED + NF + LSF + T$	
$\beta_0 + YR + ED + NF + LSF + TT$	Local/neighbourhood/landscape models
$\beta_0 + PL + RD + ED + NF + LSF + T$	
$\beta_0 + PL + RD + ED + NF + LSF + TT$	
$\beta_0 + PL + ED + T$	Neighbourhood/landscape models
$\beta_0 + PL + ED + TT$	
$\beta_0 + YR + PL + ED + T$	
$\beta_0 + YR + PL + ED + TT$	Anthropogenic features models
$\beta_0 + RD + NF + T$	
$\beta_0 + RD + NF + TT$	
$\beta_0 + YR + RD + NF + T$	Complete models
$\beta_0 + YR + RD + NF + TT$	
$\beta_0 + YR + PL + RD + ED + NF + LSF + T$	
$\beta_0 + YR + PL + RD + ED + NF + LSF + TT$	

2007) were modeled as groups to test for year effects on DSR. Also, the five individual covariates previously selected through discriminant function analysis were used to build models. We included linear (*T*) and quadratic (*TT*) time trends because DSR may vary over the course of a breeding season (Rotella 2010). We modeled a set of 27 models (Table 2) which included univariate, local habitat,

landscape, local habitat and landscape, negative edge or matrix effects and response to anthropogenic features models.

Logistic regression models were then compared using second-order Akaike information criterion (AIC_c). The relative performance of each model was assessed using ΔAIC_c . Models with $\Delta AIC_c < 2$ were considered to have substantial support (Burnham and

Anderson 2002). Finally, we calculated model weights (w_i) from ΔAIC_c scores. The relative importance of variables was assessed by summing Akaike weights of models where each variable was included. Univariate relationships were plotted to assess the strength of the corresponding variables. We examined models for each of the 5 landscape covariates, using a constant for daily survival rate within and among years. Then, nest survival probability (i.e. the probability of a nest surviving from initiation to completion) was calculated using a period of 37 days (laying: 6 days, incubation: 15 days, and nestling stage: 16 days; Hejl et al. 2002).

We analysed a larger sample of nests ($n = 81$) to investigate the effect of distance to the nearest hard edge between deciduous forest and clear-cut blocks or conifer plantations on probability of nest success (i.e. fledging at least one young). This data set included all nests found between 2005 and 2007 that were successful or depredated (binary variable). We modeled this relationship using logistic regression and identified a threshold value for distance to the nearest edge using ROC (receiver-operating characteristic) analysis (Zweig and Campbell 1993).

Results

Of the 54 nests considered in this study, 31 (57.4%) fledged at least one young and 23 (42.6%) were depredated. The proportion of successful nests decreased from 2005 to 2007 and the apparent nest success tended to be overestimated compared to the nest survival probabilities obtained using MARK (Fig. 2). Relative to depredated nests, successful nests were located in larger patches of late-seral forest ($r = 141$ m) with lower non-forest cover ($r = 141$ m), farther from the nearest forest edge, and in landscapes with lower road density ($r = 1$ km) and lower cover of spruce plantations ($r = 2$ km) (Table 3). From all possible model combinations, 4 were supported by the data ($\Delta AIC_c \leq 2$, Table 4). Models including a linear time trend received more support than those with a quadratic time trend. The best model included distance to the nearest hard edge and proportion of cone-producing plantations in the landscape (Table 4). The third and fourth best models both included a year effect. Local/neighbourhood habitat models had a greater influence on DSR than

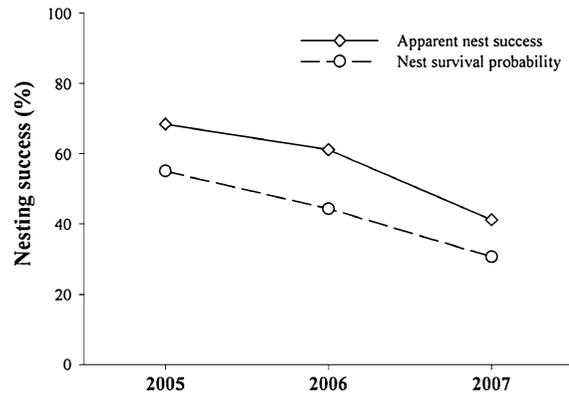


Fig. 2 Temporal changes in apparent nesting success and nest survival probability obtained from program MARK using a constant daily survival rate

Table 3 Descriptive statistics for successful and depredated Brown Creeper nests

Variables	Mean (SE)	
	Successful nests (n = 31)	Depredated nests (n = 23)
YR	n/a	n/a
LSF (ha)	4.15 (0.42)	3.61 (0.47)
NF (%)	1.30 (0.40)	3.40 (1.30)
NF (ha)	0.08 (0.13)	0.21 (0.38)
ED (m)	147.84 (18.74)	109.91 (14.12)
RD (km/km ²)	1.82 (0.14)	2.23 (0.17)
PL (%)	18.60 (2.70)	23.2 (2.90)
PL (ha)	233.74 (191.93)	291.26 (175.94)

See Table 1 for meaning of variable codes

landscape models but, as indicated above, the best model included variables from both spatial scales.

According to importance weights, the best predictors of daily nest survival were distance from nests to the nearest forest edge (0.88) and proportion of cone-producing plantations within a 2-km radius (0.87). The importance weights of other variables were as follows: YR = 0.40, NF = 0.16, RD = 0.15 and LSF = 0.14 (see Table 1 for variable codes). The relative importance of variables can be seen in univariate relationships (Fig. 3).

When using a larger subset of nests, fledging success showed a significant threshold in the distance to the nearest forest edge (99 m, area under the ROC curve = 0.73, $n = 81$, Fig. 4). The probability of

Table 4 Models predicting Brown Creeper daily nest survival rate as a function of five landscape variables and year

Model ^a	AIC _c	ΔAIC _c	w _i	K ^b	Deviance
B₀ + ED + PL + T	152.10	0.00	0.21	4	144.05
B₀ + ED + PL + TT	152.14	0.04	0.20	4	144.09
B₀ + YR + ED + PL + T	152.20	0.11	0.20	5	142.14
B₀ + YR + ED + PL + TT	153.11	1.01	0.13	5	143.04
B ₀ + ED	155.03	2.93	0.05	2	151.02
B ₀ + PL + RD + ED + NF + LSF + T	155.62	3.52	0.04	7	141.50
B ₀ + PL + RD + ED + NF + LSF + TT	155.73	3.63	0.03	7	141.61
B ₀ + YR + PL + RD + ED + NF + LSF + T	156.08	3.98	0.03	8	139.92
B ₀ + YR + PL + RD + ED + NF + LSF + TT	156.57	4.48	0.02	8	140.42
B ₀ + NF	157.73	5.64	0.01	2	153.72
B ₀	158.00	5.91	0.01	1	156.00
B ₀ + YR	158.39	6.30	0.01	2	154.38
B ₀ + RD	159.01	6.91	0.01	2	154.99
B ₀ + PL	159.10	7.00	0.01	2	155.08
B ₀ + LSF	159.14	7.05	0.01	2	155.13
B ₀ + ED + NF + LSF + T	159.42	7.32	0.01	5	149.36
B ₀ + RD + NF + T	159.46	7.37	0.01	4	151.42
B ₀ + ED + NF + LSF + TT	159.48	7.39	0.01	5	149.42
B ₀ + RD + NF + TT	159.63	7.53	0.00	4	151.59
B ₀ + YR + ED + NF + LSF + T	160.38	8.28	0.00	6	148.29
B ₀ + YR + RD + NF + T	160.52	8.42	0.00	5	150.45
B ₀ + YR + ED + NF + LSF + TT	161.03	8.93	0.00	6	148.94
B ₀ + YR + RD + NF + TT	161.25	9.15	0.00	5	151.18
B ₀ + PL + RD + T	161.42	9.33	0.00	4	153.38
B ₀ + PL + RD + TT	161.50	9.40	0.00	4	153.45
B ₀ + YR + PL + RD + T	161.86	9.76	0.00	5	151.79
B ₀ + YR + PL + RD + TT	162.76	10.67	0.00	5	152.70

The number of estimated parameters (K), scaled deviance ($-2 \log$ likelihood), second-order Akaike's information criterion (AIC_c), scaled AIC_c and AIC_c weights (w_i) are indicated

Models in bold have substantial support ($\Delta AIC_c \leq 2$)

^a See Table 1 for meaning of variable codes; B₀ intercept, T linear time trend, TT quadratic time trend

^b Parameter count includes the intercept

fledging at least one young increased significantly beyond 99 m from the nearest hard edge.

Discussion

Intensive forest management influenced Brown Creeper daily nest survival rate over different spatial scales through an increase in predation risk (Fig. 5). To our knowledge, this is one of the first studies indicating an edge effect on avian reproductive success in a managed forest landscape (see also Manolis et al. 2000;

Flaspohler et al. 2001; Malt and Lank 2009). The most important predictors of nest predation risk were the distance to the nearest forest edge and the proportion of cone-producing plantations within a 2-km radius (Fig. 6). Predation risk was lower for nests located at least 100 m away from the nearest forest edge. On the other hand, Brown Creeper reproductive success was highly variable between years (see also Poulin et al. 2010), suggesting that edge and landscape effects may vary as a function of the abundance of nest predators, itself fluctuating in response to mast seeding events (e.g. Schmidt et al. 2008).

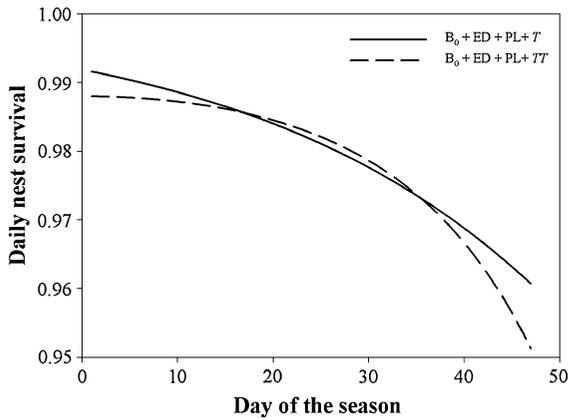


Fig. 3 Predicted influence of the two best models on daily nest survival rate

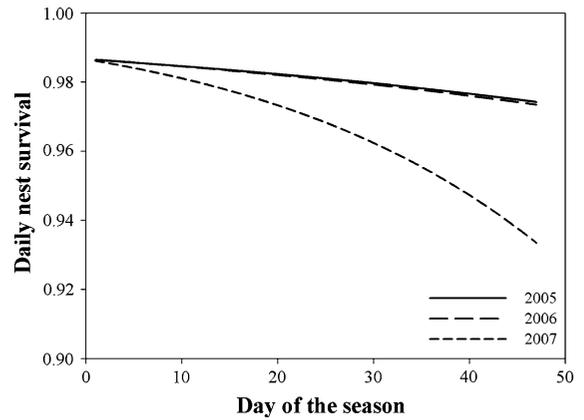
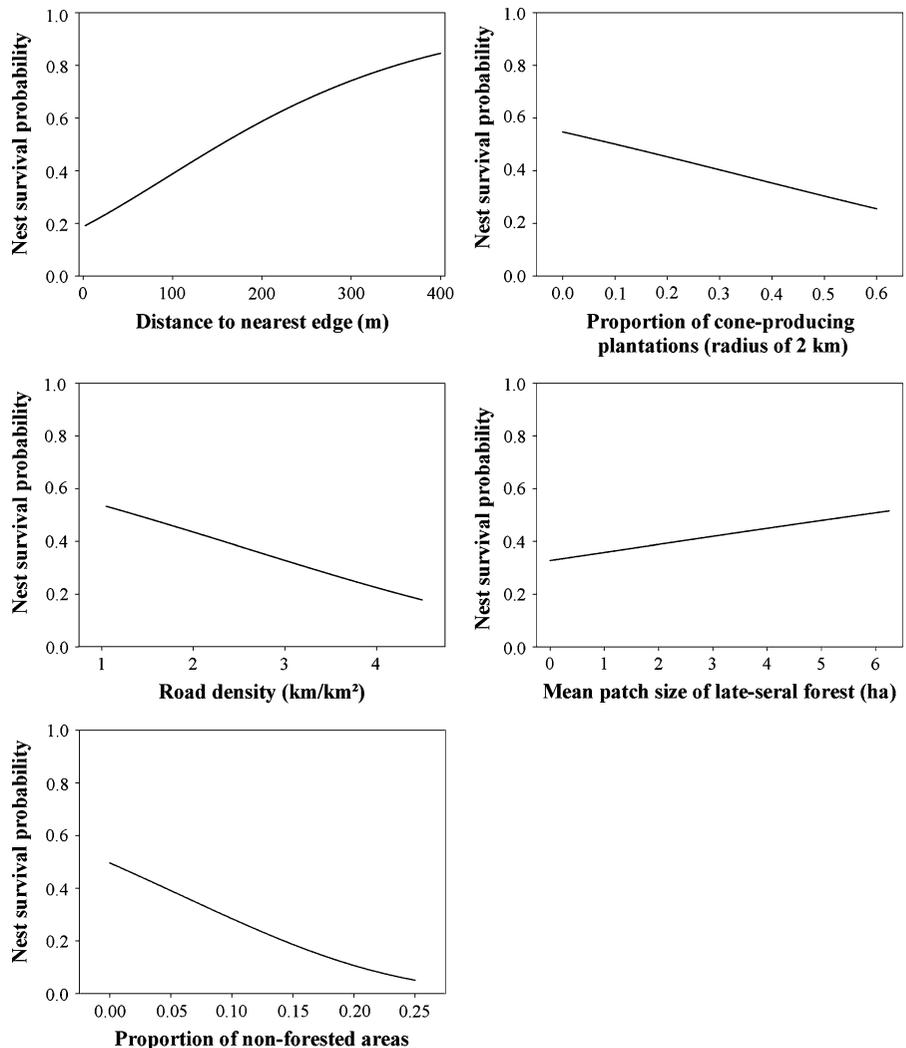


Fig. 5 Predicted influence of year on daily nest survival rate

Fig. 4 Nest survival probability as a function of the five landscape variables included in the supported models using a constant daily survival rate ($n = 54$)



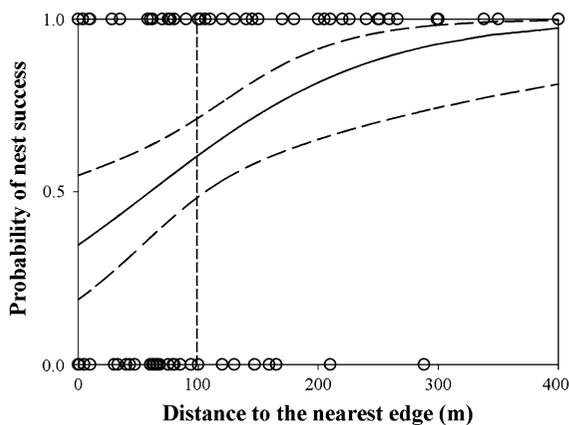


Fig. 6 Probability that a nest fledged ≥ 1 young as a function of the distance to the nearest forest edge ($n = 81$). Dashed curves represent the 95% confidence interval around estimated values and the vertical dashed line indicates the threshold value obtained using ROC analysis (see “Methods”)

Nests located farther from an edge were more likely to be successful. Although edge effects tend to vary with focal species and edge types, negative edge effects tend to be the norm rather than the exception (Hartley and Hunter 1998; Batary and Baldi 2004; but see Lahti 2001). Nonetheless, edge effects often interact with landscape type and there is less evidence for negative edge effects in managed forest landscapes than in agricultural landscapes (Andren 1992; Hanski et al. 1996; Hartley and Hunter 1998). In this study, edges were associated with clear-cuts, spruce plantations, logging roads, or skid trails in partially-harvested deciduous stands. Compared to mature untreated deciduous stands, clear-cuts and conifer plantations represent either non-habitat or extremely marginal habitat for the Brown Creeper (Guenette and Villard 2005). Clear-cut edges may increase nest predation risk, as suggested by Manolis et al. (2000). Similarly, roads and road edges create sharp and sometimes fairly wide canopy openings. Individuals nesting near edges may be forced to defend oblong territories and may thus incur higher costs when feeding nestlings, as reported for the Eurasian Treecreeper (Kuitunen and Makinen 1993, Suorsa et al. 2003). This could result in a lower reproductive success for individuals (see Huhta et al. 1999 for the Pied Flycatcher [*Ficedula hypoleuca*]) and an elevated physiological stress level and lower body condition for nestlings (Suorsa et al. 2004 for the Eurasian Treecreeper).

Nests located in (Carignan and Villard 2002) or near (Hanski et al. 1996) spruce plantations suffer higher predation rates than those located in naturally-regenerated forest stands. In this study, Brown Creeper nests were monitored in shade-tolerant deciduous stands. Thus, the influence of cone-producing spruce plantations on reproductive success is indirect, probably through its influence on nest predator populations. The red squirrel is a confirmed predator on Brown Creeper nests (Mahon and Martin 2006; Pelech et al. 2010) and its survival rate has been shown to vary with the production of conifer seeds (Halvorson and Engeman 1983). In our study area, we obtained photographs of red squirrels depredating creeper nests (J.-F. Poulin, M.-A. Villard, and E. D’Astous, unpubl. data). Red squirrel populations tend to fluctuate as a function of seed crops (Kemp and Keith 1970; Wheatley et al. 2002) and they may shift their diet to eggs and nestlings when seeds become scarce (Mahon and Martin 2006).

We also found that daily nest survival rate increased with patch size of mature forest. Larger patches may either be better buffered against nest predators from the matrix (Robinson et al. 1995; Thompson et al. 2002) or they may offer better foraging conditions (higher availability and quality of food resources), as reported in the Eurasian Tree-creeper (Suorsa et al. 2004).

Surprisingly, the distance from nests to the nearest cone-producing spruce plantation was not a good predictor of fledging success, suggesting that the relationship between cone crops and creeper nest predation manifests itself over broader spatial scales. The Blue Jay (*Cyanocitta cristata*) is thought to be more abundant near habitat edges (Graber et al. 1987) and is known to be an efficient nest predator (Pelech et al. 2010), but this species is not known to depredate Brown Creeper nests (Hejl et al. 2002) and we never caught it in the act (J.-F. Poulin, M.-A. Villard, and E. D’Astous, pers. obs.). As predicted, Brown Creeper nest survival was negatively related to the presence of anthropogenic features (here, proportion of non-forested areas and density of maintained roads). However, those two variables were not among the best predictors. At a finer scale, daily nest survival was negatively influenced by the proportion of non-forested lands (Fig. 4). Narrow forest openings like seismic lines used by the oil and gas industry or narrow roads (<8 m wide) have not been found to have a negative influence on

songbird abundance or reproductive success (King and DeGraaf 2002; Bayne et al. 2005; Machtans 2006). On the other hand, the abundance of forest birds has been shown to decrease in the vicinity of wider forest roads (Ortega and Capen 2002; Laurance 2004).

Conclusion

Most taxa respond simultaneously to local environmental conditions and to landscape context (Mazerolle and Villard 1999; Driscoll and Donovan 2004). Results from this study suggest that nest fate reflects both local (or neighbourhood) and larger-scale processes, judging from the strong influence of proximity to edge and the proportion of cone-producing spruce plantations. Edge effects on nesting success have rarely been reported in managed forest landscapes (Andrén 1992; Hanski et al. 1996; Hartley and Hunter 1998). A landscape dominated by conifer plantations could promote population fluctuations in nest predators, especially the red squirrel, as cone production is cyclical. In turn, this may result in higher nest predation rates relative to the pre-industrial landscape, where mixedwood forest was more important (Etheridge et al. 2006), especially during low mast years (e.g. Mahon and Martin 2006).

Increased predation risk has a direct influence on nest success that can be documented. However, indirect effects (e.g. through behavioural responses to nest predators) are more difficult to assess, but can also have a significant influence on songbird demography. Some bird species have been shown to modify their level of parental investment according to perceived nest predation risk (Fontaine and Martin 2006) whereas others may avoid areas with high densities of nest predators (Morton 2005). These considerations raise the possibility of large-scale negative effects of intensive forest management on certain bird species through direct and indirect effects of nest predators.

The Brown Creeper is considered to be an indicator of sustainable forest management. Nesting habitat selection was documented by Poulin et al. (2008). Here, we linked nest fate to neighbourhood and landscape features, which is critical to model population viability (Wintle et al. 2005). Although much attention has focused on agricultural landscapes, where matrix and edge effects on nest

predation appear to be stronger (e.g. Andrén 1992), our study indicates that old forest specialists may also be strongly affected by intensive forest management. Thus, conservation strategies for the Brown Creeper and ecologically similar species should integrate effects of edge and landscape matrix on reproductive success to ensure that forest management is truly sustainable.

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