Contributed Paper

Negative Effects of Habitat Loss on Survival of Migrant Warblers in a Forest Mosaic

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Abstract: Habitat loss and fragmentation in forested landscapes often negatively affect animal abundance; however, whether these factors also affect fitness is not well known. We hypothesized that observed decreases in bird occurrence and abundance in landscapes with harvested forests are associated with reduced apparent survival of adults. We defined apparent survival as an estimate of survival that accounts for an imperfect resighting probability, but not permanent emigration (i.e., dispersal). We examined the association between spatially extensive habitat loss and apparent survival of males of 2 Neotropical migrant species, Blackburnian Warbler (Dendroica fusca) and Black-Throated Green Warbler (D. virens), over 7 years in the Greater Fundy Ecosystem, New Brunswick, Canada. We estimated apparent survival among and within breeding seasons. We quantified amount of habitat in the context of individual species. In this landscape, boundaries between land-cover types are gradual rather than clearly identifiable and abrupt. Estimated apparent within-season survival of both species decreased as a function of amount of habitat within a 2000-m radius; survival was approximately 12 times (95% CI 3.43–14) greater in landscapes with 85% habitat than in landscapes with 10% habitat. Apparent annual survival also decreased as a function of amount of habitat within a 100-m radius. Over the range of habitat amount, apparent annual survival decreased 15% (95% CI 7–29%) as the amount of habitat decreased. Our results suggest that reduced species occurrence in landscapes with low proportions of habitat is due partly to lower apparent survival at these sites. This mechanism operates both directly (i.e., via effects on mortality or dispersal during breeding) and possibly through indirect effects during the nonbreeding season. Habitat loss was associated not only with a lower number of individuals, but also with lower survival of those individuals.

Keywords: apparent survival, dispersal, forest management, fragmentation, habitat loss, landscape, matrix, songbirds

Efectos Negativos de la Pérdida de Hábitat sobre la Supervivencia de Parulíidos Migratorios en un Mosaico Forestal

Resumen: La pérdida de hábitat en paisajes boscosos a menudo afecta negativamente a la abundancia de animales; sin embargo, no se sabe si estos factores también afectan a la adaptabilidad. Planteamos la hipótesis de que los decrementos observados en la ocurrencia y abundancia de aves en paisajes con bosques cosechados están asociados con la reducción de la supervivencia aparente de adultos. Definimos la supervivencia aparente como una estimación de la supervivencia que considera la probabilidad de reaparición imperfecta, pero no la emigración permanente (i.e., dispersión). Examinamos la asociación entre la pérdida extensiva de hábitat y la supervivencia aparente de machos de 2 especies de parulíidos migratorios (Dendroica fusca) y (D. virens), a lo largo de 7 años en el Ecosistema Greater Fundy. Nuevo Brunswick, Canadá. Estimamos la supervivencia aparente entre y dentro de los períodos reproductivos. Cuantificamos la cantidad de hábitat

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Paper submitted December 3, 2010; revised manuscript accepted March 5, 2011.
en el contexto de especies individuales. En este paisaje, los límites entre tipos de cobertura de suelo son graduales y no claramente identificables y abruptos. La supervivencia aparente estimada de ambas especies en el período disminuyó como una función de la cantidad de hábitat en un radio de 100 m. En el rango de la cantidad de hábitat, la supervivencia anual aparente disminuyó 15% (95% IC 7-29%) a medida que disminuyó la cantidad de hábitat. Nuestros resultados sugieren que la reducción en la ocurrencia de especies en paisajes con proporciones bajas de hábitat se debe parcialmente a la menor supervivencia aparente en esos sitios. Este mecanismo opera tanto directamente (i.e., vía efectos sobre la mortalidad o dispersión durante la reproducción) y posiblemente por medio de efectos indirectos durante la época no reproductiva. La pérdida de hábitat se asoció no solo con un menor número de individuos, sino también con una menor supervivencia de esos individuos.

**Palabras Clave:** aves canoras, fragmentación, manejo forestal, matriz, paisaje, pérdida de hábitat, supervivencia aparente

### Introduction

The combined effects of habitat loss and fragmentation may have detrimental effects on native species (Pimm et al. 1995). Both habitat loss and fragmentation usually occur as a result of forest harvest. Possible negative effects of habitat loss and fragmentation are lower recolonization rates (Wiens 1994), increased mortality rates of individuals moving between patches (Fahrig & Merriam 1994), decreased reproductive success (Robinson et al. 1995), and increased local extinction rates (Hanski & Ovaskainen 2000).

Spatially extensive habitat loss and fragmentation have moderate to strong influences on songbird occurrence, abundance, and density (McGarigal & McComb 1995; Villard et al. 1999; Lichstein et al. 2002). However, little is known about the mechanisms driving observed patterns in abundance. Leading hypotheses include reduced nest success (Robinson et al. 1995), reduced potential for conspecific attraction (Fletcher 2009), and lower adult and juvenile apparent survival (Doherty & Grubb 2002). Of these, only the nest success hypothesis has been tested extensively (e.g., Paton 1994). We defined apparent survival as an estimate of survival that accounts for an imperfect resighting probability, but not permanent emigration (i.e., dispersal) (Sandercok 2006).

Abundance can be a poor measure of habitat quality (Van Horne 1983). Animals may be drawn to sinks (Pulliam & Danielson 1991) or ecological traps (Schlaepfer et al. 2002), where reproduction or survival are low. Thus, detecting small or no effects of the amount and configuration of habitat on abundance of a species does not necessarily indicate the absence of underlying demographic effects. Few researchers have examined demographic parameters other than nest success. Yet adult and juvenile apparent survival are likely to strongly affect population viability (Lampila et al. 2005) and perhaps how species respond to habitat fragmentation (With & King 1999). Furthermore, few studies on avian survival in extensive fragmented habitat have been conducted in agricultural landscapes, where the distinction between patches and matrix is unambiguous (Porceluzi & Faaborg 1999; Doherty & Grubb 2002; but see Bayne & Hobson 2002). Although clearcuts initially create abrupt boundaries between patches and matrix, these edges often become gradients as the forest regenerates. Whether the changes in edge structure caused by timber harvesting in forested landscapes affect animal survival is not well known.

Previous efforts to detect effects of habitat loss and fragmentation on species occurrence or demography may have been hampered by the accuracy of the definition of habitat for species under consideration. Researchers have tended to rely on qualitative definitions of habitat (e.g., Homan et al. 2004) or have used general land-cover classifications (e.g., forest [Trzcinski et al. 1999]) that may not describe the actual habitat associations of individual species. Correctly assessing amount and distribution of habitat for individual species may be particularly important in forest mosaics, where gradients between vegetation types are more common than clearly identified patch boundaries (Wiens 1994).

Effects of amount and configuration of habitat on apparent survival could reflect factors both within and among breeding seasons. Within-breeding-season events include mortality in or dispersal from forest fragments, which could be affected by factors such as high predator abundance or predation success or a high frequency of among-patch movements by adults (Norris & Stutchbury 2001), which potentially entail greater risk of mortality (Turcotte & Desrochers 2003). Events that occur outside the breeding season include mortality (Sillett & Holmes 2002), which could result from the effects of poor body condition stemming from occupation of poor-quality habitat in forest fragments on breeding grounds. Also, breeding dispersal could occur between years (i.e., a bird may settle somewhere different in consecutive years).

Globally, declines in forest cover due to agricultural development and timber harvest are continuing at 0.6% per year (a loss of 1,011,000 km² from 2000 to 2005 [Hansen et al. 2010]). These rates are greater than the global average in boreal and temperate forests. Thus, we think that it is important to test whether habitat loss...
affects not only abundance, but also the demography of forest-associated species.

We used 7 years of capture-recapture data to test whether spatially extensive habitat loss affects within-season and among-season apparent survival of 2 songbirds associated with mature forests: Blackburnian Warbler (*Dendroica fusca*) and Black-Throated Green Warbler (*D. virens*).

**Methods**

**Study Area and Species**

The study area encompassed 4000 km$^2$ within the Greater Fundy ecosystem, New Brunswick, Canada (66.08–64.96$^\circ$W, 46.08–45.47$^\circ$N). Fundy National Park is a relatively small protected area (206 km$^2$) within the study area with over 80% contiguous mature (>60 years old) forest. Forest cover was primarily yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), balsam fir (*Abies balsamea*), and red spruce (*Picea rubens*), with black spruce (*P. mariana*) in some low-lying areas. Intensive forest management activities (i.e., clearcutting, planting of spruce and pine, and thinning) since the 1970s have reduced the amount of mature forest to approximately 12–50% of the landscape (NBDNRE 1998). After accounting for regrowth, the amount of mature mixed (deciduous and coniferous) forest is declining at about 1.5%/year, primarily as a result of short-rotation clearcutting (Betts et al. 2007). Spatially extensive loss of forest, particularly mixed forest, is negatively associated with songbird occurrence (Betts et al. 2006b, 2007). We hypothesized this is due to lower apparent survival of adults in isolated habitat patches.

Blackburnian Warblers are strongly associated with mixed forest (Young et al. 2005) and their abundance is declining in New Brunswick (6.11%/year [SE 1.09]) (Sauer et al. 2007), whereas Black-Throated Green Warblers have higher breeding-habitat plasticity (Collins 1983; Morse 2005), are more abundant (Betts et al. 2006b), and are not declining at a statistically significant rate in New Brunswick (1.68%/year [SE 1.45]) (Sauer et al. 2007). Thus, we expected survival of Blackburnian, but not Black-Throated Green Warblers, to decrease as the amount of habitat across extensive areas decreased.

**Study Design**

Given that Blackburnian and Black-Throated Green Warblers are dependent on mature forest during the breeding period (May–August) to differing extents (Morse 2004, 2005; Young et al. 2005), the area we sampled consisted of all mature forest in our 4000 km$^2$ study area. This area maximized our probability of encountering, and subsequently capturing, as many individual birds as possible. Patches were not selected randomly among all patches of mature forest; rather, they were chosen a priori in a stratified sampling strategy to represent the gradient of amount of mature forest cover within a 2000-m (landscape-extent) radius. This 2000 m represents the distance of natal dispersal proposed for migratory warblers (Bowman 2003) and the distance birds may travel in the breeding season to seek extrapair copulations (Norris & Stutchbury 2001). We did not attempt to separate the effects of habitat amount and fragmentation (Trzcinski et al. 1999) because we were concerned that stratifying samples along those 2 gradients would decrease our statistical power. Thus, we tested the combined effects of habitat amount and fragmentation (i.e., landscape structure) (Fahrig 2003). We focused on the amount of mature forest because effects of habitat amount on biological diversity are typically stronger than those of configuration (Fahrig 2003). We attempted to capture birds at 367 locations at which the percentage of mature (>60 years) forest cover within a 2000-m radius ranged from 7.7% to 98.1% (mean [SE] = 39.7% [1.5]) and 41.4% to 86.7% (mean = 69.7% [5.0]) for Blackburnian Warblers and Black-Throated Green Warblers, respectively.

We captured individuals between 25 May and 30 July (the most reliable time to capture territorial individuals) each year from 2000 through 2005 with a combination of audio playback of specific songs, deployment of decoys, and mistnetting (net 30-mm mesh). Within sample patches, we captured birds opportunistically. If a focal species occurred in a mature forest patch and responded aggressively to playback, a net was set up and capture was attempted. Because this target-netting method requires aggressive territorial response to con-specific playback (Betts et al. 2005), it is highly improbable that we captured individuals that did not hold a territory within a particular netting location (i.e., birds on an extraterritorial foray [Norris & Stutchbury 2001]).

Upon capture, we fitted each adult bird with a unique combination of 2 colored, plastic leg bands and 1 Canadian Wildlife Service aluminum band. We determined age and sex of birds on the basis of plumage (Pyle 1997). Our capture method was strongly male biased (Morse 2004, 2005). Of the 572 individuals of both species we captured, 11 were females, and we excluded them from our analysis.

At each capture location, we played songs of territorial males of each species to resight banded birds. If we did not resight the bird during the initial playback, we broadcast the songs at 50-m radii in each cardinal direction for 5 min. Because both mobbing and species-specific playbacks are audible by birds at >100 m (Betts et al. 2005), our search area was approximately 7 ha (radius of 150 m)—which is 5–7 times the size of a typical Blackburnian or Black-Throated Green Warbler territory (Morse 2004, 2005; Young et al. 2005). Although this search area is smaller than that in previous studies of apparent survival of songbirds (10 ha; Sillett and Holmes 2002),...
Habitat Loss and Songbird Survival

2600 ha; Bayne and Hobson [2002], 25 ha) and reduced our ability to detect dispersal events, we considered this smaller area necessary to achieve a large sample size across a full gradient of amount of mature forest cover and to avoid spatial auto-correlation as a result of all captured individuals occurring in close proximity to each other (Lichstein et al. 2002).

We spent 30–60 min attempting to resight each bird on each visit twice within each season. We recorded data only when all color bands were observed. To minimize bias, all observers were naive to band combinations and were not assigned to resight the same individual more than once.

Spatial Data

We tested whether apparent survival of both species was associated with the proportion of mature forest within a 2000-m radius of the capture location. In a separate study, we developed spatially explicit models of the distribution of both species on the basis of covariates within <100-m radius derived from a geographic information system (Betts et al. 2006a). These models performed well when validated with independent data (Betts et al. 2006a). We generated maps of the distributions (30-m² resolution) for both species (Fig. 1). We then used these maps to quantify habitat amount at local and landscape extents. To do this, we summed the estimated probability of occurrence (\( \hat{p} \)) within 30-m² pixels surrounding each sample point at 2 spatial extents: 100 and 2000 m. The 100-m extent encompassed the maximum territory size of either species (Morse 2004, 2005). To account for matrix heterogeneity, we summed the amount of poor-quality matrix within 2000 m. We defined poor-quality matrix (matrix) as areas with very low amounts of mature forest (\( \hat{p} < 0.05 \); less than an estimated 5% probability of occurrence). Throughout this paper, habitat refers to these species-specific definitions. In all analyses, covariates (i.e., habitat, matrix, mature forest) were represented as continuous proportions (Supporting Information). We conducted spatial analyses in ArcView 3.3 (ESRI, Redlands, California).

Data Analyses

We formulated models to test whether landscape structure, time, species, and age were associated with survival. Models for landscape structure included all covariates described above (i.e., habitat, matrix, mature forest) (Supporting Information). Models for time examined either variation in apparent survival across years or variation in apparent survival over time within the breeding season. Models for species tested whether apparent survival rates of the 2 species differed when mature for est proportion is high (i.e., a species \( \times \) mature forest interaction). Models for age tested whether apparent survival rates differed between first-year breeders and more experienced breeders. We aged 92% of birds reliably. We were unable to age 9 Blackburnian Warblers and 40 Black-Throated Green Warblers. To limit the number of model parameters, birds of unknown age were excluded from analyses. We followed a subset of birds in the survival data set intensively for 2 years to estimate within-season apparent survival.

We estimated annual and within-season apparent survival probabilities separately with program MARK (hereafter MARK) (White & Burnham 1999) and an open-population Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965). In the Cormack-Jolly-Seber model, estimation of survival probabilities includes losses of individuals to mortality and to dispersal, which are often confounded (Sandercock 2006). We applied a combination of the analytical strategies suggested by Lebreton et al. (1992) and Burnham and Anderson (2002). A minimum of 3 sampling periods, 1 period of capture and 2 periods of recapture (resighting), are necessary to estimate survival probabilities with capture-mark-recapture methods (Anders & Marshall 2005). We used encounter histories to estimate annual survival. We developed these histories from 7 breeding season (May–July) sampling periods, 1 each year from 2000–2006. For instance, if a bird was captured in 2001 and resighted in 2002 and 2003 but no subsequent year, the encounter history “1110000” would have been used in analyses. We captured and marked individuals from 2000–2005 and resighted individuals from 2001–2006.

In 2005 and 2006, we collected data to allow tabulation of within-breeding-season encounter histories and estimates of within-season apparent survival. We included at least 3 sampling events (1 capture and 2 resighting periods) for both focal species in each year. Resighting efforts were separated by 10- to 14-day intervals.

We fitted a global model with separate apparent survival and resight (\( p \)) parameters with group effects of species and age and time dependence (\( \Phi_{(species \times age \times t)}, \hat{p}_t \)) (Burnham & Anderson 2002). We tested for overdispersion and estimated the variance inflation factor (\( \hat{c} \)) for our global model with the parametric-bootstrap option in program MARK (White & Burnham 1999). Models testing age and year effects still fit the annual apparent survival model poorly, so we used QAICc (quasi-Akaike’s information criterion) with an adjustment of \( \hat{c} = 1.31 \) to improve fit. For all other models \( \hat{c} < 1 \), so we made no overdispersion adjustments. We estimated annual and within-season apparent survival separately. We ranked models in each candidate set from best to worst by decreasing AIC adjusted for small sample size (QAICc) (Akaike 1973).

The change in AICc (i.e., \( \Delta QAICc \)) is the difference between the most parsimonious model (smallest AICc value; \( \Delta AICc = 0 \)) and a competing model; \( \Delta AICc < 2 \) between 2 competing models indicate that these models are roughly equivalent. Models within 4–7 AICc of
the top model, although plausible, have considerably less support than the top model (Burnham & Anderson 2002). Along with AICc, we used AICc weights (\( w_i \)) to compare models. The AIC weights summed to 1 across the model set; thus, these described relative support for each model.

The validity of estimates from capture-mark-recapture models hinges on the assumption that losses of individuals from the study area are due to mortality or breeding dispersal (Williams et al. 2002; Sandercock 2006). Although the species we examined are thought to be faithful to the breeding site from 1 year to the next (Morse 2004, 2005) and most researchers have assumed no substantial among-year movement (Sillett & Holmes 2002; Jones et al. 2004), recent evidence of breeding

Table 1. Parameter estimates (\( \beta_i \)) for variables associated with apparent annual survival (\( \Phi \)) and resighting probability of male Blackburnian Warblers (\( n = 196 \)) and Black-Throated Green Warblers (\( n = 316 \)) from 2000–2006 as a function of age (experienced breeders [ASY] and inexperienced breeders [SY]) and the amount of habitat within a 100-m radius (hab100).

<table>
<thead>
<tr>
<th>Model</th>
<th>Label</th>
<th>( \beta_i )</th>
<th>SE</th>
<th>lower</th>
<th>upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \Phi (age \times hab100) p (\cdot) )</td>
<td>( \Phi: ASY )</td>
<td>-0.546</td>
<td>0.149</td>
<td>-0.838</td>
<td>-0.255</td>
</tr>
<tr>
<td></td>
<td>( \Phi: SY )</td>
<td>-0.698</td>
<td>0.255</td>
<td>-1.198</td>
<td>-0.198</td>
</tr>
<tr>
<td></td>
<td>ASY \times hab100</td>
<td>0.129</td>
<td>0.129</td>
<td>-0.122</td>
<td>0.382</td>
</tr>
<tr>
<td></td>
<td>SY \times hab100</td>
<td>0.445</td>
<td>0.290</td>
<td>-0.124</td>
<td>1.014</td>
</tr>
<tr>
<td></td>
<td>( p )</td>
<td>1.212</td>
<td>0.384</td>
<td>0.459</td>
<td>1.964</td>
</tr>
<tr>
<td>( \Phi (age + hab100) p (\cdot) )</td>
<td>( \Phi: ASY )</td>
<td>-0.549</td>
<td>0.150</td>
<td>-0.843</td>
<td>-0.257</td>
</tr>
<tr>
<td></td>
<td>( \Phi: SY )</td>
<td>-0.587</td>
<td>0.233</td>
<td>-1.044</td>
<td>-0.130</td>
</tr>
<tr>
<td></td>
<td>hab100</td>
<td>0.252</td>
<td>0.113</td>
<td>0.012</td>
<td>0.453</td>
</tr>
<tr>
<td></td>
<td>( p )</td>
<td>1.205</td>
<td>0.384</td>
<td>0.451</td>
<td>1.958</td>
</tr>
</tbody>
</table>

*Only the 2 best models (\( \Delta AICc \leq 2 \)) are shown. Parameter estimates for age in competing models (\( AICc > 2.14 \)) were qualitatively similar. Key: (\( \cdot \)), parameter constant.

**Figure.** Habitat amount, defined quantitatively with the use of species distribution models, for Blackburnian Warblers (BLBW) and Black-throated Green Warblers (BTNW) in the Greater Fundy Ecosystem. The darker the shading the higher the probability of species occurrence.
dispersal in passerines suggests that this assumption may not be correct (Cilimburg et al. 2002). To estimate the extent that permanent emigration may have underestimated survival, in 2006 we searched for marked dispersers outside the boundaries of our resight radii (50 m) within 4 areas ranging from 410–480 ha. We searched for dispersers using the methods above and the design advocated by Marshall et al. (2004). The 4 grid-based searches occurred where a total of 26 Blackburnian Warblers and 47 Black-Throated Green Warblers had been captured previously. To estimate bias in apparent survival resulting from breeding dispersal, we randomly added resighted birds to our encounter histories to reflect the proportion resighted during the extended searches. We used this approach only to reduce bias in apparent survival estimates resulting from breeding dispersal, but did not use the dispersal-adjusted data set in modeling associations between apparent survival and habitat amount. Because this approach is based on a small sample size, some caution should be used in interpretation.

Results

We captured and banded 205 male Blackburnian Warblers and 356 male Black-Throated Green Warblers over the 7 years of the study. We resighted 54 Blackburnian Warblers and 105 Black-Throated Green Warblers at least once. A subset of 143 individuals (44 Blackburnian Warblers, 99 Black-Throated Green Warblers) was tracked throughout 2005–2006 to estimate within-season survival. Apparent annual survival was similar between the 2 species (Blackburnian \( \Phi = 0.361 \) [SE 0.055], Black-throated \( \Phi = 0.341 \) [0.035]). The model including “species” had little support (\( \Sigma w_i = 0.066 \)). We found considerable support for differences in survival between age classes (\( w_i = 0.931 \)). Experienced breeders (\( n = 318 \)) had higher apparent survival rates than inexperienced breeders (\( n = 194 \); apparent survival \( [\Phi] = 0.367 \) [SE 0.035], \( \Phi = 0.224 \) [0.041]).

Annual apparent survival increased as habitat amount at the 100-m extent increased (\( \Sigma w_i = 0.53 \)) (Table 1 & Supporting Information). There was also some evidence that apparent annual survival increased as habitat amount at the 2000-m extent increased (\( \Sigma w_i = 0.20 \)). Support for inclusion of habitat amount at one or the other spatial extent was high (\( \Sigma w_i = 0.69 \) for models of the hypothesis that habitat amount at either 100- or 2000-m extents was associated with warbler survival). Over the range of habitat amount observed, apparent annual survival decreased 15% (95% CI 7–29) as a function of habitat loss at the local extent; the survival probability dropped from 0.42 to 0.36. There was also some evidence that survival of inexperienced breeders was associated differentially with habitat loss at the 100-m extent (Table 1 & Supporting Information), but confidence intervals around age \( \times \) habitat parameter estimates incorporated zero. We found little support for an association of area of mature forest or matrix with apparent survival at either extent (mature \( \Sigma w_i = 0.06 \), matrix \( \Sigma w_i = 0.08 \)). We did not detect differences in the way each species responded to matrix, mature forest, or habitat amount at either spatial extent; interactions between species and these covariates had similarly low support (\( \Sigma w_i = 0.006 \)).

Apparent within-season survival was strongly associated with habitat amount at the landscape extent (Table 2 & Supporting Information). Amount of habitat within 2000 m was included in all of the top six models. Summed AIC\(_c\) weights for models including habitat amount at the landscape extent were 0.84 versus 0.07 for models including only habitat amount at the 100-m extent. The effect of landscape-extent habitat loss on apparent within-season survival was substantial. Apparent survival decreased from 0.65 to 0.05 over the range observed. Thus, apparent survival was about 12 times (95% CI

### Table 2. Parameter estimates (\( \beta_i \))\(^{a}\) for variables associated with apparent within-season survival (\( \Phi \)) and resighting probability (\( p \)) of male Blackburnian Warblers (BLBW, \( n = 44 \)) and Black-Throated Green Warblers (BTNW, \( n = 99 \)) in 2005 and 2006 as a function of species, year, and the amount of habitat within a 2000m radius (hab2000).

<table>
<thead>
<tr>
<th>Model (^b)</th>
<th>Label</th>
<th>( \beta_i )</th>
<th>SE</th>
<th>lower</th>
<th>upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \Phi ) (species * year + hab2000) ( p ) (t)</td>
<td>BLBW 2005</td>
<td>10.750</td>
<td>3.225</td>
<td>4.429</td>
<td>17.071</td>
</tr>
<tr>
<td></td>
<td>BLBW 2006</td>
<td>-3.972</td>
<td>1.741</td>
<td>-7.383</td>
<td>-0.560</td>
</tr>
<tr>
<td></td>
<td>BTNW 2006</td>
<td>8.385</td>
<td>(-c)</td>
<td>(-c)</td>
<td>(-c)</td>
</tr>
<tr>
<td></td>
<td>hab2000</td>
<td>4.676</td>
<td>1.479</td>
<td>1.778</td>
<td>7.574</td>
</tr>
<tr>
<td>( p: t_1 )</td>
<td>1.257</td>
<td>0.264</td>
<td>0.739</td>
<td>1.776</td>
<td></td>
</tr>
<tr>
<td>( p: t_2 )</td>
<td>-0.030</td>
<td>0.188</td>
<td>-0.398</td>
<td>0.339</td>
<td></td>
</tr>
<tr>
<td>( p: t_3 )</td>
<td>-0.792</td>
<td>0.206</td>
<td>-1.195</td>
<td>-0.388</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)Estimates reflect changes in \( \Phi \) and \( p \) over 10- to 14-day intervals throughout the breeding season.

\(^b\)Only the best model (\( \Delta \text{AIC}_c \leq 2 \)) is shown. Parameter estimates for hab2000 in lower ranked (\( \Delta \text{AIC}_c > 2.75 \)) models were qualitatively similar.

Key: t, time.

\(^c\)Inestimable in MARK due to confounding in the fully time-dependent model.
between species (species \times year \sum w_i = 0.63). Average within-season survival estimates for the entire breeding season were qualitatively greater for Blackburnian Warbler (\(\Phi = 0.976 \pm 0.083\)) than Black-Throated Green Warbler (\(\Phi = 0.928 \pm 0.083\)), but confidence intervals around survival estimates were quite broad and overlapped, presumably due to the high interannual variation in survival in each species (Supporting Information). We found little evidence that associations between within-season survival and habitat amount varied between species (species \times landscape-extent habitat amount \sum w_i = 0.03).

Species- and year-dependent models for resighting probability received little or no support. However, in all top-ranked models resighting probabilities decreased over the 3 sampling events (14 days) within a breeding season (model-averaged estimates during time 1 [15 June–28 June] = 0.787 [SE 0.048], time 2 [29 June–12 July] = 0.492 [0.049], time 3 [13 July–26 July] = 0.313 [0.156]), which indicates that birds were more difficult to detect as the season progressed.

During searches for birds that had dispersed from initial capture locations, we resighted 2 individual Blackburnian Warblers (2/26 = 7.7%) and 5 individual Black-Throated Green Warblers (5/47 = 10.6%) that had not been resighted previously. These individuals moved 65–650 m from the locations where they were originally captured. Including these individuals increased annual survival estimates (\(\Phi = 0.475 \pm 0.092\), corrected versus \(\Phi = 0.301 \pm 0.049\), uncorrected).

Discussion

Habitat loss at local and landscape extents was associated with a decrease in the apparent annual and breeding season survival of Blackburnian and Black-Throated Green Warblers. Thus, differential apparent survival as a function of habitat amount may be partly responsible for the lower probability of occurrence of these species in landscapes with low amounts of habitat. Habitat loss was associated with not only a decrease in the total number of individuals in a landscape, but also a reduction in survival. Our results support the hypothesis that habitat loss on the breeding grounds reduces apparent survival of Blackburnian Warblers and Black-Throated Green Warblers. Mortality in forest fragments could result from factors such as greater predator abundance or predation success and greater frequency of movements among patches by adults (Norris & Stutchbury 2001) than in contiguous landscapes with large amounts of habitat. Alternatively, greater breeding dispersal from forest fragments than from contiguous forest could indicate higher nest predation risk in fragments.

Studies that relate occurrence or density of animals to vegetation structure have been criticized for not considering survival and reproduction (Van Horne 1983; Bock & Jones 2004). We observed a positive correlation between the estimated probability of occurrence (from Betts et al. 2006b) at local and landscape extents and annual and within-season apparent survival of both species. This indicates that these fairly vagile species are efficient at finding sites that enhance their survival. As a result of our expanded grid-based searches, we found evidence of long-term breeding dispersal away from the boundaries of our resighting area. Such long-term emigration shows that our survival estimates were biased low for both species in landscapes with different amounts of habitat. By simulating new data that matched our observed likelihood of breeding dispersal, we corrected apparent survival estimates for this bias. The corrected estimate (\(\Phi = 0.475 \pm 0.092\)) was
similar to those in other studies of *Dendroica* warblers ($\Phi = 0.45–0.54$) (Stewart 1988; Sillett & Holmes 2002) and is possibly closer to the “true” survival value than our uncorrected estimates.

Relatively long-distance breeding dispersal has been observed in warblers (Cilimb ung et al. 2002). Evidence is thus accumulating that migratory passerines are not as site faithful as initially thought (Morse 2004, 2005). The variation in apparent survival we observed across a gradient of habitat amount could be attributed at least partly to breeding dispersal or true mortality. The survival difference between experienced and inexperienced breeders could be due to actual higher survival rates or higher site fidelity of experienced breeders. Reproductive success, the other key measure of habitat quality beyond abundance, may also decrease as habitat is lost across large landscapes (e.g., Robinson et al. 1995; Por neluzzi & Faaborg 1999). If breeding success of Blackburnian Warblers and Black-Throated Green Warblers was lower in landscapes with fragmented habitat, it is possible that reproductively unsuccessful birds emigrated in search of higher quality habitat.

The association between habitat loss at landscape extents and annual and within-season survival was substantial and changes in survival may affect the population viability of both species. However, because Black-Throated Green Warblers appear to be more plastic in their habitat requirements, few areas of our study region were characterized by low amounts of predicted habitat for this species (mean habitat area within 2000 m = 69.7% [SE 5.0], range 41.4–86.7). In contrast, except in Fundy National Park, Blackburnian Warbler habitat comprises a relatively low percentage of the region (12–50% mature forest in the Greater Fundy Ecosystem compared with >80% mature forest in Fundy National Park). Decreased apparent survival rates in this species on the breeding grounds could thus be a cause of declining abundances in eastern Canada (Sauer et al. 2007). Current forest management continues to apply shorter harvest-rotation periods (<50 years); thus, timber is harvested (often via clearcutting) before the stand has grown sufficiently to provide Blackburnian Warbler habitat (Young et al. 2005; Betts et al. 2006a). We suggest that implementing management treatments (e.g., selective cutting, longer harvest rotations) that maintain more mature coniferous-deciduous mixed forest that is characteristic of the historical Acadian Forest in New Brunswick may slow or reverse population declines. Maintaining relatively high amounts of habitat at multiple spatial extents may not only maintain the total number of individuals in a region, but also increase their apparent survival.

**Acknowledgments**

We gratefully acknowledge A. Breton for invaluable advice on the mark-recapture modeling. We also thank B. Sandercoc k, S. Sillett, the editor, and 3 anonymous reviewers for their constructive comments on earlier drafts of this manuscript. Thanks are due to many field assistants involved in the study. Financial support was provided by the New Brunswick Wildlife Trust Fund, Fundy National Park, Canadian Wildlife Service, New Brunswick Environmental Trust Fund, and the Fundy Model Forest.

**Supporting Information**

Covariates and other factors incorporated into models fitted in program MARK and models fitted to the Blackburnian Warbler and Black-throated Green Warbler data set used to assess variation in apparent annual survival and within-season survival and resighting probabilities (Appendix S1) are available online. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

**Literature Cited**


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