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Survival of Adult Songbirds in Boreal Forest Landscapes Fragmented by Clearcuts and Natural Openings

Taux de survie d'oiseaux adultes dans des paysages forestiers boréaux fragmentés par la coupe à blanc et les ouvertures naturelles

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ABSTRACT. There exists little information on demographic responses of boreal songbirds to logging. We conducted a 4-yr (2003-2006) songbird mark-recapture study in western Newfoundland, where land cover is a naturally heterogeneous mosaic of productive spruce-fir forest, stunted taiga, and openings such as bogs, fens, and riparian zones. We compared apparent survival and rate of transience for adults of 14 species between areas having forests fragmented primarily by either natural openings or 3-7 yr-old clearcuts. Data were collected on three landscape pairs, with birds being marked on three 4-6 ha netting sites on each landscape (total = 18 netting sites). Survival rates were estimated using multi-strata mark-recapture models with landscape types specified as model strata. Landscape type was retained in the best model for only two species, Ruby-crowned Kinglet and Yellow-rumped Warbler, in both cases indicating lower apparent survival in landscapes having clearcuts. Though parameter estimates suggested lower survival in clearcut landscapes for several species, meta-analysis across all species detected no general difference between landscape types. Further, we did not detect any relation between landscape differences in survival and a species' habitat affinity, migratory strategy, or the proportion of transients in its population. Although sensitivity to logging was limited, we observed high interspecific variation in rates of breeding season apparent survival (48% [Dark-eyed Junco] to 100% [several species]), overwinter apparent survival (0.3% [Ruby-crowned Kinglet] to 86.5% [Gray Jay]), and transience (≈0% [several species] to 61% [Ruby-crowned Kinglet in clearcut landscapes]). For Lincoln's and White-throated Sparrows, over-winter apparent survival was >2× higher for males than females, and rate of transience was > 8× higher for White-throated Sparrow males than females. Moderately male-biased sex ratios suggested that both lower mortality and higher site fidelity contributed to higher apparent survival of males. Overall, variability in our estimates of survival was too great to be explained by mortality alone, suggesting a large influence of landscape-scale movement by adults, e.g., breeding dispersal, extra-territorial forays, and transience, on the dynamics of boreal songbird populations. These movement patterns may also confer resilience to localized disturbance in boreal landscapes.

RÉSUMÉ. Peu d'informations nous permettent de mesurer la réponse démographique des oiseaux boréaux à l'exploitation forestière. Afin de pallier à cette situation, nous avons effectué une étude par capture-recapture d'une durée de 4 ans (2003-2006) dans l'ouest de Terre-Neuve, où l'on retrouve une mosaïque naturellement hétérogène de peuplements forestiers productifs d'épinettes-sapins, de taïga rabougrie et d'ouvertures telles que des tourbières, fens et zones riveraines. Nous avons comparé le taux de survie apparent et la proportion d'individus en transit pour des adultes de 14 espèces entre des zones de forêts principalement fragmentées par des ouvertures naturelles versus des coupes à blanc de 3 à 7 ans. Les données ont été récoltées dans trois paires de paysages, les oiseaux étant marqués dans trois sites de capture

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de 4 à 6 ha dans chaque paysage (total = 18 sites de capture). Les taux de survie ont été estimés en utilisant des modèles de capture-recapture multi-strates, les types de paysages représentant les dites strates. La variable « type de paysage » a été retenue dans le meilleur modèle chez seulement deux espèces, soit le Roitelet à couronne rubis et la Paruline à croupion jaune. Dans les deux cas, le taux de survie apparent était inférieur dans les paysages présentant des coupes à blanc. Bien que les estimés de paramètres suggéraient un taux de survie inférieur dans les paysages sous exploitation forestière pour plusieurs espèces, une méta-analyse pour toutes les espèces n'a permis de détecter aucune différence générale entre les types de paysages. De plus, nous n'avons pas détecté de relation entre les différences inter-paysages dans le taux de survie et l'affinité des espèces pour différents types d'habitat, leur stratégie migratoire ou la proportion d'individus en transit dans la population. Bien que la sensibilité à la coupe était limitée, nous avons observé une variation interspécifique élevée dans les taux de survie apparents durant la saison de nidification (48% [Junco ardoisé] à 100% [plusieurs espèces]), les taux de survie apparents durant l'hiver (0,3% [Roitelet à couronne rubis] à 86.5% [Mésangeai du Canada]) et la proportion d'individus en transit (≈0% [plusieurs espèces] à 61% [Roitelet à couronne rubis dans les paysages sous exploitation forestière]). Pour le Bruant de Lincoln et le Bruant à gorge blanche, le taux de survie apparent durant l'hiver était >2× plus élevé pour les mâles que les femelles et la proportion d'individus en transit était > 8× plus élevée chez les Bruants à gorge blanche mâles que chez les femelles. Des rapports des sexes modérément biaisés vers les mâles suggèrent que la mortalité plus faible et la plus grande fidélité au site ont contribué au taux de survie apparent plus élevé chez les mâles. Dans l'ensemble, la variabilité de nos taux de survie estimés était trop élevée pour s'expliquer uniquement par la mortalité, ce qui suggère une grande influence des mouvements des adultes à l'échelle des paysages (ex., dispersion, mouvements exploratoires extra-territoriaux et itinérance) dans la dynamique des populations d'oiseaux boréaux. Ces patrons de mouvements peuvent aussi leur conférer une résilience aux perturbations locales dans les paysages boréaux.

Key Words: *boreal forest; clearcutting; demographics; forest management; mark-recapture; resilience; songbirds; apparent survival; transience.*

INTRODUCTION

Survival rate strongly influences population growth rate (Robinson et al. 2004, Stahl and Oli 2006) and habitat factors can affect local survival both through direct effects on mortality and indirectly through influences on dispersal behavior (e.g., Porneluzi and Faaborg 1999, Yoder et al. 2004, Devers et al. 2007). Thus demographic responses play an important role in determining the extent to which habitat change affects populations. Research has documented local numerical changes to land bird populations resulting from boreal forest management activities (e.g., Niemi et al. 1998, Whitaker and Montevecchi 1999, Imbeau et al. 2000). However, demographic responses are harder to measure, and at present little information is available linking changes in the distribution and abundance of boreal birds to demographic and population processes (Downes et al. 2000, Rich et al. 2004, Anders and Marshall 2005, Lampila et al. 2005).

As other authors in this special section have pointed out, boreal forest birds may be relatively resilient to habitat management practices that mimic natural disturbance regimes (Rempel 2007, Belisle et al. 2007). In line with this, previous research based on occurrence rates has suggested that bird communities are relatively resilient to logging in the boreal forest (e.g., Schmiegelow et al. 1997, Niemi et al. 1998, Schieck and Song 2006). Still, population-level demographic responses cannot be inferred from distributional studies alone, as source-sink population dynamics may mask any influence of landscape change on local populations of highly mobile wildlife such as birds (VanHorne 1983, Vickery et al. 1992, Robinson et al. 1995, Porneluzi and Faaborg 1999). For example, Bayne and Hobson (2002*a*) reported that fragments of boreal forest isolated by agriculture are often occupied by Ovenbirds (*Seiurus aurocapilla*; hereafter see Table 1 for scientific names), but that individuals within these patches have reduced annual apparent survival compared to conspecifics occupying similarly sized stands isolated by clearcutting. Elevated losses in agricultural landscapes were associated with a higher proportion and turnover of first time breeders. Thus matrix habitat influenced demographic parameters and likely affected habitat quality in fragments, but effects on incidence were less pronounced (Bayne and Hobson 2002*a*). As this demonstrates, knowledge of demographic responses affords a more complete understanding of the resilience of bird populations to landscape-scale habitat management, facilitating development of sound conservation guidelines (Sallabanks et al. 2001, Bayne and Hobson 2002*b*, Donovan et al. 2002, Lampila et al. 2005).

Movement of individuals is an important process affecting both the dynamics of local songbird populations and inferences drawn from studies of songbird demography. Analytical methods for processing mark-recapture data, as used here, can correct for failure to detect individuals that are alive and have remained in the study area, but cannot distinguish mortality from emigration. Consequently estimates are of apparent survival, i.e., local survival, and are minimal estimates of true survival rates (Lebreton et al. 1992). From an ecological point-of-view, local- and landscape-scale movements are important to the dynamics of local populations because movement of individuals into or out of an area can have a large effect on habitat occupancy, population structure, synchrony of population processes, and population persistence. Dispersal is critical for the colonization of new or unpopulated habitat patches, and is of central importance to spatially structured population processes, e.g., source-sink dynamics, demographic rescue, and metapopulations (Harrison 1993, Walters 1998). Even temporary movements such as transience and extra-territorial forays can be important in facilitating such processes as information gathering, mate selection, extra-pair mating, and gene flow. Recent research has made it clear that regular landscape-scale extra-territorial movements are typical behavior for most forest songbird species, that nonterritorial “floaters” are common in some situations, and that the expression of both of these behaviors is often influenced by landscape structure (Norris and Stutchbury 2001, Fraser and Stutchbury 2004, Woolfenden et al. 2005, Leonard et al, *in press*). All of these forms of movement can be affected by a species’ population status and likely play an important role in synchronizing the dynamics of forest songbird populations on a scale of kilometers to tens of kilometers (Toms et al. 2004, Tittler et al. 2006). Consequently, consideration of patterns of space use will enhance interpretation of information on the demographics and resilience of local songbird populations.

Here we present the results of a 4-yr mark-recapture study that compared apparent survival rates of 14 species of boreal forest songbirds between landscapes characterized by either natural forest openings, i.e., mainly peatlands, or anthropogenic openings, i.e., clearcuts. We realize that peatlands and clearcuts differ in many ways, particularly vegetation and site productivity, but given the importance of movement in demographic studies we felt it was important to compare landscapes that were composed of structurally analogous matrices of open and forested habitats. Interspecific comparisons of demographic responses to habitat change can improve our understanding of avian life history strategies and the manner in which different species respond to and compensate for environmental change (Martin 1995, Lampila et al. 2005), so we expanded our analyses to include tests for patterns across species.

A priori predictions of interspecific patterns in responses are fraught with difficulty. Generally, if boreal forest bird populations are resilient to moderate levels of anthropogenic landscape change then within and between year survival should be similar in natural landscapes and landscapes modified by clearcutting. However, one might also predict that apparent survival would differ if patterns of movement vary with landscape type and resource distribution. Furthermore, individual species will likely differ in both the manner and degree to which they compensate for landscape change. As a simple starting point, we suggest three behavioral attributes that may relate to a species’ compensatory ability. First, some species may be intolerant of a given habitat type, and so individuals must either relocate or endure greater risk if they remain in a landscape characterized by that habitat. Based on this we predicted that any effect of clearcutting on apparent survival would differ between species that either selected or avoided clearcuts. Second, resident birds must endure any adverse consequences of landscape change year-round and winter is a critical period for their survival. This led to the prediction that, if clearcutting affects survival, the effect would be more pronounced for residents than for migrants. Third, pairing success or territory density may be lower in unfavorable landscapes, leading to more extensive movements by individuals that settle in these areas (e.g., Fraser and Stutchbury 2004). Individuals that wander widely can be identified as “transients” in mark-recapture analyses, so we predicted that an inverse relation would exist

Table 1. List of study species and range of previously published estimates of annual survival. Estimates printed in italics are return rates and would likely be higher if mark-recapture analytical methods had been used to estimate apparent survival. [†] American Ornithologists Union species code, used to denote species throughout this manuscript. Source of published estimate: [1] DeSante and Kaschube (2006); [2] Strickland and Ouellet (1993); [3] Rosenberg et al. (1999); [4] Nott and DeSante (2002); [5] Gardali et al. (2003); [6] Roberts (1971); [7] Stewart (1988); [8] DeSante et al. (1998); [9] Sandercock and Jaramillo (2002); [10] Karr et al. (1990); [11] Nolan et al. (2002). [§] Calculated by averaging the annual survival estimates presented in Table 3 across landscape types and (where applicable) sexes.

Species	spcd [†]	Temperate locations[‡]	Boreal locations[‡]	This study[§]
Yellow-bellied Flycatcher *Empidonax flaviventris*	YBFL	na	na	0.69
Gray Jay *Perisoreus canadensis*	GRAJ	0.75[1]	0.54-*0.83*[1,2]	0.73
Boreal Chickadee *Poecile hudsonicus*	BOCH	na	0.49[1]	0.38
American Robin *Turdus migratorius*	AMRO	0.38-0.58[1]	0.35[1]	0.42
Hermit Thrush *Catharus guttatus*	HETH	0.45-0.46[1]	0.50[1]	0.44
Swainson’s Thrush *Catharus ustulatus*	SWTH	0.59-0.75[3,4,5]	0.42-0.57[1,3]	0.40
Ruby-crowned Kinglet *Regulus calendula*	RCKI	0.26[1]	na	0.01
Blackpoll Warbler *Dendroica striata*	BLPW	0.34[1]	0.31[1]	0.28
Northern Waterthrush *Seiurus noveboracensis*	NOWA	0.40-0.72[1,6]	0.53[1]	0.35
Yellow-rumped Warbler *Dendroica coronata*	MYWA	0.29-0.70[1,4,7,8]	0.37[1]	0.23
Fox Sparrow *Passerella iliaca*	FOSP	0.35-0.55[1,9]	0.52[1]	0.20

(con'd)

Lincoln’s Sparrow *Melospiza lincolnii*	LISP	0.43[1,4,9]	0.35[1]	0.26
Dark-eyed Junco *Junco hyemalis*	SCJU	0.39-*0.54*[1,4,10,11]	0.31[1]	0.23
White-throated Sparrow *Zonotrichia albicollis*	WTSP	0.29-0.61[1,10]	0.50[1]	0.29

between any effect of clearcutting on apparent survival and the proportion of transients in a population.

We conducted a meta-analysis across all species to assess the overall resilience of the assemblage to clearcutting, and then tested for relations between our estimates of the effect of clearcutting on apparent survival and each species’ habitat association, migratory strategy, and rate of transience. This study should offer insight into whether common boreal species have the capacity to compensate demographically for broad-scale environmental change, which is a fundamental component of resilience (Walker et al. 2006).

METHODS

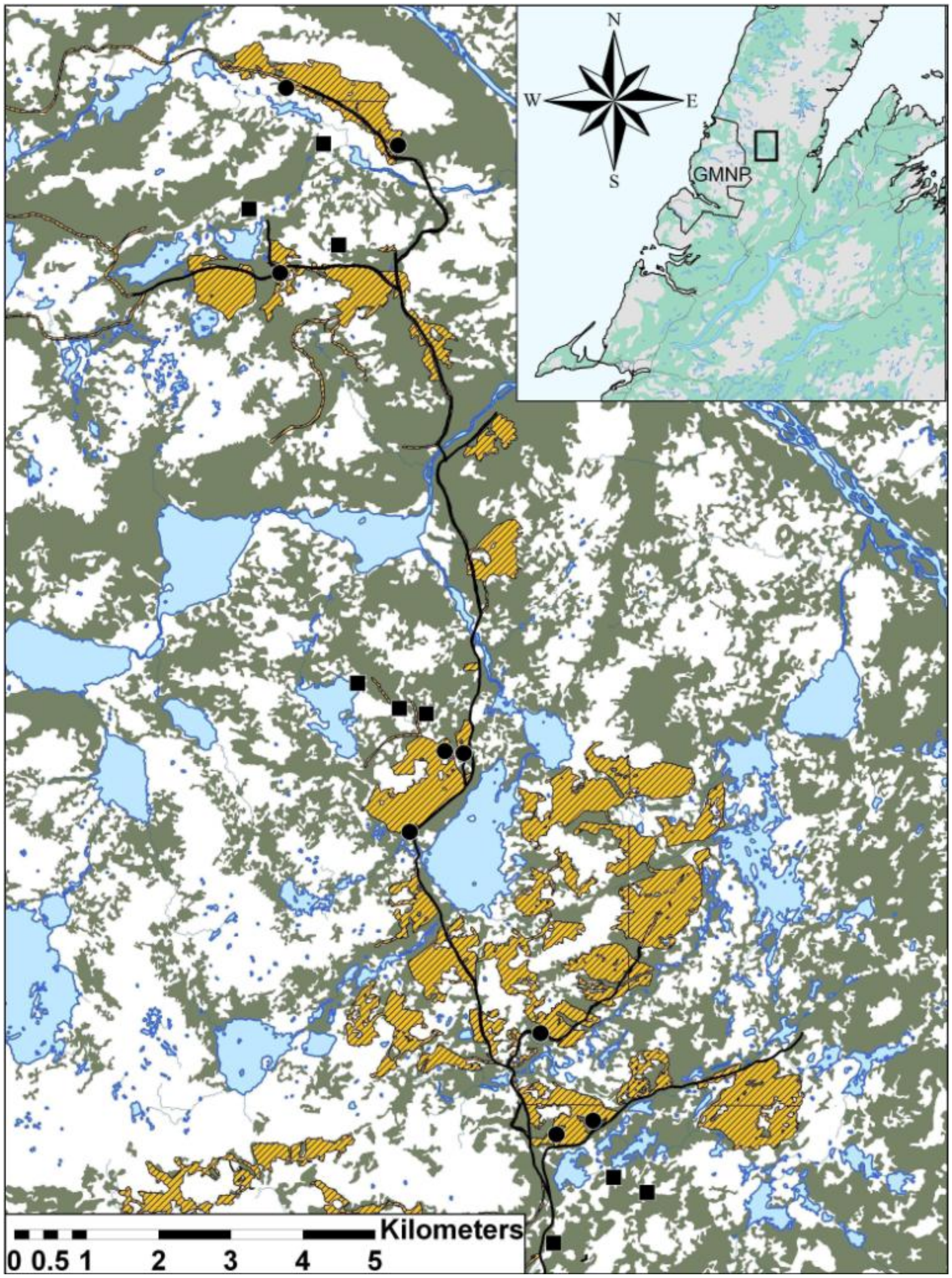
Data collection

Our study site was the Upper Main River watershed, situated on the eastern slope of the Long Range Mountains in western Newfoundland, Canada (57º 15´ W; 49º45´N; elevation range 400–525 m; Fig. 1). The 338 km² study area was a naturally heterogeneous mosaic that had been modified by clearcut timber harvesting; during this study, land cover comprised 8% surface water, 11% peatlands and other natural openings, 36% scrub forest, 40% mature productive forest, and 6% clearcut forest. Timber harvesting occurred during 1999 and 2000 and clearcuts ranged in size from 20–100 ha, whereas natural openings ranged in size from 1–50 ha. Both productive and scrub forests were typically dominated by balsam fir (*Abies balsamea*) with a significant representation of black spruce (*Picea mariana*), particularly on saturated soils. Most of the study area had never been logged, and wildfire and stand-killing outbreaks of defoliating insects have been rare due to the wet climate and cold winters. This lack of recent largescale disturbance led to prevalence of gap-dynamic old-growth coniferous forests on productive sites (McCarthy and Weetman 2006).

Data were collected on six landscapes; these were grouped into three pairs that were approximately equally spaced along a 15 km north-south gradient. Landscapes were ≈4 km², and paired adjacent landscapes were located within ≈500 m of one another. One landscape in each pair was characterized by forest cover interspersed with natural openings, i.e., peatlands; (NAT), whereas forest cover on the other was broken primarily by clearcuts, though some natural openings were also present (CUT); open habitats comprised 30–50% of each landscape. Two constant effort mist-netting sites were sampled on each landscape in the south and middle landscape pairs during 2003 (total = 8 netting sites), and in 2004 these eight sites as well as two sites on each of the two northern landscapes were sampled (total = 12 netting sites). For 2005 and 2006, a third netting site was added to each of the 6 landscapes, for a total of 18 netting sites (Fig. 1). Note that for logistical reasons there was some interspersion of netting sites on the northern landscapes. Each netting site consisted of 25 mist nets dispersed over 4–6 ha, and nets on each site were approximately equally distributed between forest, forest edge, and open habitats. Mist nets measured 12 × 2.6 m, and had four shelves and a mesh size of 30 mm.

Constant effort mist netting began during the first week of June and finished in mid-August each year. Sampling was carried out as a series of net rounds, within which each netting site was sampled once. Six net rounds were completed in 2003, 2005, and 2006, whereas nine net rounds were completed in

Fig. 1. Distribution of netting sites across three paired landscapes in the Upper Main River watershed, 2003-2006. Each landscape included three netting sites located in areas having forest cover broken either by natural openings (squares) or by clearcuts (circles). Productive forest cover (green) was interspersed with clearcuts (hatched orange), scrub forest and peatlands (white), and lakes and rivers (blue). The rectangle in the inset map depicts the location of the study area, east of Gros Morne National Park (GMNP) on the island of Newfoundland, Canada.



2004 (total = 27 net rounds); netting ran from 05:30–11:30 h each day. The order in which netting sites were visited within each net round was kept relatively constant each year, ensuring that the interval between consecutive visits to a site was ≥6 d. For the 3 yr in which we conducted six netting rounds, the mean interval between the start of consecutive netting rounds was 12.4 d, whereas the mean interval was 8.3 d in 2004. Often some or all mist nets on a site were closed due to wind or rain, and as a minimum we required a total of 75 net-hr of effort, of a possible 150 net-hr, in a single day to consider a site as having been adequately sampled. We calculated effort for each net round as the total number of net-hours sampled across all sites divided by the total possible net-hr.

During netting each captured bird was classified by species and whenever possible by sex and age according to criteria in Pyle (1997), and unbanded birds were fitted with a numbered aluminum leg band. All field procedures were approved by the Animal Care Committee of Acadia University in accordance with Canadian Council on Animal Care.

Data analysis

Survival analyses were carried out using multi-strata mark-recapture models (Brownie et al. 1993) in which harvested and unharvested landscapes were specified as strata (CUT and NAT). Multi-strata models are an elaboration of open population Cormack-Jolly-Seber models that allow estimation of three parameters; stratum-specific apparent survival probability (S_i^s; the probability that an individual alive in stratum s at time i is alive and in that stratum at time i+1), stratum-specific detection probability (p_i^s; the probability that an individual alive in stratum s at time i is recaptured at time i), and transition probabilities for movement between strata (Ψ_i^{rs}; the probability that an individual in stratum r at time i is in stratum s at time i+1, given that it is alive at time i+1) (White et al. 2006). Models were fit in program MARK using a logit link function (White and Burnham 1999, White et al. 2006). To account for the fact that nine net rounds were completed in 2004, whereas six were completed in all other years, we set the time interval for the eight within-breeding season survival intervals in 2004 to 0.625, i.e., 5/8ths the duration of within-season intervals in other years.

All captures of hatch-year birds were dropped, after which a capture history was generated for each adult after-hatch-year bird. We generated two capture history datasets for each species. In the first we coded males and females as separate groups, whereas in the second we included all birds in a single group, including any additional individuals of unknown sex. Known mortalities were coded as having not been released following their final capture (*n* = 7).

Estimates of apparent survival will be biased downwards if samples include transient individuals that are not resident on the study site. In this context “resident” refers to individuals showing fidelity to the study site, i.e., territory holders, not migratory strategy. Similarly, “transient” refers to individuals that are not resident on the study site, though they may maintain territories elsewhere and be captured while on an extra-territorial forays, i.e., they are not necessarily nonterritorial floaters. To segregate bias occurring due to the presence of transients, survival rates were estimated separately for newly marked and previously marked individuals (Pradel et al. 1997). We further subdivided our estimates of apparent survival by parameterizing intervals occurring within a breeding season vs. those spanning the overwinter period separately. This was done for both the period following initial captures and for subsequent time intervals, yielding four apparent survival estimates for each sex and stratum: (1) breeding season *S* for newly marked individuals, (2) breeding season *S* for local residents, (3) overwinter *S* for newly marked birds, and (4) overwinter *S* for local residents.

Transition probabilities (Ψ) were parameterized for males and females moving from a CUT to a NAT site or a NAT to a CUT site during either the breeding season or the overwinter period. We did not control for year when estimating either apparent survival or transition probabilities.

Estimates of capture probability were not of direct interest in the context of this study (White et al. 2006), and yet there were several reasonable alternative parameterizations of *p*. Consequently we used a two-stage model selection process (Lebreton et al. 1992). First we fit a series of candidate global models to identify the best parameterization of capture probability (*p*) for that species. We then fit a series of reduced models starting from that best global model.

We began by fitting the set of candidate global models to the sex-specific capture history database for a species. Each global model included full parameterization of apparent survival, i.e., $S_{\text{land*sex*tp4}}$, (see Table 2 for an explanation of parameter footnotes) and an additive parameterization for the transition probabilities, i.e., $\Psi_{\text{land+sex+t2}}$. Alternative parameterizations of capture probability in the candidate global models included full time dependence in *p*, a linear trend in *p* over each breeding season, independent estimation of *p* for each net round within seasons, and constant capture probability across net rounds. Each of these parameterizations of *p* was fit using various additive and multiplicative combinations of landscape type, sex, effort, and year.

Once this set of candidate global models had been fit, we took the model having the lowest value of Akaike's Information Criterion corrected for sample size (AIC_c; Burnham and Anderson 2002) and used a bootstrap goodness-of-fit test to evaluate model fit and estimate a variance inflation factor (c-hat; Lebreton et al. 1992, White and Burnham 1999). If the fit of this candidate global model was acceptable, we used it as the global model for that species; if the fit was poor (i.e., $p < 0.05$ or c-hat < 0.9 or > 1.5) we tested the fit of increasingly general candidate global models until we identified one that adequately fit the data. If none of the candidate models was acceptable we switched to the capture history for that species in which sexes were pooled, and repeated the process with a set of candidate global models that were similar except for the absence of any terms for sex.

Once an acceptable global model was identified we fit a series of reduced models, with simplifications being first based on stratum-transition terms (Ψ), followed by capture probability (*p*) and finally apparent survival (*S*) (Lebreton et al. 1992). For *S* we fit all additive and interactive combinations of landscape type, sex, and time phase (tp4). We used the estimate of c-hat from the global model to correct for over-dispersion in our data by adjusting the deviance used to calculate the information criteria for each sub-model (i.e., quasi-likelihood Akaike's Information Criterion corrected for sample size, or $QAIC_c$; Burnham and Anderson 2002). If the estimate of c-hat was < 1, we set c-hat to 1 (Burnham and Anderson 2002). Models were ranked based on $QAIC_c$, where models having a smaller $QAIC_c$ were considered better. Finally, once the model having the lowest $QAIC_c$ was identified we attempted to reduce this model further by combining records for overwinter resident and newly marked individuals into a single parameter for overwinter survival (i.e., tp3). If this yielded an improvement in fit we applied this reduced parameterization to all models in the set.

For each species we report a subset of competing models that includes all models having either $\Delta QAIC_c < 2$ or $QAIC_c$ weight ($QAIC_c\omega$) > 0.10, as well as the global model. We also report the model-averaged estimates of apparent survival for each group and stratum, i.e., sex and landscape type. Model-averaged estimates were calculated as the weighted average across all models, with weighting based on $QAIC_c\omega$. Standard errors reported with these estimates are unconditional, incorporating both sampling variance and model selection uncertainty.

We estimated the proportion of transients for each species by assuming that transients are never recaptured (i.e., $p_{\text{transient}} = 0$); the proportion of transients in captures of unbanded individuals (τ) can then be estimated as $1 - (S_{\text{newly marked}} / S_{\text{resident}})$, where $S_{\text{newly marked}}$ is the estimate for the first interval following marking and S_{resident} is the survival rate during subsequent intervals (Pradel et al. 1997). As this does not take into account the proportion of marked residents in the population it is an estimate of the proportion of transients in the unmarked population (Pradel et al. 1997, Jessop et al. 2004).

We carried out a meta-analysis to test for a general difference in apparent survival across all species between NAT and CUT landscapes. For this we used apparent survival estimates from the model in each species' set specifying $S_{(\text{land+t4})}$, as this was the simplest model that provided landscape-specific estimates and, by excluding sex, was common to all species. For each species we calculated the difference in breeding season and overwinter *S* between NAT and CUT landscapes by subtracting S_{NAT} from S_{CUT}, and estimated the standard error of these differences as:

$$\text{SE} = \sqrt{\text{Variance}_{(\text{CUT})} + \text{Variance}_{(\text{NAT})} - 2 \times \text{Covariance}_{(\text{CUT,NAT})}} \quad (1)$$

(Crawley 2002). We estimated the average difference in breeding season or overwinter apparent survival between landscape types, with each species' difference weighted by the associated

Table 2. Sets of competing best multi-strata mark-recapture models for 14 species of songbirds breeding in boreal forests of western Newfoundland, 2003-2006. Best models are highlighted in bold. The last model reported in each set is the most general global model, which was used to calculate the variance inflation factor for that model set (c-hat). Effective n is the number of releases of marked individuals back into the population up to the penultimate net round, whereas % CUT indicates the percentage of captures that occurred on netting sites located in clearcut landscapes, i.e., vs. naturally fragmented landscapes. Species codes are from Table 1. [†] Terms in models are as follows: *land* = landscape type (CUT or NAT); *sex* = sex; *tp4* = 4 time phases for *S* (breeding season newly-marked, breeding season resident, over winter newly-marked, and over winter resident); *tp3* = as with tp4, but with residents and newly marked birds combined to estimate only one over winter survival rate; *year* = year; *trend* = linear trend in *p* within each breeding season; *round* = independent estimation of *p* for each net round within a season; *effort* = net effort; *time* = independent estimate of *p* for every net round in every year; *t2* = Ψ for two periods, i.e., breeding season and over winter.

Model[†]	*K*	Q dev.	QAIC$_c$	Δ_i	ω_i
YBFL (n = 181; % CUT = 59%; effective n = 231; c-hat = 1.00)					
$S_{(\text{tp3})}p_{(\text{year+effort})}\Psi_{(\text{land})}$	**10**	**313.55**	**474.32**	**0.00**	**0.23**
$S_{(\text{land*tp3})}p_{(\text{year+effort})}\Psi_{(\text{land})}$	13	306.97	474.43	0.11	0.22
$S_{(\text{land+tp3})}p_{(\text{year+effort})}\Psi_{(\text{land})}$	11	311.83	474.81	0.49	0.18
$S_{(\text{tp4})}p_{(\text{year+effort})}\Psi_{(\text{land})}$	11	312.90	475.88	1.56	0.10
$S_{(\text{land+tp4})}p_{(\text{year+effort})}\Psi_{(\text{land})}$	12	310.93	476.14	1.82	0.09
$S_{(\text{land*tp4})}p_{(\text{year+effort})}\Psi_{(\text{land})}$	15	304.22	476.23	1.91	0.09
$S_{(\text{land*tp4})}p_{(\text{year+effort})}\Psi_{(\text{land+t2})}$	16	303.91	478.23	3.91	0.03
GRAJ (n = 59; % CUT = 38%; effective n = 103; c-hat = 1.00)					
$S_{(\text{tp4})}p_{(.)}\Psi_{(\text{land+t2})}$	**8**	**294.72**	**397.35**	**0.00**	**0.69**
$S_{(\text{land+tp4})}p_{(.)}\Psi_{(\text{land+t2})}$	9	294.27	399.30	1.95	0.26
$S_{(\text{land*tp4})}p_{(.)}\Psi_{(\text{land+t2})}$	12	291.06	403.62	6.27	0.03
BOCH (n = 59; % CUT = 32%; effective n = 120; c-hat = 1.25)					
$S_{(\text{tp3})}p_{(\text{land*trend})}\Psi_{(.)}$	**8**	**143.75**	**220.30**	**0.00**	**0.52**
$S_{(\text{tp4})}p_{(\text{land*trend})}\Psi_{(.)}$	9	143.10	221.99	1.69	0.22
$S_{(\text{land+tp3})}p_{(\text{land*trend})}\Psi_{(.)}$	9	143.74	222.62	2.32	0.16
$S_{(\text{land*tp4})}p_{(\text{effort+land*trend})}\Psi_{(\text{land+t2})}$	16	142.25	238.98	18.68	0.00
AMRO (n_{male} = 90, n_{female} = 77; % CUT = 63%; effective n = 229; c-hat = 1.00)					

(con'd)

$S_{(tp3)}p_{(round)}\Psi_{(land)}$	**11**	**387.62**	**553.86**	**0.00**	**0.39**
$S_{(sex+tp3)}p_{(round)}\Psi_{(land)}$	12	387.22	555.70	1.84	0.15
$S_{(land+tp3)}p_{(round)}\Psi_{(land)}$	12	387.59	556.07	2.21	0.13
$S_{(tp4)}p_{(round)}\Psi_{(land)}$	12	387.61	556.09	2.23	0.13
$S_{(land*sex*tp4)}p_{(sex+round+effort)}\Psi_{(land+sex+t2)}$	28	377.99	585.14	31.28	0.00
HETH (n_{male} = 79, n_{female} = 71; % CUT = 56%; effective n = 302; c-hat = 1.21)					
$S_{(tp4)}p_{(round+effort)}\Psi_{(sex)}$	**13**	**604.13**	**780.14**	**0.00**	**0.47**
$S_{(sex+tp4)}p_{(round+effort)}\Psi_{(sex)}$	14	603.66	781.87	1.73	0.20
$S_{(land+tp4)}p_{(round+effort)}\Psi_{(sex)}$	14	603.91	782.12	1.98	0.18
$S_{(land*sex*tp4)}p_{(land+sex+round+effort)}\Psi_{(land+sex+t2)}$	29	596.94	810.08	29.94	0.00
SWTH (n = 162; ; % CUT = 48%; effective n = 229; c-hat = 1.23)					
$S_{(tp3)}\ p_{(land+round+effort)}\Psi_{(land)}$	**13**	**283.66**	**430.50**	**0.00**	**0.49**
$S_{(land+tp3)}\ p_{(land+round+effort)}\Psi_{(land)}$	14	282.95	432.05	1.55	0.23
$S_{(land+tp4)}\ p_{(land+round+effort)}\Psi_{(land)}$	14	283.66	432.76	2.26	0.16
$S_{(land*tp4)}p_{(land+round+effort)}\Psi_{(land+t2)}$	19	280.89	441.67	11.17	0.00
RCKI (n_{male} = 93, n_{female} = 67; % CUT = 36%; effective n = 197; c-hat = 1.00)					
$S_{(land+tp3)}p_{(trend)}\Psi_{(.)}$	**7**	**151.41**	**279.25**	**0.00**	**0.41**
$S_{(land+tp4)}p_{(trend)}\Psi_{(.)}$	8	151.15	281.16	1.91	0.16
$S_{(land+sex+tp3)}p_{(trend)}\Psi_{(.)}$	8	151.33	281.34	2.09	0.14
$S_{(land*sex+tp3)}p_{(trend)}\Psi_{(.)}$	9	149.48	281.69	2.44	0.12
$S_{(land*sex*tp4)}p_{(land+sex+trend+year)}\Psi_{(land+sex+t2)}$	27	143.32	319.51	40.26	0.00
BLPW (n_{male} = 248, n_{female} = 179; % CUT = 52%; effective n = 655; c-hat = 1.17)					
$S_{(tp3)}p_{(round+effort)}\Psi_{(.)}$	**11**	**805.11**	**1310.26**	**0.00**	**0.25**
$S_{(tp4)}p_{(round+effort)}\Psi_{(.)}$	12	804.07	1311.29	1.03	0.15
$S_{(sex+tp3)}p_{(round+effort)}\Psi_{(.)}$	12	804.47	1311.69	1.43	0.12
$S_{(land*sex*tp4)}p_{(land+sex+round+effort)}\Psi_{(land+sex+t2)}$	29	792.46	1335.99	25.73	0.00
NOWA (n = 117; % CUT = 36%; effective n = 142; c-hat = 1.24)					
$S_{(tp3)}p_{(land+trend)}\Psi_{(land)}$	**8**	**157.27**	**229.93**	**0.00**	**0.41**

(con'd)

$S_{(\text{tp4})}p_{(\text{land+trend})}\Psi_{(\text{land})}$	9	156.04	230.99	1.06	0.24
$S_{(\text{land+tp3})}p_{(\text{land+trend})}\Psi_{(\text{land})}$	9	157.24	232.18	2.25	0.13
$S_{(\text{land*tp4})}p_{(\text{land+trend+effort})}\Psi_{(\text{land+t2})}$	15	149.35	238.74	8.81	0.00
MYWA (n_{male} = 278, n_{female} = 232; % CUT = 48%; effective n = 705; c-hat = 1.12)					
$\boldsymbol{S_{(\text{land+tp4})}p_{(\text{time})}\Psi_{(.)}}$	**32**	**646.43**	**1320.01**	**0.00**	**0.37**
$S_{(\text{tp4})}p_{(\text{time})}\Psi_{(.)}$	31	649.62	1321.01	1.00	0.22
$S_{(\text{land+sex+tp4})}p_{(\text{time})}\Psi_{(.)}$	33	646.33	1322.16	2.09	0.13
$S_{(\text{land*sex+tp4})}p_{(\text{time})}\Psi_{(.)}$	34	644.30	1322.34	2.28	0.12
$S_{(\text{land*sex*tp4})}p_{(\text{land+sex+time})}\Psi_{(\text{land+sex+t2})}$	48	637.52	1347.18	27.12	0.00
FOSP (n = 84; % CUT = 62%; effective n = 122; c-hat = 1.00)					
$\boldsymbol{S_{(\text{tp3})}p_{(\text{trend})}\Psi_{(.)}}$	**6**	**186.26**	**278.40**	**0.00**	**0.42**
$S_{(\text{land+tp3})}p_{(\text{trend})}\Psi_{(.)}$	7	184.89	279.29	0.89	0.27
$S_{(\text{tp4})}p_{(\text{trend})}\Psi_{(.)}$	7	185.97	280.36	1.96	0.16
$S_{(\text{land*tp4})}p_{(\text{land+trend+effort})}\Psi_{(\text{land+t2})}$	15	180.92	294.86	16.46	0.00
LISP (n_{male} = 124, n_{female} = 67; % CUT = 44%; effective n =384; c-hat = 1.05)					
$\boldsymbol{S_{(\text{sex*tp3})}p_{(\text{land+sex+year+trend*effort})}\Psi_{(.)}}$	**16**	**668.79**	**1009.94**	**0.00**	**0.22**
$S_{(\text{land*sex+sex*tp3})}p_{(\text{land+sex+year+trend*effort})}\Psi_{(.)}$	18	665.25	1010.80	0.86	0.14
$S_{(\text{sex+tp3})}p_{(\text{land+sex+year+trend*effort})}\Psi_{(.)}$	14	674.10	1010.91	0.97	0.14
$S_{(\text{land+sex*tp3})}p_{(\text{land+sex+year+trend*effort})}\Psi_{(.)}$	17	668.34	1011.68	1.74	0.09
$S_{(\text{land*sex*tp4})}p_{(\text{land+sex+year+trend*effort})}\Psi_{(\text{land+sex+t2})}$	29	661.66	1032.24	22.30	0.00
SCJU (n_{male} = 115, n_{female} = 57; % CUT = 67%; effective n = 275; c-hat = 1.00)					
$\boldsymbol{S_{(\text{tp4})}p_{(\text{land+trend})}\Psi_{(.)}}$	**8**	**433.86**	**700.82**	**0.00**	**0.32**
$S_{(\text{tp3})}p_{(\text{land+trend})}\Psi_{(.)}$	7	436.37	701.20	0.39	0.27
$S_{(\text{sex+tp4})}p_{(\text{land+trend})}\Psi_{(.)}$	9	433.73	702.82	2.00	0.12
$S_{(\text{land+tp4})}p_{(\text{land+trend})}\Psi_{(.)}$	9	433.79	702.88	2.06	0.12
$S_{(\text{land*sex*tp4})}p_{(\text{land+sex+trend+effort})}\Psi_{(\text{land+sex+t2})}$	25	430.47	732.72	32.86	0.00
WTSP (n_{male} = 242, n_{female} = 143; % CUT = 53%; effective n = 728; c-hat = 1.07)					
$\boldsymbol{S_{(\text{sex*tp3})}p_{(\text{land+time})}\Psi_{(\text{sex})}}$	**35**	**1095.41**	**1896.66**	**0.00**	**0.45**

(con'd)

$S_{(\mathrm{land+sex*tp3})}p_{(\mathrm{land+time})}\Psi_{(\mathrm{sex})}$	36	1094.14	1897.60	0.94	0.28
$S_{(\mathrm{sex*tp4})}p_{(\mathrm{land+time})}\Psi_{(\mathrm{sex})}$	37	1093.76	1899.44	2.77	0.11
$S_{(\mathrm{land*sex*tp4})}p_{(\mathrm{land+sex+time})}\Psi_{(\mathrm{land+sex+t2})}$	48	1085.80	1916.33	19.67	0.00

standard error (rmeta package [Lumley 2006]; R statistical package, The R Development Core Team, version 2.4.1).

In an effort to explain interspecific variation in responsiveness to landscape, we also fit generalized linear models with either the breeding season or overwinter landscape differences in apparent survival as the response variable, and explanatory variables relating to three life history traits: habitat association, migration strategy, and proportion of transients. Based on extensive bird surveys conducted in the study area (D. M. Whitaker, *unpublished data*), we classified each species' habitat affinity as positively, negatively, or not associated with the amount of clearcut within 1 ha. These same habitat affinities were also generally evident in the proportion of captures occurring in CUT vs. NAT landscapes (% CUT; Table 2). We quantified migration strategy as the median latitude of each species' wintering range; for Gray Jay and Boreal Chickadee we used the latitude of our study site, as it was assumed that these nonmigratory species wintered there. Finally, if species are adversely affected by landscape change then pairing success and territory density may be reduced, leading to a higher incidence of nonterritorial floaters and extra-territorial forays. Consequently we fit our estimate of the proportion of transients, which we hypothesized would be positively related to sensitivity to landscape change.

RESULTS

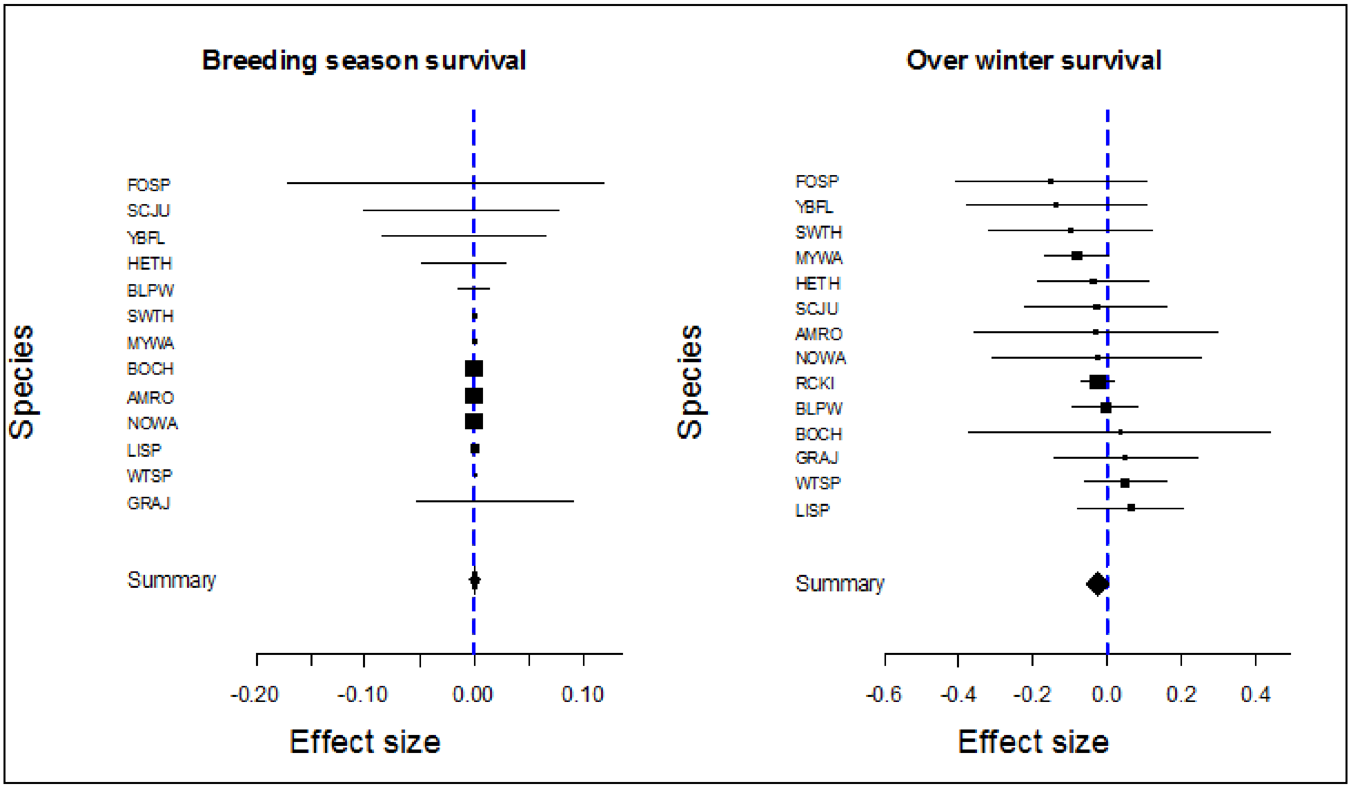
Bootstrap goodness of fit tests indicated that satisfactory global models were identified for sex-specific capture histories of seven species and for an additional six species after sexes were pooled (Table 2). For one common species, Blackpoll Warbler, we were unable to identify a suitable global model using our original model structure. However a good global model fit was obtained for the sex-specific capture histories after switching to a constant time interval for all net rounds, i.e., not setting the time step for 2004 to 0.625. We tested to see if this biased estimates of breeding season survival for this species by including a separate survival parameter for the 2004 breeding season; this term did not improve model fit and so was not retained.

Sample sizes varied across these 14 species, and in some cases there was as much as a two-fold difference in number of captures between CUT and NAT landscapes (Table 2). Small, unevenly distributed sample sizes limited the resolution of some parameter estimates and consequently the power of comparisons between landscapes for those species (e.g., Table 3, Fig. 2). However, we took this uncertainty into account wherever appropriate, e.g., in model averaging and meta-analyses, and encourage readers to do the same when evaluating our results. Given that we screened each species for inclusion using rigorous model selection criteria, we believe that our findings are useful if assessed with due caution.

Across the 14 species there was high variability in estimates of apparent survival during both the breeding and overwinter periods (Table 3). Although estimates suggested that breeding season survival was near 100% for most species, estimated S_{breeding} per net round was substantially lower for Hermit Thrush (< 0.94) and Dark-eyed Junco (< 0.87) indicating season-long apparent survival rates of 73% and 47%, respectively. Estimates of overwinter apparent survival were even more variable, exceeding 0.6 for Yellow-bellied Flycatcher, Hermit Thrush, and Gray Jay, but being as low as <0.03 for Ruby-crowned Kinglet. Overwinter apparent survival ranged from 0.2–0.5 for most other species.

Only Ruby-crowned Kinglet showed an unambiguous effect of landscape type on apparent survival; the three best models all included an additive effect of landscape type on *S* (Tables 2 and 3). These models indicated that breeding season apparent survival of kinglets was higher in NAT landscapes; extremely

Fig. 2. Meta analyses of landscape differences in breeding season and over-winter apparent survival (S) ± 95% CI of boreal songbirds in western Newfoundland, 2003-2006. Observations for each species represent the difference in apparent survival between naturally fragmented landscapes and landscape modified by clearcutting (SNAT-SCUT), and are ordered based on the magnitude of the difference. Negative values indicate lower apparent survival in CUT landscapes. Squares vary in size to reflect the precision of each estimate, which was calculated as $1/SE^2$ and used to weight each species during meta analyses. Note that in cases in which weights were very low, the square was so small as to be obscured by the horizontal line, which represents the 95% confidence interval on the difference. The black diamond at the bottom of each plot, labeled summary, is centered on the overall mean difference, and its width indicates the 95% confidence interval on the mean difference (breeding season mean = 0.000, 95% CI = -0.001-0.001; over-winter mean = -0.023, 95% CI = -0.054-0.009). Ruby-crowned Kinglet was dropped from the within-year plot because the species' large confidence interval (-0.49-0.33) overwhelmed estimates for other species. Species codes are from Table 1.



low estimates of apparent survival during the overwinter period made inferences for this period biologically trivial. The best model and two of three competing models for Yellow-rumped Warbler also included the term for landscape, again indicating higher apparent survival in NAT landscapes (Tables 2 and 3). Models including a landscape-specific survival term also had some support for seven other species (i.e. $\Delta_i < 2$; Table 2).

Although meta-analysis across species-level estimates from our $S_{(land+t4)}$ models did not detect an overall effect of landscape type on breeding season apparent survival (summary effect = 0.000, 95% CI = -0.001-0.001), there was some evidence of a difference in overwinter apparent survival (summary effect = -0.023, 95% CI = -0.054-0.009) (Fig. 2). For 10 of 14 species, the estimate of between year apparent survival was lower in CUT landscapes than in NAT landscapes and for 5 of 6

Table 3. Model-averaged apparent survival estimates ± SE by species and when applicable, sex for birds inhabiting boreal forest landscapes having either natural open areas (NAT) or clearcuts (CUT), 2003–2006. We report unconditional standard errors, which take variance from each model and model selection uncertainty into account. Species codes are from Table 1, whereas model sets used to calculate model-averaged survival estimates are presented in Table 2. † As the seasonal survival rates were estimated for five breeding season intervals and one over winter interval, annual survival was calculated as ((breeding season$S$)^5×(over winter S)).

Species	Newly-marked birds S ± SE		Breeding season S ± SE		Over-winter S ± SE		Annual $S^{\dagger}$	
	NAT	CUT	NAT	CUT	NAT	CUT	NAT	CUT
YBFL (all)	0.581 ± 0.203	0.639 ± 0.202	0.998 ± 0.031	0.995 ± 0.055	0.823 ± 0.196	0.581 ± 0.194	0.815	0.567
GRAJ (all)	1.000 ± 0.000	1.000 ± 0.000	0.963 ± 0.052	0.972 ± 0.044	0.861 ± 0.224	0.865 ± 0.207	0.713	0.750
BOCH (all)	0.536 ± 0.150	0.543 ± 0.194	1.000 ± 0.004	0.998 ± 0.033	0.371 ± 0.109	0.384 ± 0.156	0.371	0.380
AMRO male	1.000 ± 0.001	1.000 ± 0.000	1.000 ± 0.000	1.000 ± 0.002	0.437 ± 0.100	0.431 ± 0.086	0.437	0.431
AMRO female	1.000 ± 0.000	1.000 ± 0.004	1.000 ± 0.000	1.000 ± 0.000	0.410 ± 0.106	0.408 ± 0.088	0.410	0.408
HETH male	0.768 ± 0.095	0.756 ± 0.094	0.937 ± 0.044	0.933 ± 0.044	0.635 ± 0.128	0.631 ± 0.131	0.459	0.446
HETH female	0.757 ± 0.099	0.742 ± 0.099	0.935 ± 0.047	0.930 ± 0.047	0.614 ± 0.130	0.608 ± 0.134	0.439	0.423
SWTH (all)	0.623 ± 0.137	0.596 ± 0.145	0.998 ± 0.023	1.000 ± 0.000	0.421 ± 0.108	0.379 ± 0.098	0.417	0.379
RCKI male	0.863 ± 0.214	0.362 ± 0.190	0.992 ± 0.049	0.931 ± 0.228	0.027 ± 0.029	0.003 ± 0.008	0.026	0.002
RCKI female	0.855 ± 0.230	0.431 ± 0.234	0.992 ± 0.048	0.934 ± 0.219	0.021 ± 0.025	0.003 ± 0.008	0.020	0.002
BLPW male	0.498 ± 0.054	0.502 ± 0.054	0.965 ± 0.047	0.963 ± 0.047	0.350 ± 0.103	0.343 ± 0.101	0.293	0.284
BLPW female	0.485 ± 0.057	0.491 ± 0.058	0.973 ± 0.044	0.971 ± 0.044	0.309 ± 0.089	0.303 ± 0.086	0.269	0.262
NOWA (all)	0.435 ± 0.177	0.435 ± 0.192	1.000 ± 0.013	1.000 ± 0.000	0.365 ± 0.134	0.338 ± 0.146	0.365	0.338
MYWA male	0.687 ± 0.095	0.606 ± 0.095	0.996 ± 0.025	0.993 ± 0.044	0.275 ± 0.068	0.211 ± 0.049	0.270	0.204
MYWA female	0.675 ± 0.095	0.616 ± 0.098	1.000 ± 0.018	1.000 ± 0.020	0.251 ± 0.051	0.206 ± 0.055	0.251	0.206
FOSP (all)	0.986 ± 0.077	0.960 ± 0.173	0.991 ± 0.108	0.977 ± 0.135	0.240 ± 0.133	0.180 ± 0.100	0.229	0.160

(con'd)

LISP male	0.773 ± 0.101	0.787 ± 0.103	0.981 ± 0.046	0.982 ± 0.044	0.414 ± 0.115	0.434 ± 0.114	0.376	0.396
LISP female	0.754 ± 0.171	0.825 ± 0.149	0.989 ± 0.067	0.992 ± 0.050	0.119 ± 0.082	0.173 ± 0.100	0.113	0.166
SCJU male	0.890 ± 0.144	0.888 ± 0.142	0.862 ± 0.062	0.861 ± 0.059	0.479 ± 0.143	0.471 ± 0.137	0.228	0.223
SCJU female	0.895 ± 0.140	0.893 ± 0.139	0.866 ± 0.063	0.865 ± 0.061	0.485 ± 0.144	0.477 ± 0.139	0.236	0.231
WTSP male	0.689 ± 0.070	0.714 ± 0.068	0.971 ± 0.040	0.977 ± 0.033	0.422 ± 0.091	0.445 ± 0.086	0.364	0.396
WTSP female	0.966 ± 0.102	0.970 ± 0.092	1.000 ± 0.001	1.000 ± 0.000	0.193 ± 0.055	0.210 ± 0.056	0.193	0.210

species that showed a difference in within year survivorship between landscape types, apparent survivorship was also lower in CUT landscapes (Fig. 2). General linear models did not detect any relation between either breeding season or overwinter landscape differences in apparent survival and a species' median wintering latitude, association with clearcut habitat, or the proportion of transients in populations.

We detected clear differences in survival between sexes for only two of the eight species for which we were able to fit sex-specific models. Best models for both Lincoln's and White-throated Sparrows included interactions between time phase and sex; for both species overwinter survival estimates were > 2× higher for males compared to females, while estimates of breeding season survival were marginally higher for females than for males (Tables 2 and 3).

Our estimates of τ, the proportion of transients in captures of unmarked individuals, were highly variable (Table 4). For some species, proportions of transients were negligible, e.g., American Robin and Fox Sparrow. Our analyses even suggested that apparent survival during the first interval after marking exceeded that of subsequent breeding season intervals for Gray Jay and Dark-eyed Junco, suggesting either declining survival or, more likely, declining site fidelity through the breeding season. In contrast, transients exceeded 40% of unmarked birds for Boreal Chickadee, Blackpoll Warbler, and Northern Waterthrush. As mentioned above, we observed lower apparent survival of Ruby-crowned Kinglets in CUT landscapes, and our estimates of τ suggested that the proportion of transients for this species was 4× higher in CUT than NAT landscapes. Overwinter *S* was higher for male than female White-throated Sparrows, and proportion of transients within the breeding season was also much higher for males of this species. In contrast, though overwinter *S* was also higher for male than female Lincoln's Sparrows, estimates of breeding season transience were similar between sexes.

DISCUSSION

Diversity in life-history strategies among forest songbird species has important consequences for how landscape management influences populations. The dearth of information about key demographic parameters for boreal songbirds and how these may mediate or contribute to any effects of environmental change on these species is a critical knowledge gap. We observed a high degree of variation in the parameters we studied; estimates of breeding season apparent survival ranged from 48% (SCJU; see Table 1 for a list of species codes) to 100% (several species), overwinter apparent survival ranged from 0.3% (RCKI) to 86.5% (GRAJ), and the estimated proportion of transients among unmarked birds ranged from being negligible for several species to 61% (RCKI in CUT landscapes). Further, differences in overwinter apparent survival between males and females of a species ranged from negligible to being 3.5× higher for males (LISP). Although the proportion of transients was similar between sexes for most species, this value was > 8× higher for male than female White-throated Sparrows. This heterogeneity was observed even though (1) all of our study species were small-bodied songbirds, (2) all form socially monogamous pair bonds and maintain defended territories, (3) only adult, after-hatch-year

Table 4. Estimated proportions of transients (τ) in captures of unmarked birds by landscape type and, when possible, sex for each species during the breeding period in western Newfoundland, 2003–2006. Proportions were estimated from model averaged survival rates (reported in Table 3) using the formula (1-($S_{\text{newly marked}}$/ $S_{\text{breeding season}}$)). Species codes are from Table 1.

Species & sex	τ_{NAT}	τ_{CUT}
YBFL (all)	0.418	0.358
GRAJ (all)	-0.038	-0.029
BOCH (all)	0.464	0.456
AMRO male	0.000	0.000
AMRO female	0.000	0.000
HETH male	0.180	0.190
HETH female	0.190	0.202
SWTH (all)	0.376	0.404
RCKI male	0.130	0.611
RCKI female	0.138	0.539
BLPW male	0.484	0.479
BLPW female	0.502	0.494
NOWA (all)	0.565	0.565
MYWA male	0.310	0.390
MYWA female	0.325	0.384
FOSP (all)	0.005	0.017
LISP male	0.212	0.199
LISP female	0.238	0.168
SCJU male	-0.032	-0.032

(con'd)

SCJU female	-0.033	-0.032
WTSP male	0.290	0.269
WTSP female	0.034	0.030

birds were included in our analyses, and (4) data were collected concurrently on the same sites and analyzed using common methods.

Our estimates of apparent survival were generally comparable to or lower than the lowest estimates previously reported for our study species (Table 1). In line with this observation, DeSante and Kaschube (2006) analyzed data from the continent-wide Monitoring of Avian Productivity and Survivorship program (MAPS) and found that apparent survival of landbirds was generally lower in Alaska and boreal Canada than in more southerly regions of North America (cf., Bayne and Hobson 2002*b*). Similarly, Rosenberg et al. (1999) reported that estimates of annual apparent survival for Swainson's Thrush declined from 0.75 to 0.42 along a south-north gradient from northern California to Alaska. DeSante and Kaschube (2006) suggested that longer migration routes and severe winter weather faced by resident species may lead to higher mortality in populations of birds breeding in northern forests. However, even if this is true the overwinter apparent survival rates we observed for most species are too low to be explained by mortality alone. This suggests an important role for landscape-scale movement of adults, possibly including breeding dispersal, transience, and extra-territorial forays, in the dynamics of local populations of many songbird species (e.g., Cilimburg et al. 2002; Fig. 3). Our results are consistent with recent observations that most boreal songbirds use home ranges far larger than their defended territories, that individuals respond to landscape-scale habitat, and that populations are synchronized on a scale of kilometers to tens of kilometers (Toms et al. 2004, Betts et al. 2006*a*, Taylor and Krawchuk 2006, Tittler et al. 2006, Leonard 2007, Rempel 2007).

Central to this explanation for generally lower overwinter apparent survival rates of songbirds in northern forests is the suggestion that boreal landscapes have favored relatively low interannual territory fidelity. Boreal forests are naturally heterogeneous systems where regular largescale disturbance creates a shifting mosaic of stands in varying successional stages and where productive forests are interspersed with persistent open habitats such as peatlands, scrub forests, rock barrens, and water bodies (Niemi et al. 1998, McCarthy and Weetman 2006; Fig. 1). Further, breeding seasons in boreal forests are typically brief and subject to extended periods of adverse spring weather, particularly in mountainous and coastal regions such as our study area. These conditions may have favored patterns of site fidelity, local space use, and dispersal that allow individuals to exploit or colonize suitable habitat at a broad spatial scale and to relocate when a site becomes unsuitable (e.g., Betts et al. 2006*b*, Leonard 2007).

Response to forest harvesting

Our analyses suggested that apparent survival was lower in harvested landscapes for Ruby-crowned Kinglet and Yellow-rumped Warbler (Tables 2 and 3) and pointed to weak support for lower survival in harvested landscapes for several additional species (Fig. 2). We observed that occurrence rate of kinglets was negatively associated with clearcuts in our study area (D. M. Whitaker, *unpublished data*; see also Table 2 and Ingold and Wallace 1994) offering an obvious explanation for reduced local survival and increased transience in CUT landscapes. However simply attributing this observation to avoidance of clearcuts is overly simplistic; occurrence of several other species considered here was also positively or negatively related to clearcuts (D. M. Whitaker, *unpublished data*; Table 2), yet these species showed no clear influence of landscape on apparent survival. Further, apparent survival of Yellow-rumped Warbler was lower in CUT landscapes, though occurrence of this habitat generalist is typically unaffected by clearcuts (Table 2; Hunt and Flaspohler 1998, Whitaker and Montevecchi 1999,

Fig. 3. This male Blackpoll Warbler was banded in a clearcut as an adult and recaptured one year later while on territory in a natural forest opening 820 m away.

Taylor and Krawchuk 2006). Thus, if local habitat selection was important, it may be contingent on a species' relative affinity for natural openings vs. clearcuts, as contrasted here. Along these lines, Taylor and Krawchuk (2006) reported that occurrence of Ruby-crowned Kinglet in our study area was positively related to the amount of forest cover in the landscape, but that the nature of this response depended on whether the nonforest cover consisted of natural openings or clearcuts.

Previous research has pointed to links between age and reproductive success and reduced apparent survival in disturbed or fragmented forest habitat, likely mediated through breeding dispersal (Porneluzi and Faaborg 1999, Bayne and Hobson 2002*a*). Unfortunately we were unable to reliably assess age or monitor reproductive success of kinglets. The fact that the proportion of transient Ruby-crowned Kinglets was 3–4 times higher in CUT landscapes (Table 4) suggests a link to lower site fidelity, though this may at least in part have been an artifact of a lower density of locally resident individuals on our netting sites. The extremely low overwinter apparent survival we observed for this species may also reflect high rates of interannual breeding dispersal. Only 1 of 108 adult Ruby-crowned Kinglets marked prior to our last year of banding was recaptured in a subsequent year. The resulting estimates of overwinter apparent survival for this species (< 3%) cannot be reflective of its true survival rate, given the continued existence of kinglets in the area. Previously it has been suggested that the extremely thin legs of kinglets may lead to high rates of band loss (Brewer et al. 2000). However, to address this concern a smaller band size has been used on this species since 1993, and interannual recapture rates in northwestern USA are much higher than observed here, indicating that in that region many kinglets do return with these bands (DeSante and Kaschube 2006).

Variation in survival and transience

Consistent with other studies (e.g., Powell et al. 2000, Sillett and Holmes 2002, Jones et al. 2004, Leonard 2007) we observed high breeding season survival rates for adult songbirds of most species. Consequently the relatively low rates we observed for junco (≈48%) and Hermit Thrush (≈70%) are noteworthy. It seems implausible that such high losses to local breeding populations resulted from mortality alone, implicating high rates of territory abandonment or breeding dispersal within the breeding season. This is consistent with our seemingly unlikely observation of negative rates of transience for juncos, i.e., higher apparent survival during the first interval after marking than during subsequent intervals. A parallel study of nesting success found that nesting phenology for these species was similar to most other songbirds in our study area (Dalley 2007). Thus these movements were not simply a result of these species completing breeding earlier than other species. However this may be a reasonable explanation for our observation of negative rates of transience for Gray Jay (Table 4); this species breeds much earlier than other boreal passerines (Strickland and Ouellet 1993) and in our area most pairs had fledged young by mid-June. Adult dispersal during the breeding period is relatively unstudied in songbirds, although Dale et al. (2006) reported that more than half of all breeding dispersal in a population of Ortolan Buntings (*Emberiza hortulana*) occurred at this time. Also, Nott and DeSante (2002) reported that peak recapture rates for known-resident (Oregon) juncos occurred at the start of the breeding season, whereas captures of known-residents of nine other species remained high until much later. Similarly, our models for juncos included a declining trend in capture probability through the breeding season, whereas models for Hermit Thrush included a nonlinear trend in which capture probability peaked early in the breeding season. However, our estimates of breeding season apparent survival were low even though we controlled for this variability in capture probability. These findings suggest that patterns of within-year territory fidelity were strikingly different for juncos and possibly Hermit Thrush than for most other boreal songbirds, though identification of the mechanism leading to this difference was beyond the scope of this study.

Although breeding season survival rates were similar between sexes for both Lincoln’s and White-throated Sparrows, overwinter apparent survival rates were 2.1–3.5× higher for males than for females (Table 3). Higher apparent survival of males can result either from lower male mortality, which should be reflected in male-biased sex ratios, and/or higher male site fidelity. For example, Bayne and Hobson (2002b) reported that apparent annual survival was lower for female than male Ovenbirds (0.21 vs. 0.60) and, though populations were likely male-biased, the authors felt that such an extreme difference could only be explained by lower female site fidelity. Sandercock and Gratto-Trevor (1997) also reported lower apparent survival for female than male Semipalmated Sandpipers (*Calidris pusilla;* 0.56 vs. 0.61). In this case there was direct evidence of lower site fidelity of females, as median female dispersal distances was greater than that of males (174 m vs. 41 m), and also anecdotal evidence for higher female mortality.

Our mark-recapture analyses indicated that capture probabilities were similar between sexes for both White-throated and Lincoln’s Sparrows. However, we captured 1.92 male White-throated Sparrows per female (*n* = 449 individuals), and 1.88 male Lincoln’s Sparrows per female (*n* = 193 individuals), indicating that populations were male-biased on our study sites. Other studies have documented a comparable male-bias in Lincoln’s Sparrow populations (Ammon 1995), and possibly an interactive color morph×sex bias in mortality of White-throated Sparrows (Falls and Kopachena 1994), suggesting that biased sex ratios may be widespread for these species and consequently that mortality is higher for females than males. However the biased sex ratios we observed would reflect the accumulated effect of higher male survival over the life spans of these species (≥7 yr; Falls and Kopachena 1994, Ammon 1995), so although substantial they are insufficient to fully account for the 2.1–3.5-fold higher local survival of males over a single winter that we observed. This suggests that, as with many passerines (Clarke et al. 1997), interannual site fidelity was also higher for males than for females.

Other phenomena that may be associated with biased sex ratios are high rates of transience and extra-territorial forays for males, as many males will remain unpaired (e.g., Fraser and Stutchbury 2004). Though similar between males and females in Lincoln's Sparrow, the proportion of transients (τ) was > 8× higher for male than female White-throated Sparrows (Table 4). This suggests that, for this species, males encountered on our netting sites were less likely to be local residents than were females; this may also account in part for the male-biased sex ratio in captures.

We observed proportions of transients in excess of 20% of newly marked individuals for at least one class, by sex or landscape type, for 10 of 14 species we studied (Table 4). Nott and DeSante (2002) observed a similar range of rates of transience across 10 species of temperate songbirds. Note: Nott and DeSante (2002) define τ as the proportion of residents in captures, i.e., $1 - \tau$ as defined here and in Pradel et al. (1997). Although our estimates of τ could reflect a high proportion of nonterritorial "floaters" in populations, we suspect that most transients were on forays from territories located off of our study sites. Nur et al. (2004) reported that recapture probability was strongly inversely related to territory proximity to netting sites, so individuals captured while on forays from nearby territories were unlikely to be recaptured. Recent research has also shown that most temperate passerines make regular long distance extra-territorial forays in search of extra-pair mates and to forage (e.g., Norris and Stutchbury 2001, Fraser and Stutchbury 2004, Woolfenden et al. 2005). For example, although our analyses indicated that approximately 50% of newly marked Northern Waterthrush and Blackpoll Warblers were transient, Leonard (2007) used radiotelemetry to study movements of breeding males of these species on our study area and reported that only 1 of 30 waterthrush and 1 of 35 blackpolls were nonterritorial floaters. However, both species made regular extra-territorial forays that at times exceeded 1000 m from their territory centers (Leonard et al., *in press*).

CONCLUSIONS

Findings from this study suggest that populations of many common species of boreal songbirds are resilient to a moderate amount of clearcutting with respect to breeding season and overwinter apparent survival. These patterns hold true regardless of migratory strategy, affinity for clearcut habitat, or the proportion of transients in the population (Fig. 2; see also Lampila et al. 2005). However 2 of 14 species we studied did experience lower apparent survival in landscapes altered by clearcutting, and for several others there was some suggestion of reduced apparent survival. The relatively low sensitivity to clearcutting we observed is noteworthy given that local survival rates during both the breeding season and overwinter periods and proportions of transients were highly variable across species and sexes. Low sensitivity to habitat change caused by logging has been reported in a number of studies of boreal songbirds (e.g., Bayne and Hobson 2002*a*, Dalley 2007, Leonard 2007), and this pattern may be a general feature of boreal songbird communities (Schmeigelow et al. 1997, Niemi et al. 1998, Imbeau et al. 2000, Lampila et al. 2005).

A general pattern we observed was that, even within species, annual apparent survival appeared to be lower in boreal forests than in more temperate regions (Table 1; see also DeSante and Kaschube 2006), likely indicative of extensive landscape-scale movement (e.g., Fig. 3). We speculate that this reflects adaptation to an ecosystem subject to regular largescale disturbance, whereby individuals use the landscape at a scale that exceeds that of major disturbance events (Walters 1998, Mazerolle and Hobson 2003, Ibarzabal and Desrochers 2004, Leonard et al., *in press*). In other words, we suggest that boreal songbird populations maintain resilience to naturally occurring landscape change through adaptable movement behaviors. If true, such behavior would also confer a degree of resilience to forest harvest when it occurred within the same range of spatial and temporal scales. Indeed there is increasing evidence that boreal birds and other animals alter movement behavior in response to moderate changes in landscape structure (e.g., Pither and Taylor 1998, Belisle and St. Clair 2001, Leonard 2007). In line with this, we suggest that our observation of a moderate reduction in apparent survival for several species in landscapes altered by clearcutting may be the result of changes to patterns of settlement, return, or space use within these species. We caution however that there are likely thresholds to landscape change beyond which animals can no longer compensate and where resilience will break down (e.g., Jonsen and Taylor 2000). Broader-scale knowledge of patterns of movement of boreal songbirds, in particular, interannual movement, will be necessary to elucidate these relationships, uncover any mechanisms that might underlie them, and determine whether thresholds to such adaptations exist.

A commonly suggested approach for minimizing impacts of clearcutting on populations of boreal forest wildlife is to mimic natural disturbance patterns (e.g., Hunter 1992, Niemi et al. 1998). It seems intuitive that boreal forest wildlife should be adapted to persist in heterogeneous, dynamic landscapes and consequently relatively more resilient to landscape change resulting from timber harvesting than are species adapted to systems typified by continuous closed canopy forest and infrequent disturbance (Schmiegelow et al. 1997, Niemi et al. 1998, Imbeau et al. 2000). However, extrapolating our observation that a number of common species were resilient to a moderate amount of clearcutting to other species, locations, and management regimes in the boreal forest may be problematic. For example, we have reported estimates for all species for which data were sufficient to yield a reasonable model fit. This constraint may have biased us against including species that declined in abundance following logging or avoid both natural and anthropogenic open habitats. Also, the extent of clearcutting in our study area, i.e., 5.9% of the landscape; ≈12.9% of productive woodlands, was much lower than is typical of other managed boreal forests. For example, the Upper Humber River watershed lies to the immediate south of our study area, and 27.5% of this 516 km² landscape, including >50% of productive woodlands, was clearcut between 1990 and 1999.

In conclusion, our findings suggest that populations of boreal songbirds are characterized by regular landscape-scale movement of individuals, leading to relatively low apparent local survival and largescale mixing and synchrony in populations. This also affords resilience to localized habitat change resulting from natural and anthropogenic disturbance. Studies of the distribution of other taxa in the same region, in relation to landscape structure, suggest that other organisms interact with the landscape at these same, broad spatial scales (Miner and Taylor 2002, Krawchuk and Taylor 2003) suggesting that such resilience may be widespread, taxonomically. However it is worth noting that some species likely still experience reduced local survival in landscapes modified by clearcutting, and even with some level of resilience there may be thresholds to both forest fragmentation and outright loss of habitat beyond which adverse demographic effects and local extinctions will occur (Porneluzi and Faaborg 1999, Jonsen and Taylor 2000, Stephens et al. 2003, Guénette and Villard 2005, Lampila et al. 2005).

Responses to this article can be read online at:
http://www.ace-eco.org/vol3/iss1/art5/responses/

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