

SUCCESS OF MIGRATORY SONGBIRDS BREEDING IN HARVESTED BOREAL FORESTS OF NORTHWESTERN NEWFOUNDLAND

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Abstract. The consequences of forest harvest to birds nesting in spatially and temporally dynamic landscapes are poorly understood. The boreal forests of Newfoundland have a low density of nesting birds, are naturally heterogeneous, and experience extreme annual variation in weather. Against this backdrop, we tested whether breeding success of passerines was affected by forest harvest or whether natural heterogeneity masked potential consequences of harvesting. During 2004 and 2005, we monitored 98 nests and banded 439 hatch-year (HY) birds of three migratory passerines in landscapes that varied in the extent of natural or human-induced heterogeneity: the White-throated Sparrow (*Zonotrichia albicollis*), Yellow-rumped Warbler (*Dendroica coronata*), and Blackpoll Warbler (*Dendroica striata*). We monitored nest-initiation date, clutch size, hatching success, nests' daily survival rates, fledging success, and productivity (ratio of HY to adults captured) relative to proportion of forest harvested within radii of 20 m (local scale), 115 m (neighborhood scale), and 1250 m (landscape scale). Local habitat and year significantly predicted nest-initiation date. Hatching success, fledging success, and productivity were significantly influenced by year and proportion of harvest at all scales, although associations varied by species. Nests' daily survival rates were significantly related to proportion of harvest at all three scales for the White-throated Sparrow; for all species they were consistently higher in 2005, and the direction of the harvest's effect differed by species. Our results reveal that larger scales are important later in breeding and that spatial and temporal heterogeneity may not only conceal consequences of forest harvest, they may also have complex interactions that make predictions difficult in these dynamic landscapes.

Key words: boreal forest, breeding success, forest harvest, passerines, productivity, spatial scale.

Éxito de Aves Canoras Migratorias en Bosques Boreales Explotados en el Noroeste de Newfoundland

Resumen. Las consecuencias de la cosecha forestal sobre las aves de bosque que nidifican en paisajes espacial y temporalmente dinámicos son poco conocidas. Los bosques boreales de Newfoundland tienen densidades bajas de aves que nidifican, son naturalmente heterogéneos y presentan variaciones climáticas anuales extremas. Bajo este escenario, probamos si el éxito de cría de aves paseriformes era afectado por la cosecha forestal o si la heterogeneidad natural de estos bosques enmascaraba las potenciales consecuencias de la cosecha. Durante 2004 y 2005, monitoreamos 98 nidos y anillamos 439 individuos en su año de eclosión (AE) de tres especies de paseriformes migratorias (*Zonotrichia albicollis*, *Dendroica coronata* y *Dendroica striata*) en paisajes que variaron en el grado de heterogeneidad natural o inducida por humanos. Monitoreamos la fecha de iniciación del nido, el tamaño de la nidada, el éxito de eclosión, las tasa de supervivencia diaria de los nidos, el éxito de emplumamiento y la productividad (proporción de captura de individuos del AE y adultos) con relación a la proporción de árboles cosechados dentro de radios de 20 m (escala local), de 115 m (escala de vecindario) y de 1250 m (escala de paisaje). El hábitat local y el año predijeron significativamente la fecha de iniciación del nido. El éxito de eclosión, el éxito de emplumamiento y la productividad estuvieron influenciados significativamente por el año y la proporción de cosecha en todas las escalas, aunque las asociaciones variaron entre especies. Las tasas de supervivencia diaria de los nidos estuvieron significativamente relacionadas con la proporción de cosecha a las tres escalas para *Z. albicollis*; para todas las especies estas tasas fueron consistentemente más altas en 2005, y la dirección del efecto de la cosecha difirió entre especies. Nuestros resultados muestran que las escalas mayores son importantes durante las etapas más tardías de la reproducción y que la heterogeneidad temporal y espacial no sólo puede enmascarar las consecuencias de la cosecha de árboles, sino que también pueden interactuar de forma compleja haciendo más difícil hacer predicciones en estos paisajes dinámicos.

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INTRODUCTION

On both wintering and breeding grounds forest harvesting is influencing populations of migrant songbirds dramatically (Askins et al. 1995, Robbins et al. 1989, Robinson et al. 1995), and such harvesting is considered one of the most important threats to these species in boreal forests (Imbeau et al. 2001). Demographic data from all periods of the annual cycle are required for migratory birds to be managed and conserved (Green 1999, Sillett and Holmes 2002) and for the effects of human-induced forestry changes on North American breeding birds to be predicted and mitigated (Thompson et al. 1999, Hobson and Bayne 2000). Here, we focus on breeding populations.

Forestry practices can influence breeding songbirds in many ways. Forest-dwelling birds may avoid deforested landscapes (Bélisle et al. 2001), and edges created by forestry can be associated with increased depredation of ground nests (Gates and Gysel 1978, Paton 1994, Manolis et al. 2002, Ibarzabal and Desrochers 2004). Also, foraging success in clear-cuts can be reduced, leading to reduced provisioning, slower chick growth, and reduced chick survival (Buehler et al. 2002, Stauss et al. 2005, Tremblay et al. 2003, 2005). As a consequence of these and other influences, Lampila et al. (2005) reported that 41.9%, 55.5%, and 2.6% of studies on forest birds found significantly negative, nonsignificant, and significantly positive responses, respectively, to forest fragmentation. Fragmentation and its consequences are not restricted to one scale (Lord and Norton 1990). Hence, studies at multiple scales have become increasingly common (Sisk et al. 1997, Stephens et al. 2003, Bourque and Desrochers 2006). Different patterns may emerge at different spatial scales (Zanette and Jenkins 2000), and factors at larger scales may determine the degree of response to factors at smaller scales (Mazerolle and Villard 1999, Robinson et al. 1995) or vice versa. The spatial scale at which forestry influences songbird populations must be considered carefully, particularly in a system such as the boreal forest where small- and large-scale heterogeneities are inherent.

There is a recognized need for studies of demographic responses of breeding birds at broad scales (Schmiegelow et al. 1997), especially in areas made up of a natural patchwork of stands of diverse ages, such as boreal forests (Tewksbury et al. 1998). In this study, we consider measures of breeding phenology and breeding success of boreal songbirds in relation to forest harvest in northwestern Newfoundland. In Newfoundland, as elsewhere, forest harvest affects the abundance, assemblage composition, movement, space use, and survival of songbirds at multiple scales (Powell 2005, Taylor and Krawchuk 2005, Leonard et al. 2008), but it is not known how forest harvest influences productivity of these birds. We focus on avian breeding success as one part of a multifaceted study (Taylor et al. 2006) on movement and demographic responses to human-induced heterogeneity (i.e., forest harvest).

Specifically, we tested how the proportion of harvest at the local (20-m radius), neighborhood (115-m radius), and landscape (1250-m radius) scales were related to six variables: (1) initiation date, (2) clutch size, (3) hatching success, (4) fledging success, (5) nests' daily survival rates (nDSR), and (6) productivity [ratio of juvenile (hatch-year, HY) to adult (after-hatch-year, AHY) birds captured]. Radii of 115 and 1250 m were chosen because, in our study area, they correspond to the typical territory size and maximum average distance moved from the territory center, respectively, by Blackpoll Warblers (*Dendroica striata*) during breeding (Leonard 2007).

METHODS

STUDY AREA

The study took place in western Newfoundland, Canada, in the Main River watershed of the Gros Morne Greater Ecosystem (49.78° N, 57.29° W; fig. 1 in Dalley et al. 2008). The majority of the island of Newfoundland is dominated by tracts of continuous second-growth forest remaining from past logging (Sturtevant et al. 1996) so that most areas are in early successional stages (Thompson 1991). The Main River area encompasses some of the few remaining nonharvested forests in Newfoundland, is dominated by black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) (Belanger et al. 2003), and has scrub, peat lands, and ponds. Parts of the study area were harvested between 1997 and 2001, but operations ceased in 2001, in part to help maintain ecological integrity of the greater ecosystem of Gros Morne and the Main River UNESCO world heritage site. The post-harvest landscape contains riparian buffer strips, patches of trees not viable commercially, a low density of hardwood patches, primarily paper birch (*Betula papyrifera*), and dead woody debris from tree branches removed on site.

Within this area, we chose three sets of study plots ~2 km × 2 km (fig. 1 in Dalley et al. 2008), with one natural plot of heterogeneous habitat (as described above) paired with a plot that contained openings harvested between 1999 and 2000. We focused efforts on finding nests within these paired study plots.

NESTING DATA

Between early June and late July 2004 and 2005, we observed adult birds' behavior for cues of breeding (e.g., carrying nesting material and flushing brooding females) while searching terrestrial habitats (Ralph et al. 1993). We recorded stage and content upon finding the nest and on subsequent visits every three days. To reduce attraction of predators, we approached and vacated nests from different directions to avoid leaving dead-end trails (Martin and Geupel 1993). We used poles with mirrors to view nests that were difficult to approach or too high to observe directly.

We deemed nests active when females were brooding, young were observed, or adults were visiting nests with food.

If we observed no activity at nests with eggs on three consecutive visits, or if nests contained intact dead young, we deemed them abandoned. We considered nests depredated if found empty before the expected date of fledging, damaged, or containing injured young. We defined number of young fledged as the number of young observed in the previous visit if we did not observe signs of nest loss. We considered nests successful if young were present on the visit previous to the expected date of fledging. We used visual or auditory observations of fledglings with adults to confirm nest success (Ralph et al. 1993). No nests in our analyses were of uncertain fate.

STUDY SPECIES

We collected data on all species encountered, but we analyzed in detail only those for the Yellow-rumped Warbler (*Dendroica coronata*), Blackpoll Warbler, and White-throated Sparrow (*Zonotrichia albicollis*) because we obtained too few data (<20 nests) for other species (Dalley 2007). The three focal species breed commonly in the northern boreal forests of Canada. Each species nests in an open cup constructed by the female. The species are territorial and considered socially monogamous, with females incubating and both sexes feeding mostly insects to the young. Yellow-rumped Warblers breed primarily in coniferous forests, building nests >1 m above the ground. Blackpoll Warblers breed in coniferous scrub and forests, nesting generally within 1 m of the ground. White-throated Sparrows nest along edges and in openings of coniferous forests, usually on the ground (Ehrlich et al. 1988, Falls and Kopachena 1994, Hunt and Flaspohler 1998, Hunt and Eliason 1999).

MEASURES OF PRODUCTIVITY

We followed the North American Banders' Council's (NABC 2001) protocol for all procedures. With constant effort, we mist-netted passively in each of three paired (i.e., six) study plots as part of a larger project (Taylor et al. 2006). In each study plot, there were three netting sites for a total of 18 sites. We monitored each netting site with 25 12-m mist-nets, with three sites monitored per day. In both 2004 and 2005, we began netting in early June and ended in early- to mid August. Netting commenced at 05:30 NST on each day that weather permitted (minimal wind so that nets were not billowing, no rain, and no extreme temperatures to reduce bird stress), and ended at 11:30. After six suitable days, each site had been netted once. We fitted each netted bird with a numbered aluminum Canadian Wildlife Service leg band, identified each bird to species, and aged and sexed it according to Pyle (1997). We defined each site's productivity as the ratio of HY to AHY birds netted, where the assumption is that capture probabilities for HY and AHY birds are the same within a site (DeSante and Geupel 1987, Koford et al. 1994, Peach et al. 1996, Bart et al. 1999, Nott et al. 2002, Mazerolle et al. 2005, Gaston et al. 2006).

STATISTICAL ANALYSES

We conducted all analyses with R version 2.4.0 (R Core Development Team 2006). Response variables for each of the three focal species included day of nest initiation (day the first egg was laid), clutch size (total number of eggs laid in the nest), hatching success (proportion of eggs laid that hatched), nDSR (according to logistic exposure; Shaffer 2004; for these models, a nest was considered to be active or successful if it contained or fledged one or more young, respectively), fledging success (proportion of hatched eggs that fledged), and productivity (see above). For nests located after nest initiation, we backdated from known hatching or fledging dates, assuming that one egg was laid per day and that incubation started with the last egg laid. To determine the number of days by which to backdate nests, we calculated a nesting interval for each species; we used the modal clutch size and mean incubation and nestling periods for each species rounded to the nearest day. Nests abandoned prior to completion of building were excluded from analyses.

We used a GIS data set provided by Gros Morne National Park to quantify the proportion of forest harvest within 20, 115, and 1250 m of each nest. The GIS data contained detailed information about habitat types (e.g., forest-stand type, clear-cut, bog type, barren, waterway). Narrow unmaintained roads in natural areas were lumped with natural areas because these roads are not associated with decreased productivity of forest passerines or increased nest predation (King and DeGraaf 2002, Ortega and Capen 2002). We calculated area of harvest with ArcGIS 9.1 (Environmental Systems Research Institute 2005). The proportion of area harvested ranged from 0.0 to 1.0 at both the 20- and 115-m scales and from 0.0 to 0.37 at the 1250-m scale. At the 20-m scale we scored habitat height from 1 to 5 for vegetation 0.0–3.5 m, 3.6–6.5 m, 6.6–9.5 m, 9.6–12.5 m, and 12.6–15.5 m high, respectively. For simplicity in representing data and potential curvilinear relationships, in figures measurements with significant interactions by year are divided in three even-sized ranges of predictor variables and depicted as “low,” “moderate,” and “high.”

We modeled all response variables with proportion of harvest within radii of 20, 115, and 1250 m of each nest site as continuous predictors. We developed statistical models in a stepwise backward approach, including in the full model year, habitat height (for models at the 20-m scale only), proportion of harvest at each of the 20-m, 115-m, and 1250-m scales, and all interactions with year. When a model did not converge, we fit all main effects and used a stepwise forward approach by sequentially adding year interactions that were most significant as determined by univariate tests. We assessed a model's overall fit by examining residual plots and the quality of parameter estimates (i.e., no poorly estimated parameters with large standard errors). We eliminated predictors with the highest *P* values and contributing the least to a model's overall deviance from the model first. When a candidate model

TABLE 1. Nest habitat, breeding (sample sizes or mean \pm SD), and capture data for the Yellow-rumped Warbler, Blackpoll Warbler, and White-throated Sparrow. Nest-habitat assignments are based on observations from this study and the literature (Ehrlich et al. 1988, Falls and Kopachena 1994, Hunt and Flaspohler 1998, Hunt and Eliason 1999, Whitaker and Montevecchi 1999).

	Yellow-rumped Warbler	Blackpoll Warbler	White-throated Sparrow
Nest habitat	Wooded	Mixed ^a	Open
Nests	26	39	33
Clutch size	3.70 \pm 0.93	3.85 \pm 0.63	3.85 \pm 0.44
Number hatched	3.46 \pm 1.10	3.69 \pm 0.61	3.12 \pm 1.34
Proportion of clutch that hatched	0.94 \pm 0.21	0.96 \pm 0.09	0.92 \pm 0.34
Number fledged	1.55 \pm 1.82	2.56 \pm 1.59	2.85 \pm 1.50
Proportion of hatched young that fledged	0.40 \pm 0.47	0.72 \pm 0.43	0.92 \pm 0.26
Juveniles captured	94	160	185
Juveniles as a proportion of total captures	0.14 \pm 0.31	0.20 \pm 0.36	0.19 \pm 0.34

^aIncludes scrub and edge habitats as well as wooded and open habitats.

included only parameters significantly different from zero (t -test, maximum P of a type-1 error = 0.05) and marginally different from zero ($0.05 < P < 0.10$), we compared models with and without marginally significant terms to determine if those terms contributed significantly to reducing model deviance (F test for continuous or χ^2 test for categorical variables). If a term did not, we removed the marginal term and proceeded likewise until the model included only significant terms and terms that contributed significantly to overall deviance (Crawley 2005).

We analyzed initiation dates (only the first nesting attempts, determined by visual inspection of the spread of initiation dates) by using generalized linear models with a Gaussian family (Crawley 2005). We modeled clutch size with the Poisson family and hatching success and fledging success with the binomial family (i.e., logistic regression). Models for White-throated Sparrow hatching success and Blackpoll Warbler fledging success were overdispersed (residual deviance was much larger than the residual degrees of freedom), so we fit them with the quasibinomial family (Crawley 2005). We modeled nDSR with a user-specified family (logit model for p_{days}) by following the logistic-exposure model (Shaffer 2004) as suggested by the help file for “family” (R Core Development Team 2006).

To test for variation in productivity with proportion of harvest at different scales, we used generalized linear mixed models (glmmPQL function) with a binomial family. We included netting site as a random effect and day of year, proportion of harvest, and year as fixed effects. Since netting sites covered an area larger than the 20-m scale, we used only the 115-m and 1250-m scales for these analyses.

RESULTS

GENERAL OBSERVATIONS

In 2004 and 2005, we located 169 nests of 13 species. Of these, 139 (82%) fledged one or more young and 30 (18%)

were abandoned or depredated. Nest success was similar in 2004 (79%) and 2005 (85%) (Fisher's exact test, $P = 0.20$). We attributed most losses (75% and 79% in 2004 and 2005, respectively) to predation, the rest to abandonment. Yellow-rumped Warblers, Blackpoll Warblers, and White-throated Sparrows collectively accounted for 98 (58%) of the nests monitored and 439 (46%) of 956 juveniles captured (Table 1). Of the Yellow-rumped Warbler, there were 16 nests in 2004 and 10 in 2005, 23 juveniles captured in 2004 and 71 in 2005. Corresponding numbers were 16, 23, 33, and 127 for the Blackpoll Warbler, and 22, 11, 77, and 108 for the White-throated Sparrow.

ASSOCIATIONS WITH MEASURES OF REPRODUCTIVE SUCCESS

Nests were initiated significantly earlier in 2005 (Fig. 1; median dates 15, 18, and 11 June for the Yellow-rumped Warbler, Blackpoll Warbler, and White-throated Sparrow, respectively) than in 2004 (corresponding median dates 24, 25, and 17 June, respectively). For the Yellow-rumped and Blackpoll Warblers, year was the only significant predictor of initiation date (Table 2). For the White-throated Sparrow, initiations were earlier in 2005 than in 2004 in habitats with low and moderately tall vegetation, but later in 2005 than in 2004 in habitats with tall vegetation (Table 2, Fig. 2A).

Clutch sizes of the three focal species were similar (Table 1). Modal clutch size of each species was four, as occurred 48%, 67%, and 79% of the time for the Yellow-rumped Warbler, Blackpoll Warbler, and White-throated Sparrow, respectively. Clutch sizes ranged from two to five for the Yellow-rumped and Blackpoll Warblers and three to five for the White-throated Sparrow. We identified no significant predictors of clutch size for these species.

For all three focal species hatching success was similar ($\geq 92\%$; Table 1), and we identified no significant predictors

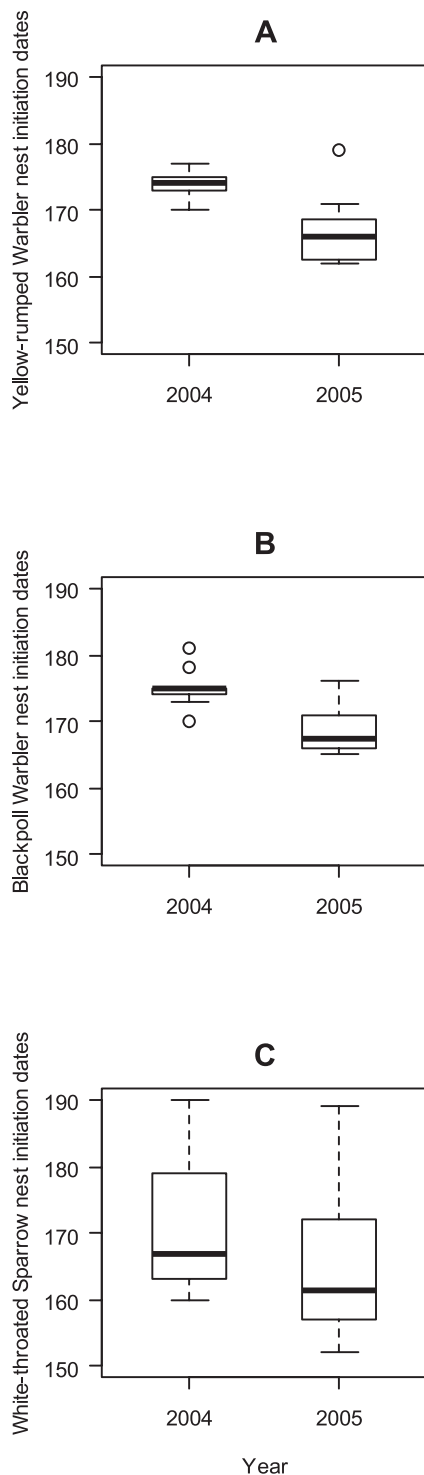


FIGURE 1. Box plot of nest-initiation dates in 2004 and 2005 for the (A) Yellow-rumped Warbler, (B) Blackpoll Warbler, and (C) White-throated Sparrow. Date is given as day of year where 1 = 1 January and 160 = 9 June. The horizontal bar in the middle indicates the median initiation date, and the box indicates the middle 50% of all observations. Whiskers show the range of the data, excluding out-liers shown as points beyond the whiskers.

of hatching success for the Yellow-rumped or Blackpoll Warbler. For the White-throated Sparrow (Table 3), hatching success was lower where more forest had been harvested within 20 m of nests. Furthermore, White-throated Sparrow hatching success decreased with a moderate proportion of harvest within 1250 m in 2004 and increased with proportion of harvest within 1250 m in 2005 (Fig. 2B).

We identified no significant predictors of nDSR for the two warblers. For the White-throated Sparrow, proportions of harvest at the 20-m, 115-m, and 1250-m scales were all marginally important ($P < 0.10$) and contributed significantly to the models' overall fit (Table 4). The White-throated Sparrow's nDSRs were negatively associated with increased proportion of harvest at both the 20-m and 115-m scales but positively associated with increased proportion of harvest at the 1250-m scale (Table 4, Fig. 3). For all species at all scales, nDSRs were marginally higher in 2005 than in 2004 ($\beta = 0.79$, $SE = 0.46$, $P = 0.09$; Fig. 3), but this effect was not significant for any of the individual species.

Fledging success was lower for Yellow-rumped Warblers than for the other two species (Table 1). For this species, an interaction between year and proportion of harvest at the 1250-m scale was not significant but contributed significantly to overall reduction of model deviance ($P = 0.004$), suggesting temporal differences in effects of harvest on fledging success. For Blackpoll Warblers, fledging success was higher with more harvest within 20 m (Table 5). For White-throated Sparrows, fledging success was lower with more harvest within 20 m and 115 m but higher with more harvest within 1250 m (Table 5).

Yellow-rumped Warbler productivity was the lowest of all three species (Table 1) and higher in 2005 than in 2004. Productivity increased with moderate and high amounts of harvesting at the 1250-m scale in 2005 but decreased at low and high proportions of harvest at this scale in 2004 (Fig. 2C). Productivity was higher in 2005 than in 2004 for Blackpoll Warblers (Table 6). Productivity of White-throated Sparrows was best predicted by interactions between year and proportion of harvest at both the 115-m and 1250-m scales (Figs. 2D and 2E). At these scales, productivity was positively influenced by high proportions of harvest.

PATTERNS IN OTHER EXPLANATORY VARIABLES

Species' habitat associations differed. High proportions of forest harvest had negative (although insignificant) associations with Yellow-rumped Warbler nDSR, while productivity varied by year. White-throated Sparrows appeared to do better with higher proportions of harvest in 2005, and for this species there were more significant interactions between harvesting and year. Yellow-rumped Warbler success was negatively associated, Blackpoll Warbler success was not associated or positively associated, and White-throated Sparrow success was positively or negatively associated with increases in proportions of harvest, depending on year.

TABLE 2. Summary of best generalized linear models (family = Gaussian) for day of nest initiation for the Yellow-rumped Warbler, Blackpoll Warbler, and White-throated Sparrow after stepwise elimination of nonsignificant predictors. Estimates (β) of significant parameters and terms that contributed significantly to the models' overall deviance are followed by their standard error (SE) and associated probabilities (P). Only first nest attempts (see Methods) are included in analyses. Sample sizes are given in Table 1.

Parameter	Yellow-rumped Warbler			Blackpoll Warbler			White-throated Sparrow		
	β	SE	P	β	SE	P	β	SE	P
Year	-9.0	1.3	<0.001	-6.3	1.1	<0.001	-22.6	7.6	<0.01
20-m habitat height							-8.0	4.1	0.06
Year \times habitat height within 20 m							6.7	2.7	0.02

Associations in the two years also differed. Variation in hatching success and productivity between years was greater with moderate and high proportions of harvest. Initiation dates, hatching success, nDSR, and capture rates of juveniles

were earlier or higher in 2005 (even when not significant) for all three focal species.

Finally, associations were influenced by scale. Nest initiation was significantly associated only with proportion of

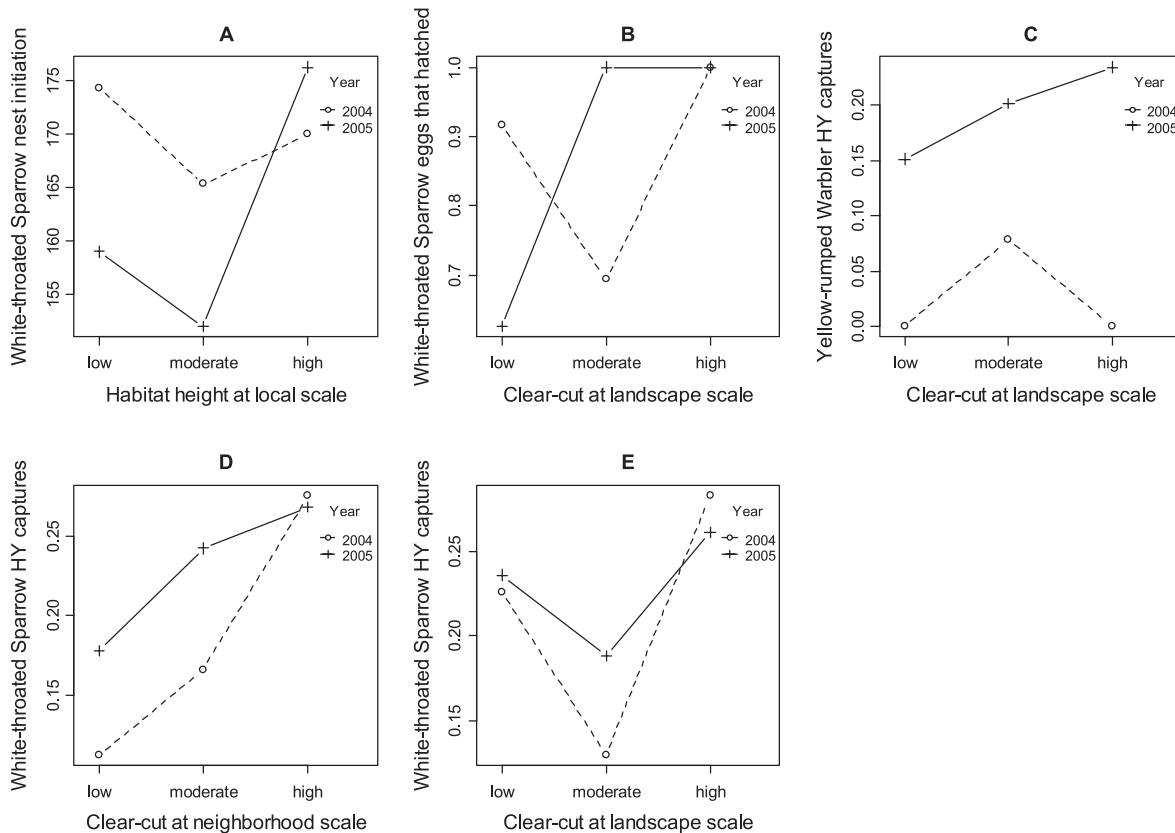


FIGURE 2. Significant interactions between habitat variables and year. (A) Interaction between habitat height at the 20-m (local) scale and year for White-throated Sparrow nest-initiation dates. Initiation dates are given as day of year where 1 = 1 January and 160 = 9 June. Values of habitat height range from 0.0 to 15.5 m with low, moderate, and high representing values from the lower, middle, and upper third of predictor values, respectively. (B) Interaction between proportion of harvest at the 1250-m (landscape) scale and year for White-throated Sparrow hatching success (proportion of eggs that hatched). Values of proportion of harvest at the landscape scale range from 0.0 to 0.37. (C) Interaction between proportion of harvest at the 1250-m (landscape) scale and year for Yellow-rumped Warbler productivity (proportion of birds captured that were juvenile). Values of proportion of harvest at the neighborhood scale range from 0.0 to 1.0. (D) Interaction between proportion of harvest at the neighborhood scale and year for White-throated Sparrow productivity. Values of proportion of harvest at the neighborhood scale range from 0.0 to 1.0. (E) Interaction between harvesting at the landscape scale and year for White-throated Sparrow productivity. Values of proportion of harvest at the landscape scale range from 0.0 to 0.37.

TABLE 3. Summary of best generalized linear model (family = quasibinomial) for White-throated Sparrow hatching success after stepwise elimination of nonsignificant predictors. Estimates (β) of significant parameters and terms that contributed significantly to the model's overall deviance are followed by their standard error (SE) and associated probabilities (P). Sample sizes are given in Table 1.

Parameter	β	SE	P
Year	-7.7	3.6	0.04
20-m proportion forest harvest	-4.1	1.9	0.04
1250-m proportion forest harvest	-54.7	26.2	0.05
Year \times 1250-m proportion forest harvest	43.1	19.6	0.04

harvest within 20 m. As the breeding season progressed from initiation to hatching and ultimately to juveniles' independence, associations with the 20-m scale were still evident, and only late in the season when we measured ratios of juveniles to adults did associations with harvesting emerge at the 115-m and 1250-m scales (Table 6).

DISCUSSION

This study is one of the few to test for influences of forest harvest on multiple measures of breeding phenology and breeding success extending from clutch initiation to independence of young. As we have illustrated, it is important to consider influences of harvesting on breeding birds at multiple temporal and spatial scales because differences in these influences may more clearly point to mechanisms underlying songbirds' population changes. It is evident from this study that some breeding parameters are rooted in life history (clutch size) and not easily influenced by external factors such as forest harvest and weather, whereas others are influenced by a species' specific habitat requirements (hatching success, nDSR, and productivity), and still others are influenced regardless of species-specific requirements (initiation date and fledging success). These results need to be considered relative to several variables.

FRAGMENTATION, SCALE, AND HARVEST

We found that associations with forest harvest emerged at different scales depending on nest stage. As the season progressed and young birds required more resources for survival, larger scales became more important as adults and fledglings presumably traveled more widely to acquire resources (Naef-Daenzer 2000).

We found no compelling evidence of negative effects of forest harvesting on the breeding of the three species we studied in northwestern Newfoundland. Because these landscapes are naturally heterogeneous, however, these populations may already be adapted to patchily distributed resources, various matrix types (Bélisle and St. Clair 2001, Jonsen et al. 2001, Jules and Shahani 2003), and various degrees of landscape connectivity (Taylor et al. 1993). The human-induced heterogeneity in northwestern Newfoundland

TABLE 4. Summary of best logistic exposure models for White-throated Sparrow nests' daily survival rates (nDSR) after stepwise elimination of nonsignificant predictors. Estimates (β) of significant parameters and terms that contributed significantly to the models' overall deviance are followed by their standard error (SE) and associated probabilities (P). Sample sizes are given in Table 1.

Parameter	β	SE	P
20-m proportion forest harvest	-3.1	1.7	0.07
115-m proportion forest harvest	-7.8	4.2	0.07
1250-m proportion forest harvest	47.8	24.9	0.05

creates a matrix of different-aged forests and regeneration. The matrix apparently contains functionally connected resources for Blackpoll Warblers and White-throated Sparrows in that these species obtained sufficient resources in this landscape (otherwise a negative influence on reproductive measures should have been observed). Similarly, other studies have found that birds cross and use regenerating clearcuts (Andren 1994, Pagen et al. 2000, Norris and Stutchbury 2001, but see Bélisle et al. 2001). For this reason, some songbirds' responses to changes in boreal forests are weaker than to changes in other landscape types (Schmiegelow et al. 1997). Nonetheless, some species nesting in the boreal forest, such as the Yellow-rumped Warbler, may be sensitive to some aspects of forest harvesting. In addition, effects of forest harvest may be masked by extreme annual variation in weather, so that only long-term monitoring would detect consequences.

ANNUAL WEATHER VARIATION

Average daytime temperatures on our study site in the two years differed significantly, with 2004 being cooler. Proportion of days with measurable precipitation and total rainfall were also highest in June 2004 (Powell et al. unpublished data). In 2004, when weather was highly variable and inclement, productivity of Yellow-rumped Warblers was less than 10% (Fig. 2C). With more favorable weather in 2005, overall productivity was higher, but this relationship varied depending on the proportion of forest harvested.

Gaston et al. (2006) also found that timing and success of reproduction are affected by weather. Poor weather may limit food availability, leading to slower nestling growth, later fledging (leading to lower recruitment), and higher nestling mortality (Wright et al. 1998, Shutler et al. 2006). Recruitment can also be related to productivity in previous years (Magrath 1991). Measuring recruitment in our study area in relation to weather variability may give insight into the quality and survival of young produced at these sites, although typically for passerines local recruitment is only ~5% (Weatherhead and Forbes 1994), making it difficult to accumulate sufficient data.

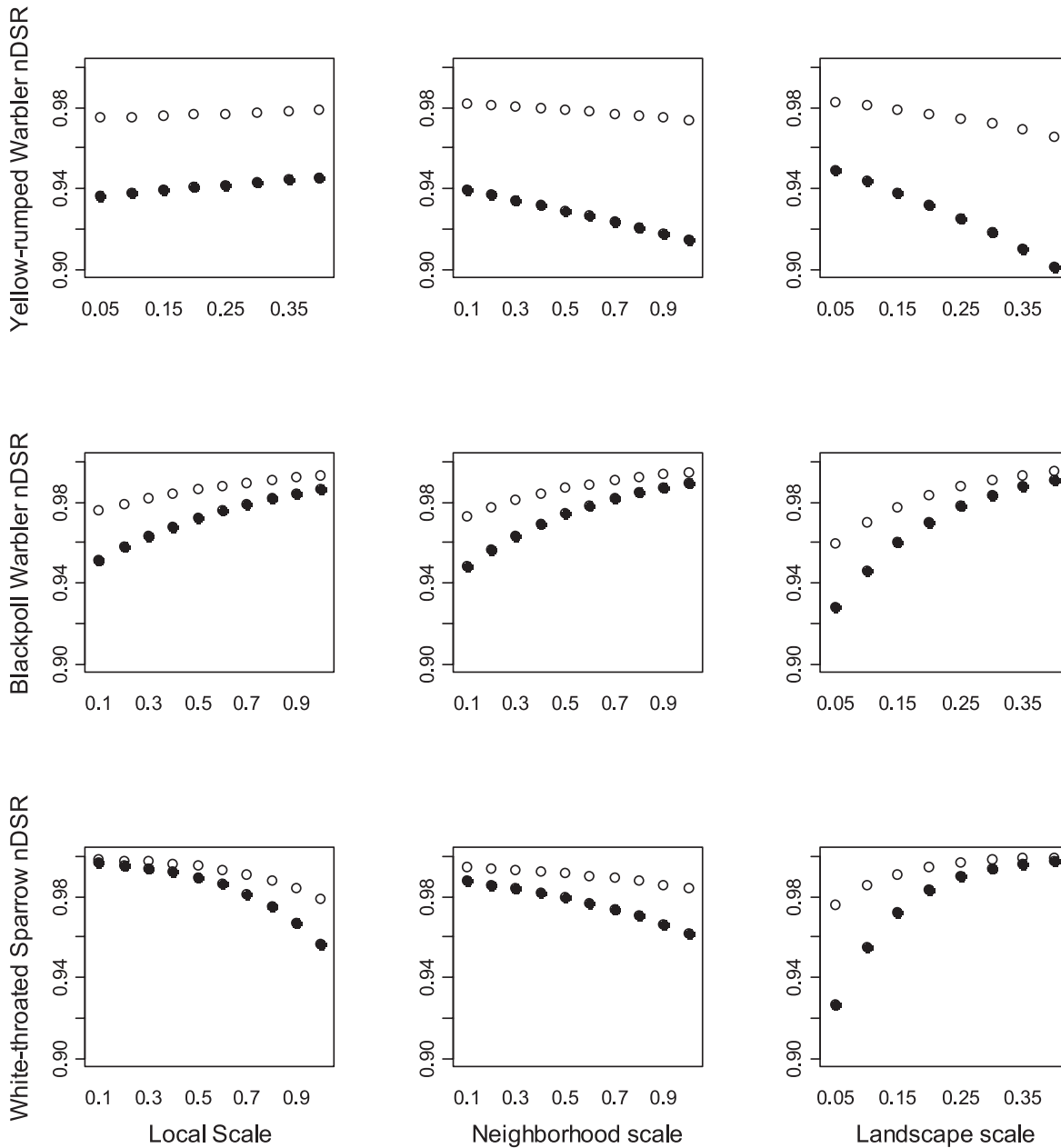


FIGURE 3. Daily survival rates (nDSR) of nests of three well-sampled species relative to proportion of harvest at the 20-m (local), 115-m (neighborhood) and 1250-m (landscape) scales. The x axis represents a continuous variable of proportion of harvest at the 20-m (left panels), 115-m (middle panels), and 1250-m (right panels) scales. Top panels are for Yellow-rumped Warblers, middle for Blackpoll Warblers, and bottom for White-throated Sparrows. Filled circles are data for 2004 and unfilled circles are data for 2005.

Global climate is increasingly recognized as being subject to the North American Oscillation (NAO) index and the El Niño Southern Oscillation (SOI). Influences of NAO differ on each side of the Atlantic; positive NAO indices are associated with increased temperature and precipitation in northern Europe, but the opposite is true in eastern Canada (Ottersen et al. 2001). Weatherhead (2005) reported high NAO values associated with higher productivity of successful nests, and

Mazerolle et al. (2005) reported both adult survival and productivity of Yellow Warblers (*Dendroica petechia*) positively correlated with SOI. For islands such as Newfoundland, climate is significantly influenced by the surrounding ocean. Island air temperatures thus fluctuate with changes in temperature of adjacent waters. For our study area, documentation of oceanic influences will likely be critical to predicting, and thus planning for, consequences of climate changes to avian

TABLE 5. Summary of best generalized linear models (family = binomial for the Yellow-rumped Warbler and White-throated Sparrow, and quasibinomial for the Blackpoll Warbler) for fledging success after stepwise elimination of nonsignificant predictors. Estimates (β) of significant parameters and terms that contributed significantly to the models' overall deviance are followed by their standard error (SE) and associated probabilities (P). Sample sizes are given in Table 1.

Parameter	Yellow-rumped Warbler			Blackpoll Warbler			White-throated Sparrow		
	β	SE	P	β	SE	P	β	SE	P
Year	21.4	16.8	0.22						
20-m proportion forest harvest				2.0	1.2	0.10	-4.7	1.7	<0.01
115-m proportion forest harvest							-9.1	5.4	0.09
1250-m proportion forest harvest	122.6	83.1	0.16				65.3	32.2	0.04
Year \times 1250-m proportion forest harvest	-104.6	80.9	0.22						

population dynamics (Mitrus 2003, Both and Visser 2005, Visser and Both 2005).

SPECIES TRENDS

Yellow-rumped Warblers had lower fledging success and lower productivity associated with low and high proportions of forest harvest, particularly in cold weather. Similarly, others have found more Yellow-rumped Warblers with more forest cover at the 115-m scale regardless of whether heterogeneities in the landscape were natural or human-caused (Taylor and Krawchuk 2005), and that adults' apparent survival was lower in harvested landscapes (Whitaker et al. 2008). We found the Yellow-rumped Warbler's breeding parameters positively associated with moderate levels of harvest, in contrast to Drolet et al. (1999), who found the species did not respond significantly to any landscape scale measures. In our study, it is important to note that lower rates of capture of juveniles were also associated with lowest proportions of forest harvest. It is possible that although the level of harvest is low, the amount of forest is also low (areas of natural openness), possibly explaining the observed interaction between capture probability and level of forest harvest.

We found either no effect or positive effects of harvesting on the breeding success of Blackpoll Warblers, in contrast to Drolet et al. (1999), who found that this species was

among four of 14 whose occurrence correlated with the combined effect of landscape measures (forest cover, edge, and core area). Similarly, Taylor and Krawchuk (2005) found that this species occurred most often in natural areas but, conversely and in accordance with the results of our study, that its occurrence was highest at low and moderate amounts of forest cover.

We found more year and harvest interactions with the White-throated Sparrow than with the other two species. Some of these results are similar to those of Taylor and Krawchuk (2005), who found that White-throated Sparrow occurrence was highest in areas of low forest cover. Lampila et al. (2005) found that ground-nesting species like the White-throated Sparrow were most sensitive to fragmentation. Our study does not support that finding, but fragmentation in connection with weather may cause dramatic differences in breeding success.

Our study suggests that forest-nesting species such as the Yellow-rumped Warbler may be most threatened by high levels of harvesting in this temporally dynamic system. Further, associations between external factors such as forest harvesting and weather, as we found, may not be easily predicted. It will be important in future management plans to consider enhanced influences of human-caused habitat changes in highly variable and unpredictable environmental conditions.

TABLE 6. Summary of best generalized linear mixed models (family = binomial) for productivity (ratio of juveniles to adults captured) after stepwise elimination of nonsignificant predictors. Estimates (β) of significant parameters are followed by their standard error (SE) and associated probabilities (P). Netting site was included as a random variable, and net-hours and day of year were included as fixed effects to control for effort and seasonal variation. Sample sizes are given in Table 1.

Parameter	Yellow-rumped Warbler			Blackpoll Warbler			White-throated Sparrow		
	β	SE	P	β	SE	P	β	SE	P
Year	5.5	1.3	<0.001	0.6	0.3	0.03			
115-m proportion forest harvest							3.2	0.9	<0.01
1250-m proportion forest harvest	28.2	7.6	<0.01				-15.6	6.0	0.02
Year \times 115-m proportion forest harvest							-1.9	0.8	0.01
Year \times 1250-m proportion forest harvest	-18.0	6.9	0.01				10.8	5.6	0.05

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