

LANDSCAPE STRUCTURE AND SPATIAL SCALE AFFECT SPACE USE BY SONGBIRDS IN NATURALLY PATCHY AND HARVESTED BOREAL FORESTS

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Abstract. Knowledge of how landscape structure influences patterns of animal space use is critical to developing sustainable landscape management practices. For breeding songbirds that defend a territory embedded within a larger home range, effects of structural change on movement may be manifested at multiple spatial scales. We used radio-telemetry to assess within-territory and home range space use as functions of the proportion of clearcut-harvested versus naturally unforested land for two species of Neotropical migrant songbirds. We tested whether these relationships varied with spatial scale by assessing landscape structure in both the local neighborhood (115 m radius around an individual's territory center) and across the landscape (1250 m radius). Territory size for riparian-associated male Northern Waterthrushes (*Seiurus noveboracensis*) was curvilinearly related to the proportion of harvested versus naturally unforested land and varied by greater than two orders of magnitude. Waterthrush territories were largest in the most heavily harvested landscapes. Home range space use by male Blackpoll Warblers (*Dendroica striata*), which are habitat generalists, was influenced by the ratio of clearcuts to natural gaps in both the neighborhood and landscape. Blackpolls may modify their behavior as a result of anthropogenic processes acting at both small and larger spatial scales, but we observed considerable interannual variability. Our results suggest that boreal forest–breeding passerines may be capable of modifying their space use behavior in response to moderate levels of structural change caused by forestry.

Key words: boreal forest, clearcut, home range, movement, songbird, territory.

La Estructura del Paisaje y la Escala Espacial Afectan el Uso del Espacio por parte de las Aves Canoras en Bosques Boreales Naturalmente Fragmentados y Cosechados

Resumen. El conocimiento sobre la influencia de la estructura del paisaje sobre los patrones de uso del espacio por parte de los animales es de gran importancia para el desarrollo de prácticas de manejo sustentable del paisaje. Para las aves canoras, que defienden durante el período reproductivo un territorio incluido en un ámbito de hogar mayor, los efectos de los cambios estructurales sobre sus movimientos pueden manifestarse a diferentes escalas. Utilizamos radio-telemetría en dos especies de aves migratorias neotropicales para determinar el uso del espacio dentro del territorio y dentro del ámbito de hogar en función de la proporción de bosque talado-cosechado y de la proporción de áreas deforestadas naturalmente. Evaluamos si estas relaciones variaron con la escala espacial considerando la estructura del paisaje tanto a escala de la vecindad local (radio de 115 m desde el centro del territorio de un individuo) como a escala del paisaje (radio de 1250 m). El tamaño de los territorios de los machos de *Seiurus noveboracensis*, especie asociada a áreas ribereñas, se relacionó de forma curvilínea con la proporción de áreas cosechadas y de áreas deforestadas naturalmente, y varió por más de dos órdenes de magnitud. Los territorios más grandes de *S. noveboracensis* se encontraron en los paisajes con mayor intensidad de cosecha. El uso del espacio en el ámbito de hogar de *Dendroica striata*, una especie generalista de hábitat, fue influenciado por el cociente entre áreas taladas y áreas deforestadas naturalmente, tanto a escala local como de paisaje. Los individuos de esta especie pueden modificar su comportamiento como resultado de los procesos antropogénicos que actúan a escalas espaciales pequeñas y grandes, aunque observamos una variabilidad interanual considerable. Nuestros resultados sugieren que las aves paseriformes que se reproducen en hábitat de bosque son capaces de modificar su comportamiento de uso del espacio en respuesta a cambios estructurales moderados producidos por actividades forestales.

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INTRODUCTION

In heterogeneous landscapes, individual-level processes such as space use are dictated by an organism's ability to move among patches of varying quality (Dunning et al. 1992, Ims 1995). However, space use patterns also result from interactions between landscape structure and an organism's response to that structure at multiple temporal and spatial scales (With 1994, Wiens 1997, Taylor et al. 2006). In turn, the propensity for movement can influence higher-level ecological processes such as recruitment, emigration, and gene flow (Kareiva 1990, Hanski 1999, Russell et al. 2003). Thus, both space use patterns and associated ecological processes may be altered in landscapes being managed for the extraction of resources such as timber. These changes result from modifications to the structure and composition of forest stands, where habitat characteristics, quality, or amount may be altered (Robinson et al. 1995, Burke and Nol 2000, Huhta et al. 2004) to the benefit of some species (Bourque and Villard 2001, Robichaud et al. 2002, Gram et al. 2003) and detriment of others (Bayne and Hobson 2002, Cooper and Walters 2002, Manu et al. 2007). A better understanding of the factors that influence space use and the consequences of disturbance has the potential to improve conservation-oriented management prescriptions.

An animal's use of space is frequently described through measures of territory and home range size and shape (Kenward 2001). During the breeding season, most migratory passerines defend a nest and a mate in a territory (*sensu* Mayr 1935). This territory is embedded within a larger home range that is typically used for activities such as foraging, mating, searching for extra-pair mates, and prospecting for future potential breeding sites (Hanski and Haila 1988, Woolfenden et al. 2005, Dale et al. 2006). Passerine behavior differs between these two areas. While in their territories, male passerines are conspicuous and vocal, and aggressive toward conspecific males. During extra-territorial forays into the home range, however, both male and female songbirds are usually quiet and furtive (Neudorf et al. 1997, Stutchbury et al. 2005). Spatial requirements of passerines during the breeding season thus exist on a range of scales, extending from that of the area immediately surrounding the nest, to the intermediate area used for territorial display and defense, to the broader home range. Consequently, the effects of structural landscape change on forest songbirds may be variably manifested at multiple spatial scales.

Territory and home range dimensions are influenced by factors that reflect both the distribution of resources and interactions among conspecifics. The size and shape of an individual's territory can be dictated by the availability and distribution of resources such as song and lookout perches (Sedgwick and Knopf 1992, Yosef and Grubb 1994, Burke and Nol 1998), as well as the preemptive behavior of neighboring conspecifics (Nice 1941, Brown 1964, Adams 2001). Such behavior can itself be influenced by conspecific density,

rates of encounter with competitors, local rules of movement, and individual characteristics reflecting competitive ability such as body size and age (Fretwell and Lucas 1969, Lambert and Hannon 2000, Mazerolle and Hobson 2004). While these variables are important at the scale of the defended territory, factors relating to the acquisition of resources such as food or extra-pair mates likely drive space use at the home range scale. For songbird home ranges, optimal search and foraging theory predicts that the ideal size and shape of a home range will minimize energy expenditure and predation risk while maximizing energy gain (Schoener 1968, Mace and Harvey 1983, Ims 1995). Positive correlations between home range area and an individual's resource needs have been reported, and resource availability and individual fitness are known to be inversely related to home range size for a variety of taxa, including forest birds (Bloom et al. 1993, Rolstad et al. 1998, Relyea et al. 2000).

The study of individual space use patterns in response to landscape structure is important for an understanding of the mechanisms underlying previously documented patterns of songbird distribution and abundance in managed forests (Edenius and Elmberg 1996, Drolet et al. 1999, Taylor and Krawchuk 2005). Further, identifying causes of variation in space use can in turn identify population-limiting factors (Whitaker et al. 2007).

We used radio-telemetry to investigate space use by two species of boreal-breeding passerines in a heterogeneous landscape. The majority of radio-telemetry studies have focused on habitat associations, the extent and duration of extra-territorial forays, and the prevalence of extra-pair mating (Hanski and Haila 1988, Vega Rivera et al. 1999, Norris and Stutchbury 2001). For some passerines, radio-telemetry has demonstrated that patterns of space use change in response to altered heterogeneity of forested landscapes (Fraser and Stutchbury 2004, Bayne et al. 2005, Machtans 2006). Here, we compare territories and home ranges of breeding adult male Northern Waterthrushes (*Seiurus noveboracensis*) and Blackpoll Warblers (*Dendroica striata*) occupying naturally heterogeneous, unharvested forests with areas where clearcut harvesting has created anthropogenically patchy landscapes. We test whether relationships between space use and landscape structure vary with the primary source of landscape heterogeneity (natural versus anthropogenic) or spatial scale.

METHODS

STUDY AREA

The Main River watershed of insular northwestern Newfoundland and Labrador, Canada (49°47'N, 57°16'W), is a mosaic of naturally and anthropogenically heterogeneous landscapes. The area is part of the wet boreal forest biome of the Western Newfoundland ecoregion (Rowe 1972). It is dominated by old-growth balsam fir (*Abies balsamea*), but contains moderate amounts

of black (*Picea mariana*) and white spruce (*P. glauca*), and white birch (*Betula papyrifera*; Damman 1983). Large-scale natural disturbance is absent in this cool, moist region, and forest fires and insect outbreaks are uncommon (Thompson et al. 2003, McCarthy and Weetman 2006). Large tracts of contiguous forest are naturally interspersed with a high density of rivers, ponds, lakes, peatlands, and patches of stunted coniferous scrub. The area is also characterized by saturated soils and an abundance of nonriparian surface water in the form of intermittent streams, outflows from peatlands, wet, productive seeps in mature forest, and numerous wetlands. Mechanized clearcut harvesting performed in 1999 and 2000 created irregularly shaped anthropogenic gaps in woodland cover (here defined as forest or coniferous scrub) that range from 20 to 150 ha; on-site delimiting left abundant slash in cleared patches, and a low density of mature white birch was left unharvested.

Study landscapes were contained within a 10 × 20 km (20 000 ha) area of the watershed, characterized by approximately 5% peatland, 7% surface water (rivers, ponds, lakes; excluding peatland pools), 34% scrub forest, 44% productive forest, and 10% clearcuts. Data were collected within three 4 km² unharvested, naturally heterogeneous landscapes and three adjacent 4 km² anthropogenically patchy (harvested) landscapes.

STUDY SPECIES

Responses to landscape heterogeneity are expected to differ according to species-specific life history traits (With and Crist 1995, Andr n et al. 1997, Gobeil and Villard 2002). Species having narrow habitat requirements are more likely to be sensitive to changes in landcover and landscape configuration, while generalists should be capable of using novel landcover types, thereby compensating for habitat change (Reunanen et al. 2000). Northern Waterthrushes (hereafter, waterthrushes) are Neotropical migrants that breed in boreal and temperate North America and tend to use riparian habitat (Eaton 1995, Warkentin et al. 2003). Blackpoll Warblers (hereafter, blackpolls) are also Neotropical migrants that breed in dense coniferous vegetation across boreal North America, but are capable of breeding in interior forest, wooded areas along riparian and anthropogenic edges, and disturbed habitats such as regenerating clearcuts (Whitaker and Montevicchi 1997, Hunt and Eliason 1999, Dalley 2007). We thus consider the waterthrush to be more of a habitat specialist and the blackpoll more of a generalist.

DATA COLLECTION

After-hatching-year male birds were captured in similar numbers in naturally and anthropogenically patchy landscapes during the 2004 and 2005 breeding seasons (waterthrushes: 15 in unharvested and 15 in harvested; blackpolls: 18 in

unharvested and 17 in harvested). Birds were captured using standard mist-netting techniques, both passively in a concurrent constant-effort mark-recapture study in the study area (Whitaker et al. 2008) and actively using playbacks of conspecific male song. Captured individuals were fitted with standard numbered aluminum bands, a unique combination of three plastic color bands, and a radio-transmitter (Holohil Systems Ltd., Carp, Ontario; model BD-2). Transmitters weighed 0.62 g (less than 5% body mass) and had an on-the-ground range of approximately 1 km. In 2004, transmitters were affixed to the bare patch of skin between the bird's shoulder blades using nontoxic eyelash adhesive; three or four feathers were removed to increase exposed skin area (J. Churchill and S. J. Hannon, University of Alberta, pers. comm.). Birds were released at the site of capture when the adhesive had dried; total processing time was approximately 10 min. To increase transmitter retention time, in 2005 we switched to a figure-8 harness design (Rappole and Tipton 1991). Harness loops were made from elastic thread and biodegradable cat gut suture. Loops were placed over the bird's legs and rested snugly in the hip joints so that the transmitter sat as a backpack on the bird's rump. This attachment technique greatly reduced handling time, and birds were released onsite after approximately 1 min.

After a 24 hr adjustment period, birds were radio-tracked on foot with a Telonics Inc. (Mesa, Arizona) TR-4 receiver and a two-element handheld antenna. Birds were followed from a distance of approximately 15–20 m in 30 min bouts. Each time a bird moved ≥5 m, a handheld Garmin eTrex Venture[®] global positioning system unit was used to record UTM coordinates of the previous location. Time spent by the bird at each location was also noted. Behavioral observations were recorded when a bird was not concealed by cover; these included mode of foraging (gleaning, hawking, from a source of water), whether the bird was singing or calling, remaining stationary or moving (extended period of flight, short flight burst, running), carrying food, or feeding young. The presence of, or aggressive encounters with, conspecifics was also noted. Birds were radio-tracked 1–2 times per day, every one to two days, with radio-tracking bouts distributed equally over three time periods: 05:00–11:00 (morning), 11:00–17:00 (afternoon), and 17:00–22:00 (evening; GMT –03:30). When an individual was radio-tracked twice in one day, the two bouts were separated by a minimum of 7 hr. Individuals were radio-tracked from 7 June to 31 July 2004 and from 13 June to 18 July 2005; these dates corresponded with nest initiation through to postfledging dependence in the study area (Dalley 2007). No individuals radio-tracked in 2004 were followed again in 2005.

We tested for an influence of transmitter presence on movement behavior in two ways. First, we compared maximum interstep distance per radio-tracking bout to recapture distances (distance from first to second capture) of male

conspecifics banded but not fitted with a transmitter in the concurrent passive mist-netting study. We fit linear models to log-transformed movement distances with the presence of a transmitter as the predictor variable. Second, we compared the return rate during the subsequent breeding season (2005 or 2006) between two groups of birds: (1) those that had been equipped with transmitters, and (2) conspecific males that did not have transmitters but that had been banded in the concurrent passive mist-netting study (Whitaker et al. 2008). We modeled recapture probability as a function of species, year, and presence of a transmitter using generalized linear models with binomial errors in the R statistical package (version 2.3.1; R Development Core Team 2006).

TERRITORY AND HOME RANGE AREA

To obtain more accurate estimates of daily space use patterns, we included only birds that were followed at least once in each of the three time periods. For analyses of territories, we further limited the dataset to include only those locations at which males were observed singing; all locations were used for home range analyses. Territory and home range areas were estimated using the fixed kernel method with the reference smoother (h_{ref}) in the statistical program R (version 2.3.1; R Development Core Team 2006) using package 'adehabitat' (version 1.5-1; Calenge 2006).

The kernel density estimation technique is a probabilistic, nonparametric method that delineates home range boundaries (isopleths of utilization intensity) by calculating the mean influence of data points at cell intersections of a grid superimposed on the data (Worton 1989, Seaman and Powell 1996). Each isopleth contains a fixed percentage of the utilization distribution, which describes the relative amount of time an animal spends in that area (van Winkle 1975). While there are other methods to delineate the utilization distribution (e.g., the minimum convex polygon), kernel density estimation is considered by many to be the most accurate and robust of those currently available (Seaman and Powell 1996, Kenward 2001, Marzluff et al. 2004). Numerous authors have investigated the effect of sample size on kernel density estimation performance, and have recommended minimum samples ranging from 20 to 50 locations to obtain accurate estimates of home range size (Worton 1989, Seaman and Powell 1996, Seaman et al. 1999). We used a minimum of 30 locations to estimate utilization distributions, and also included sample size as a factor in our statistical analyses to control for any effect of sample size on estimates of space use (see below).

The most critical component of kernel density estimation is specification of the smoothing parameter, h , which defines the distance over which a data point influences grid intersections (Silverman 1986, Wand and Jones 1995, Fieberg 2007). The least squares cross-validation technique ($h_{\text{ls cv}}$) for determining the value of h is currently recommended for most

studies of animal space use (Seaman et al. 1999, Kernohan et al. 2001, Horne and Garton 2006). However, it is common for $h_{\text{ls cv}}$ to fail to converge for datasets having a large number of identical points (Silverman 1986) or points that are very close together (Hemson et al. 2005); thus, it is not appropriate for territorial animals that have many observations clustered around a given point (i.e., a nest). If accuracy in the utilization distribution is not crucial, the fixed kernel method using a reference smoother (h_{ref}) may provide the necessary information needed about the utilization distribution (Worton 1989). Because we were most interested in the factors influencing variation in territory and home range areas, and not in the 'true' extent of the areas per se, we employed h_{ref} .

Kernel density estimation assumes that location data are statistically independent. Most animals, however, tend to not move randomly within their territories and home ranges (Turchin 1998), thereby generating autocorrelated datasets. Many authors advocate a time-to-independence or distance-to-independence sampling regime that ensures independence of observations (Swihart and Slade 1985, McNay et al. 1994, Powell 2000). This concern has recently been discounted (Otis and White 1999, Fortin and Dale 2005), as repeated observations of resident individuals are by definition autocorrelated, and removing autocorrelation can remove the biological signal of interest (de Solla et al. 1999, Blundell et al. 2001, Fieberg 2007). For these reasons, we did not test or control for autocorrelation among locations.

Inner density isopleths are considered to provide more accurate estimates of space use than outer isopleths (Anderson 1982, Seaman et al. 1999), as peripheral boundaries are more difficult to accurately delineate (Powell 2000). Many authors calculate "core" areas at the 50% isopleth as a quantitative tool for habitat conservation and management plans (Bingham and Noon 1997), and outer (e.g., 90%) isopleths to obtain 'true' estimates of maximal space use (Börger et al. 2006). To obtain the most biologically meaningful estimates and allow for comparisons with other studies of passerine space use requirements, we estimated territory and home range boundaries and areas based on the 50%, 70%, and 90% isopleths.

TERRITORY AND HOME RANGE SHAPE

We derived a 'compactness ratio' (Franzreb 2006) as a measure of territory and home range shape. For each bird, the perimeter of the 70% isopleth was measured using ImageTool (version 3.00; ImageTool Development Team 2002). For birds having multiple discrete 70% contours, the total perimeter of all these polygons was calculated. A circle is the most compact shape that a territory or home range can assume, because it contains the maximum area that a given perimeter can encompass. Thus, we calculated the area of a circle having the same perimeter as the 70% polygon(s) for each bird. The compactness ratio was then calculated as the area contained

within the 70% territory or home range divided by the area of the circle. The compactness ratio has a maximum value of 1.0. Values close to 1 indicate that the shape of the 70% territory or home range is approximately circular; values approach zero as space use becomes increasingly convoluted or linear.

LANDSCAPE HETEROGENEITY

The arithmetic mean singing location for each individual was calculated to represent the territory center for that bird. The proportion of harvested land in a circular area surrounding the center of each bird's territory was then measured at two spatial scales: (1) neighborhood, and (2) landscape. For the neighborhood scale, we calculated the mean distance of singing locations from the territory center for each bird. We then calculated the mean of mean distances per species; the resulting values of 115 m for waterthrushes and 92 m for blackpolls were used as the radii of circular areas (4.2 ha and 2.7 ha, respectively), which represented the typical size of each species' territory. The landscape scale was determined by the maximum distance that individuals moved from their territory centers. For each species, the average maximum distance moved was 1250 m, giving a circular area of 491 ha. This area encompassed movements that were considered 'outliers' (i.e., fell outside the 90% isopleth) in home range size analyses.

The proportion of harvested land around the center of each bird's territory was measured at neighborhood and landscape scales using digital forest inventory maps produced by the Newfoundland and Labrador Department of Natural Resources from 1:15 840 aerial photographs. Photographs were taken in 1995, but maps were updated in 2000 to include recently harvested areas. We used ArcGIS 9.1 (Environmental Systems Research Institute 2005) to quantify the total amount of unforested land (both natural gaps and anthropogenic gaps in forest and coniferous scrub cover) at each spatial scale. The proportion of this unforested land that was created by clearcut harvesting was then calculated at the neighborhood (N_HARVEST) and landscape (L_HARVEST) scales.

STATISTICAL ANALYSES

To control for variation in the number of radio-tracking bouts and locational fixes for each individual, and to investigate the influence of differing contributions of these sampling regime components on the variation in territory and home range area estimates, radio-tracking bouts were randomly subsampled without replacement for each individual (Börger et al. 2006). Based on each subsample per bird, we calculated the area contained within the 50%, 70%, and 90% territory and home range isopleths. We included only those birds for which we had at least three radio-tracking bouts. For both species, numbers of radio-tracking bouts ranged from three to eight for territory analyses (singing locations only) and from three to 10 for home range analyses (all locations). Thus, we randomly

subsampling radio-tracking bouts across the range of three to $n - 1$ bouts per bird. For example, if an individual was followed seven times, we first randomly subsampled (without replacement) three radio-tracking bouts and then calculated territory areas at the 50%, 70%, and 90% isopleths. We repeated this procedure of subsampling three radio-tracking bouts from the entire set of seven until 10 replicates were obtained, yielding 10 territory area estimates per isopleth. We then continued this procedure up to $n - 1$ bouts; that is, we subsampled 10 replicates each of four, five, and six radio-tracking bouts, yielding a total of 40 territory estimates per isopleth for this example bird.

We examined relationships between territory or home range area and the proportion of harvested versus naturally unforested land at the neighborhood and landscape scales. Models were fit to the subsampled replicates described above using the restricted maximum likelihood approach for linear mixed-effects regression (Pinheiro and Bates 2000). This modeling approach was appropriate because it allowed us to investigate factors that influenced mean territory and home range areas, as well as those that influenced the variation in area estimates. While many animal space use studies focus on determining 'true' estimates of space use (Harris et al. 1990, Kernohan et al. 2001), an understanding of the factors influencing the variance in estimates of territory or home range area is biologically important and likely to be more useful from a management perspective. Space use requirements may vary seasonally or with environmental factors that alter the distribution of resources. In short-term studies, however, variation in estimates of territory or home range area is more likely dictated by elements of the sampling regime (Kenward 2001, Börger et al. 2006, Fieberg 2007), hence our emphasis on variance.

We fit linear mixed-effects models using the package 'nlme' for R (version 3.1-73; Pinheiro et al. 2006), with either territory or home range area (both log-transformed) as the response variable. The analyses included the following nested random effects terms (from innermost to outermost): number of locations (FIXES) within number of subsampled follows (BOUTS) within individual (ID). We fit as fixed effects the covariates FIXES, BOUTS, YEAR, the proportion of unforested land created by clearcutting at the neighborhood (N_HARVEST) and landscape (L_HARVEST) scales, and the interactions $\text{FIXES} \times \text{BOUTS}$, $\text{YEAR} \times \text{N_HARVEST}$, and $\text{YEAR} \times \text{L_HARVEST}$. Because fixed and random effects account for different components of the response, it can be useful to fit an explanatory variable as both (Pinheiro and Bates 2000). The inclusion of FIXES and BOUTS as random effects accounted for the influence of these terms on the variance in area estimates, while fitting them as fixed effects accounted for their influences on the mean of area estimates. To investigate potential differences in species' space requirements, territory and home range areas were modeled separately for each species.

We examined the relationship between the compactness ratios (arcsine-transformed) of territories and home ranges and the proportion of harvested versus naturally unforested land at the neighborhood and landscape scales for waterthrushes and blackpolls using a linear modeling approach (Crawley 2002). Covariates included in the models were the sampling regime variables FIXES and BOUTS, as well as YEAR and the heterogeneity metrics N_HARVEST and L_HARVEST. We also tested for interactions between YEAR and the two heterogeneity metrics.

For all modeling procedures, scatterplots were visually assessed for curvilinear relationships between predictors and responses prior to model fitting. Quadratic terms were tested for inclusion in models when curvilinear patterns were suggested by the data. A manual backward stepwise approach to model selection was used. We retained terms that reduced the overall deviance ($P < 0.05$) and had reasonable parameter estimates (not approaching zero or infinity and having small standard errors). Plots of residuals were examined to assess model fit, and we interpreted results based on coefficients, standard errors, and the proportion of deviance explained (Crawley 2002). Values are reported as means \pm SD.

RESULTS

We could not delineate territories for two of 30 male waterthrushes and two of 35 male blackpolls. Though they had mates and nests, one individual per species (during 2004) was never observed singing. In addition, one individual per species (both during 2005) was not territorial (no nest or mate identified). Three waterthrushes and six blackpolls were radio-tracked for fewer than three bouts and were excluded from all analyses. Results are thus reported for 25 waterthrushes and 27 blackpolls. Sampling effort was balanced between species in terms of total radio-tracking time (waterthrushes: 108 hr; blackpolls: 117.5 hr), mean numbers of radio-tracking bouts (waterthrushes: 9 ± 3 ; blackpolls: 9 ± 2), and locations per individual (waterthrushes: 62 ± 21 , range 30–98; blackpolls: 74 ± 22 , range 44–158).

Movement distances of individuals without transmitters recaptured in constant-effort mist-netting were not different from those of individuals with transmitters (waterthrush: $t = -0.7$, $P = 0.46$; blackpoll: $t = 0.4$, $P = 0.65$). In our analysis of return rates, the probability of recapture during the following breeding season did not differ between conspecific males with and without transmitters or between species or years. Further, 10 of the 32 individuals fitted with transmitters using glue during 2004 were seen again during 2005, and five of 29 individuals fitted using the harness method during 2005 were resighted during 2006. No resighted individuals retained their transmitters between years.

Of the 65 individuals fitted with a transmitter, two blackpolls were known to have died from causes unlikely to

have been related to the attachment of the transmitter: one was depredated by a raptor and the other collided with a mist-net pole during foggy weather. These low rates of mortality are comparable with observations of breeding season survival obtained from the concurrent mist-netting study (Whitaker et al. 2008).

LANDSCAPE HETEROGENEITY

Birds did not always acquire territories in the area of capture; more waterthrushes occupied territories in naturally patchy compared to harvested neighborhoods, while the opposite pattern was true for blackpolls (Fig. 1a, 1b). At the landscape scale, the distribution of proportions of harvested versus naturally unforested land across individuals was similar between species (Fig. 1c, 1d). Of the 19 individuals (two waterthrushes and 17 blackpolls) that settled in territories where gaps in neighborhood woodland cover were due only to harvesting, only two blackpolls occupied territories that were entirely harvested (0% woodland cover at the neighborhood scale). The remaining 17 birds settled in areas where all the woodland gaps present in the neighborhood were

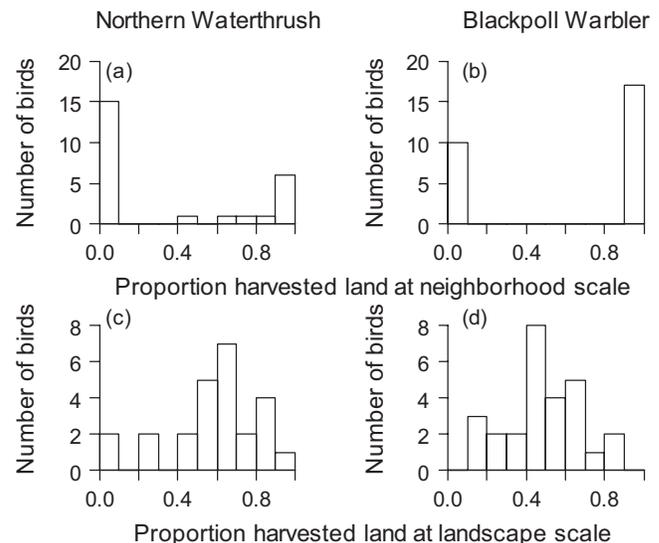


FIGURE 1. Most Northern Waterthrushes radio-tracked during the 2004 and 2005 breeding seasons in naturally patchy unharvested, and harvested boreal forests of insular Newfoundland and Labrador occupied territories in naturally patchy neighborhoods (a), while most radio-tracked Blackpoll Warblers occupied territories in harvested neighborhoods (b). The neighborhood was defined as a 115 m radius around an individual's territory center. At the landscape scale (a 1250 m radius around an individual's territory center), the proportion of naturally patchy versus harvested land contained within individual territories was similar between Northern Waterthrushes and Blackpoll Warblers (c, d). Note that a proportion of harvested land of 1.0 does not mean a complete absence of forest cover.

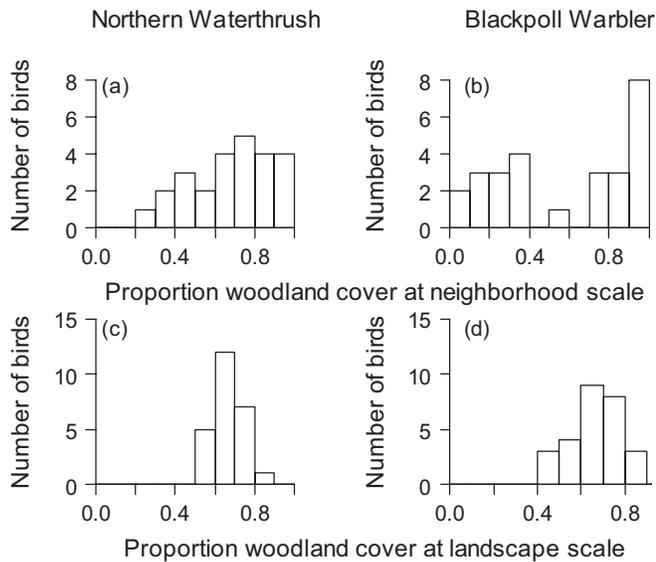


FIGURE 2. The distribution of the proportion of woodland cover contained within individual territories at both the neighborhood and landscape scales was similar between Northern Waterthrushes and Blackpoll Warblers that were radio-tracked during the 2004 and 2005 breeding seasons in naturally patchy unharvested, and harvested boreal forests of insular Newfoundland and Labrador.

created by harvesting (0% natural gaps in woodland cover), but woodland cover was present. The distribution of proportions of woodland cover in areas occupied by individual birds was similar between species at the neighborhood and landscape scales (Fig. 2).

RELATIONSHIPS BETWEEN SPACE USE AND LANDSCAPE HETEROGENEITY

Territory and home range areas. Waterthrushes and blackpolls both responded to clearcut harvesting, but in different ways. Anthropogenic gaps in woodland cover influenced waterthrush territorial space use but blackpoll home range

space use. Estimates of median territory and home range areas, and ratios of median home range to territory area, were greater for waterthrushes than for blackpolls at all density isopleths (Table 1).

Waterthrush territory area at all isopleths was curvilinearly related to the proportion of harvested versus naturally unforested land at the landscape scale (Table 2) and varied by greater than two orders of magnitude; waterthrush territories were largest in the most heavily harvested landscapes. At the 70% isopleth, mean waterthrush territory area decreased from 3.9 ha to 0.8 ha as the proportion of unforested land in the landscape due to harvesting increased from 0.04 to 0.60. Waterthrush territory area then increased in landscapes where the proportion of harvested land was greater than 0.60 up to a maximum territory area of 6.5 ha (Fig. 3). These figures represent territory shrinkage of 488% across landscapes with increasing amounts of harvest openings up to a threshold near 60% of the landscape, and subsequent maximum territory expansion of 813% in landscapes having greater than 60% of forest openings created by forest harvest. Estimates of mean waterthrush territory area were significantly related to aspects of the sampling regime at the 70% (FIXES and FIXES²) and 90% isopleths (FIXES, FIXES², and BOUTS).

In contrast, home range area for waterthrushes was not related to metrics of landscape heterogeneity (Table 3). Only terms accounting for aspects of the sampling regime (FIXES and BOUTS) influenced estimates of home range area at each of the 50%, 70%, and 90% density isopleths. Home range area decreased slightly with increasing numbers of locations and increased slightly with increasing numbers of radio-tracking bouts. The magnitude of the effects of both FIXES and BOUTS did not differ among the three density-isopleth reduced models.

We did not detect any relationship between forest harvest and our estimates of blackpoll territory area (Table 2). The sampling regime terms FIXES and BOUTS influenced territory area and were retained in each of the best-fit models for 50%, 70%, and 90% isopleths. Territory area decreased

TABLE 1. Range of territory and home range area estimates (ha) for three density isopleths, and mean compactness ratios ± 1 SD for the 70% isopleth, for male passerines during the breeding season in unharvested and harvested boreal forests in western insular Newfoundland and Labrador, 2004–2005. Values in parentheses are medians for territory and home range areas.

	Northern Waterthrush		Blackpoll Warbler	
	Territory	Home range	Territory	Home range
50% isopleth	0.1–4.6 (1.2)	0.8–10.6 (3.5)	0.1–2.7 (0.8)	0.3–8.1 (1.3)
70% isopleth	0.1–8.2 (2.3)	1.6–19.5 (6.3)	0.3–4.4 (1.5)	0.6–15.7 (2.2)
90% isopleth	0.2–15.5 (4.3)	3.5–35.9 (13.3)	0.5–7.9 (3.0)	1.2–33.2 (4.3)
Compactness ratio ^a	0.7 \pm 0.2	0.6 \pm 0.1	0.7 \pm 0.1	0.6 \pm 0.1

^aCompactness ratio = actual territory or home range area divided by maximum possible territory or home range area calculated from a circle having a perimeter equal to that of the territory or home range.

TABLE 2. Parameter estimates for fixed effects retained in reduced mixed-effects models of territory area of male passerines during the breeding season in harvested and unharvested boreal forests in western insular Newfoundland and Labrador, 2004–2005. For effects, FIXES = the number of locations per radio-tracking bout, BOUTS = the number of radio-tracking bouts per individual, and L_HARVEST = the proportion of clearcut-harvested versus naturally unforested land within a 1250 m radius from the center of an individual male bird's territory.

		Northern Waterthrush					Blackpoll Warbler					
	Parameter	df	Coefficient	SE	<i>t</i> -value	Pr(<i>t</i>)	Parameter	df	Coefficient	SE	<i>t</i> -value	Pr(<i>t</i>)
50% isopleth	INTERCEPT	173	1.16	0.67			INTERCEPT	352	-0.63	0.18		
	L_HARVEST	10	-7.87	3.02	-2.6	0.03	FIXES	352	-0.03	0.01	-5.1	<0.001
	L_HARVEST ²	10	8.77	3.05	2.9	0.02	BOUTS	50	0.20	0.03	5.9	<0.001
70% isopleth	INTERCEPT	173	2.09	0.70			INTERCEPT	352	-0.08	0.18		
	FIXES	113	-0.06	0.33	-1.9	0.06	FIXES	352	-0.03	0.01	-5.3	<0.001
	FIXES ²	113	0.00	0.00	1.9	0.06	BOUTS	50	0.21	0.03	6.0	<0.001
	L_HARVEST	10	-7.59	3.02	-2.5	0.03						
	L_HARVEST ²	10	8.50	3.05	2.8	0.02						
90% isopleth	INTERCEPT	173	2.96	0.70			INTERCEPT	352	0.50	0.19		
	FIXES	113	-0.09	0.03	-2.6	0.01	FIXES	352	-0.04	0.01	-5.2	<0.001
	FIXES ²	113	0.00	0.00	2.2	0.03	BOUTS	50	0.23	0.04	6.2	<0.001
	BOUTS	18	0.10	0.05	2.2	0.04						
	L_HARVEST	10	-8.65	2.97	-2.9	0.02						
	L_HARVEST ²	10	9.32	3.00	3.1	0.01						

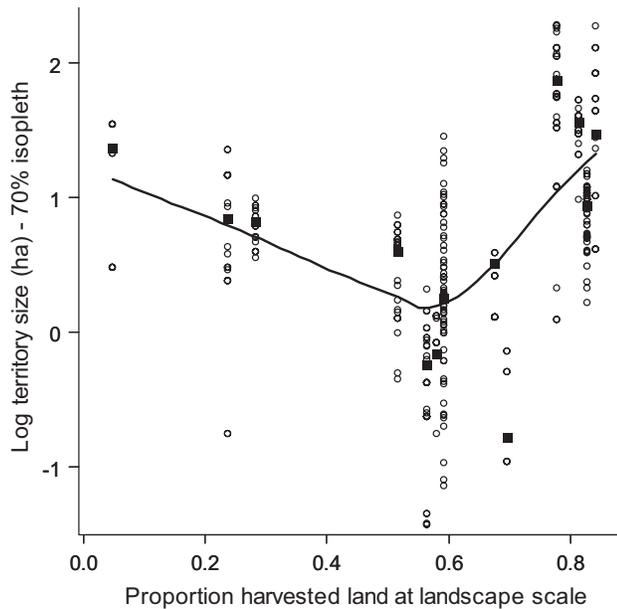


FIGURE 3. Territory areas (calculated at the 70% isopleth) of breeding Northern Waterthrushes radio-tracked in naturally patchy unharvested, and harvested boreal forests of insular Newfoundland and Labrador were curvilinearly related to the proportion of harvested versus naturally unforested land at the landscape scale. Territory areas varied by greater than two orders of magnitude and were largest in the most heavily harvested landscapes. Circles represent territory size estimated from subsampling three to $n - 1$ radio-tracking bouts with 10 replicates for each individual; squares represent territory size estimated from all radio-tracking bouts per bird; the solid line is based on locally weighted regression.

slightly with increasing numbers of locations and increased slightly with a greater number of radio-tracking bouts.

Blackpoll warbler home-range space use at the 70% and 90% isopleths was influenced by the proportion of anthropogenic gaps in woodland cover at both the neighborhood and landscape scales; these relationships varied between years (Table 3). At the neighborhood scale, median home range area was similar in both unharvested and harvested forests during 2004, while home ranges were larger in harvested compared to unharvested neighborhoods during 2005. In both years, however, home range areas were more variable in harvested compared to unharvested neighborhoods (Fig. 4). At the landscape scale, there was no clear pattern in the relationship between home range area and the proportion of unforested land that was created by harvesting during 2004. However, during 2005, blackpoll home range area was inversely related to landscape-scale forest harvest (Fig. 5). The best-fit model of blackpoll home range area at the 50% isopleth did not contain metrics of forest harvest, but did retain the term YEAR. Median home range area was larger during 2005 than during 2004, although estimates were variable in both years (Table 3). Sampling regime variables were also retained in best-fit models of blackpoll home range area at all isopleths. Home range areas were inversely related to the number of locations (FIXES) and positively related to the number of radio-tracking bouts (BOUTS). The magnitudes of these effects were relatively small (Table 3).

Territory and home range shapes. We did not detect any effect of sampling or heterogeneity metrics on territory or

TABLE 3. Parameter estimates for fixed effects retained in reduced mixed-effects models of home range area of male passerines during the breeding season in a harvested boreal forest in western insular Newfoundland and Labrador, 2004–2005. For effects, FIXES = the number of locations per radio-tracking bout, BOUTS = the number of radio-tracking bouts per individual, YEAR = the 2004 or 2005 breeding season, N_HARVEST = the proportion of clearcut-harvested versus naturally unforested land within a 115 m radius from the center of an individual male bird's territory, and L_HARVEST = the proportion of clearcut-harvested versus naturally unforested land within a 1250 m radius from the center of an individual male bird's territory. Interactions are denoted with ×.

	Northern Waterthrush						Blackpoll Warbler					
	Parameter	df	Coefficient	SE	t-value	Pr(t)	Parameter	df	Coefficient	SE	t-value	Pr(t)
50% isopleth	INTERCEPT	730	1.02				INTERCEPT	776	-0.06			
	FIXES	730	-0.01	0.00	-4.4	<0.001	FIXES	776	-0.02	0.00	-5.8	<0.001
	BOUTS	109	0.11	0.02	5.0	<0.001	BOUTS	122	0.15	0.02	6.7	<0.001
70% isopleth							YEAR	25	0.48	0.25	2.0	0.06
	INTERCEPT	730	1.59	0.14			INTERCEPT	776	-0.09	0.60		
	FIXES	730	-0.01	0.00	-4.4	<0.001	FIXES	776	-0.01	0.00	-5.3	<0.001
	BOUTS	109	0.11	0.02	5.2	<0.001	BOUTS	122	0.14	0.02	6.5	<0.001
							YEAR	21	1.17	0.75	1.6	0.13
							N_HARVEST	21	-0.26	0.41	-0.6	0.54
							L_HARVEST	21	1.48	1.35	1.1	0.28
							YEAR ×					
							N_HARVEST	21	1.13	0.62	1.8	0.09
							YEAR ×					
90% isopleth							L_HARVEST	21	-2.99	1.61	-1.9	0.08
	INTERCEPT	730	2.21	0.14			INTERCEPT	776	0.46	0.59		
	FIXES	730	-0.01	0.00	-4.3	<0.001	FIXES	776	-0.02	0.00	-6.3	<0.001
	BOUTS	109	0.11	0.02	5.4	<0.001	BOUTS	122	0.18	0.02	8.0	<0.001
							YEAR	21	1.13	0.75	1.5	0.15
							N_HARVEST	21	-0.18	0.41	-0.4	0.67
							L_HARVEST	21	1.56	1.34	1.2	0.26
							YEAR ×					
							N_HARVEST	21	1.17	0.62	1.9	0.07
							YEAR ×					
						L_HARVEST	21	-3.05	1.61	-1.9	0.07	

home range compactness ratios for either waterthrushes or blackpolls. Mean compactness ratios of territories and home ranges at the 70% isopleths did not differ within or between species (Table 1).

DISCUSSION

We observed both species- and scale-specific responses to landscape structure through breeding-season space use by our two target species. In areas with both harvested and naturally created openings, male Northern Waterthrush territory size varied by greater than two orders of magnitude. Space used for home ranges by male Blackpoll Warblers appeared to change in association with differing amounts of forest harvest at both neighborhood and landscape scales, but interannual variability was high. Similarly to the results of Lambert and Hannon (2000) for Ovenbirds (*Seiurus aurocapilla*) in pre- and postharvest landscapes, we were unable to detect any associations between landscape heterogeneity and our measure of territory and home range shape for either species.

NORTHERN WATERTHRUSH

Male Northern Waterthrush territorial space use was highly variable and curvilinearly associated with the extent of anthropogenic gaps in woodland cover at the landscape scale. As the proportion of unforested land created by harvesting increased, waterthrush territory size initially decreased by almost 500%. Beyond 60% harvest-created openings the trend was reversed and waterthrushes occupied the largest territories that we observed, resulting in a maximum territory expansion of more than 800%. We are not aware of any other studies that have documented such high variation in passerine territory size in response to changes in landscape structure. Bayne et al. (2005) observed that (congeneric) Ovenbirds occupied significantly larger territories in forests having multiple narrow seismic lines (2–3 m wide linear corridors cut through forested landscapes by the energy sector to access remote areas) than in less disturbed areas having single wider lines (8 m wide). However, mean territory size in the more disturbed forests was only slightly more than double (124%) that in less disturbed forests. Machtans (2006) also observed

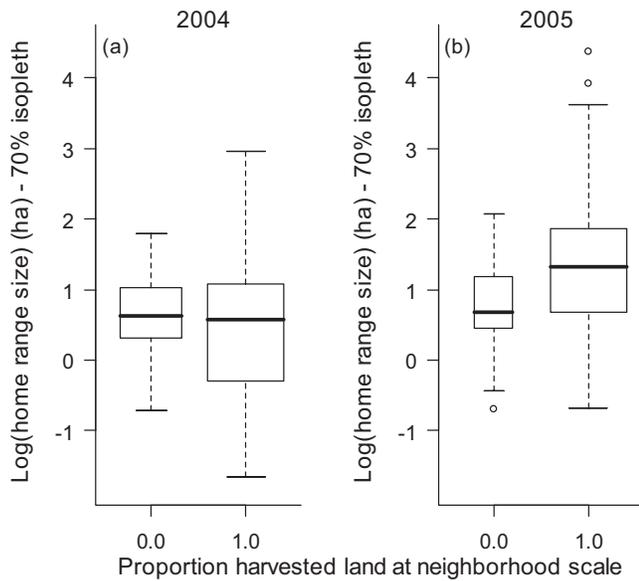


FIGURE 4. Home-range space use (calculated at the 70% isopleth) by breeding Blackpoll Warblers radio-tracked in naturally patchy unharvested, and harvested boreal forests of insular Newfoundland and Labrador was influenced by the proportion of anthropogenic gaps in woodland cover at the neighborhood scale; relationships varied between 2004 and 2005. Horizontal lines represent median home range areas and separate the 25 and 75 percentiles (lower and upper box ends), unfilled dots represent outliers, and whiskers represent 1.5 times the interquartile range. Box widths are proportional to sample size.

a significant increase in territory size for ground and shrub-level nesting passerines that incorporated seismic lines into their territories compared to birds in undisturbed forests, but territory size increased by only 30%.

Highly variable territory size and the relationship between forest harvest and territorial space use by waterthrushes in our study may have been driven by conspecific density and resource availability. These factors likely are not mutually exclusive and their effects have been documented elsewhere. Increases in conspecific density have been observed for waterthrushes in riparian buffer strips adjacent to clearcuts (Whitaker and Montevecchi 1999, Warkentin et al. 2003) and for other species of forest-dependent passerines in remnant forest patches after harvesting (Darveau et al. 1995, Gram et al. 2003). Our results may reflect differences between forest management strategies for riparian zones compared to habitat located away from sources of open water. As in many other jurisdictions, provincial government regulations require that forest managers in Newfoundland and Labrador leave riparian forests intact for the protection of water quality and to maintain habitat for riparian fauna (Canadian Forest Service 1993). Waterthrushes are typically considered riparian specialists and in harvested landscapes tend to crowd into the

remaining buffers (Eaton 1995, Whitaker and Montevecchi 1997, Warkentin et al. 2003). Consequent increases in pre-emptive behavior or energetic or time costs of defense against multiple neighbors may have led to the reduced territory area that we observed among these riparian-associated birds (Myers et al. 1979, Adams 2001).

Waterthrushes are also capable of successfully breeding in wet terrestrial forest habitat situated away from major sources of water (Warkentin et al. 2003, Dalley 2007). Wet forest habitat is common throughout the study area and provides abundant foraging habitat for waterthrushes (Thompson et al. 2003, Warkentin et al. 2003). Because riparian forest harvest regulations do not apply to wet terrestrial forest habitat, landscapes having abundant nonriparian sources of water had the greatest proportions of harvested land in our study. Removal of mature timber stands from these areas could thus result in a loss of waterthrush habitat. Nonriparian wet landscapes may have been able to support only very low densities of waterthrushes resulting in the territory expansion we observed. Alternatively, resources in these harvested, wet landscapes may have been sufficient to support individuals with small territories, but males may have required larger territories to countersing with dispersed neighbors. Inverse

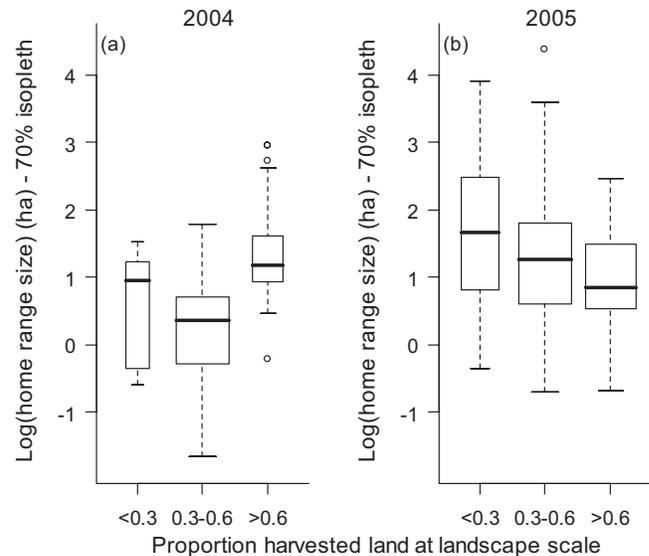


FIGURE 5. Home-range space use (calculated at the 70% isopleth) by breeding Blackpoll Warblers radio-tracked in naturally patchy unharvested, and harvested boreal forests of insular Newfoundland and Labrador was influenced by the proportion of anthropogenic gaps in woodland cover at the landscape scale; relationships varied between 2004 and 2005. Horizontal lines represent median home range areas and separate the 25 and 75 percentiles (lower and upper box ends), unfilled dots represent outliers, and whiskers represent 1.5 times the interquartile range. Box widths are proportional to sample size.

relationships between conspecific density and territory area have been observed in natural (Arcese and Smith 1988, Elchuk and Wiebe 2003) and experimentally manipulated bird populations (Krebs 1971, Both and Visser 2000).

The abundance of foraging habitat may also explain why waterthrush territory area did not vary with the amount of harvest at the neighborhood scale. We frequently observed waterthrushes foraging outside their territory boundaries. It may also explain, in part, why home range area for this species did not vary with forest harvest at either spatial scale. This result indicates that waterthrush home range resources were likely in adequate supply in both naturally and anthropogenically patchy landscapes. In addition, waterthrushes incorporated both anthropogenic and natural openings into their home ranges and we regularly radio-tracked waterthrushes flying directly across large lakes, peatlands, patches of harvested forest, and roads.

The scale-specific responses to anthropogenic heterogeneity that we observed for waterthrushes suggest that territory size for this species is driven in part by landscape-level habitat characteristics, but is less sensitive to the neighborhood-scale conditions measured. In a study of congeneric male Ovenbird territory size in fragmented and contiguous boreal forests, Mazerolle and Hobson (2004) observed higher levels of territory overlap by neighbors in fragments compared to those in contiguous forest. In our study, territory overlap is likely a consequence for waterthrushes in the most heavily harvested landscapes. However, we did not sample neighboring birds and cannot assess the degree to which this may have occurred.

In other studies, breeding Ovenbirds compressed or moved their territories away from disturbed areas, apparently to 'compensate' for changes in landscape structure (Lambert and Hannon 2000, Machtans 2006). Similarly to our observation that the largest territories occurred in the most heavily harvested landscapes, breeding Hooded Warblers (*Wilsonia citrina*), Ovenbirds, and Scarlet Tanagers (*Piranga olivacea*) have been observed to move more extensively in fragmented landscapes compared to continuous forest, and sometimes occupy discontinuous territories comprising multiple fragments (Bayne and Hobson 2001a, Norris and Stutchbury 2001, Fraser and Stutchbury 2004).

BLACKPOLL WARBLER

Blackpoll territory area was not associated with the proportion of harvested land at either the neighborhood or the landscape scale. This suggests that resources required for territory maintenance were sufficient in both unharvested and harvested neighborhoods and landscapes. Blackpolls were regularly observed singing, foraging, engaging in agonistic behavior with conspecifics, carrying food, and moving with females during provisioning in both naturally patchy and harvested areas. In

addition, blackpolls nested in the regenerating vegetation of five- to six-year-old clearcut patches and successfully fledged young (Dalley 2007). Further, apparent survival of blackpolls was similar between harvested and naturally fragmented landscapes (Whitaker et al. 2008).

Blackpoll home range area was associated with the proportion of unforested land that was created by harvesting at both the neighborhood and landscape scales, although these relationships differed between years. This interannual variation may reflect unbalanced samples within and between years. Equal numbers of blackpolls were radio-tracked in unharvested ($n = 6$) and harvested ($n = 7$) neighborhoods during 2004, but during 2005 only three of 14 birds occupied territories lacking cleared patches. Alternatively, blackpoll response to forest harvest at the landscape scale through home range space use may be attributable to factors such as resource availability, particularly in the context of interannual differences in weather. Avian home range area can be positively related to resource needs and inversely related to resource availability (Schoener 1968, Ims 1995, Springborn and Meyers 2005). Forest harvesting can affect prey availability for passerines by removing foraging habitat or decreasing arthropod abundance (Burke and Nol 1998, Zanette et al. 2000). Likewise, arthropod abundance can be negatively affected by rainfall (Moran et al. 1987, Weisser et al. 1997). Inclement weather during 2004 (both seasonal and June precipitation levels were significantly higher than 2005; Environment Canada 2005) may have led to delayed breeding and decreased availability of food throughout the study area. This in turn may have caused blackpolls in both unharvested and harvested landscapes to focus space use more on foraging for survival rather than reproduction (songbird productivity in the study area was lower in 2004 than 2005; Dalley 2007), leading to no trend in home range area relative to extent of harvested land at either spatial scale that year. During 2005, median home range area was larger in landscapes with 0%–30% of openings created by harvesting compared to those same landscapes during 2004. Further, blackpoll home range area decreased with higher amounts of landscape-scale forest harvest in 2005. It is possible that the change in mode of transmitter attachment between years influenced blackpoll home range area. However, we did not detect an effect of year (and thus mode of attachment) on space use by waterthrushes, and Bayne and Hobson (2001b) found no effect of transmitter attachment method (glue versus harness) on movement patterns of Ovenbirds.

Blackpolls were frequently observed foraging on regenerating balsam fir and in remnant, nonmerchantable timber in harvested patches. In a concurrent passive mist-netting study conducted in our study area, blackpoll capture rates did not differ between harvested and naturally patchy forests (Whitaker et al. 2008). This indicates that forest harvesting has created habitat for blackpolls, possibly by providing food resources and an abundance of potential extra-pair mates

in a more densely populated landscape. If harvested patches provide more resources for blackpolls than natural gaps, then the birds may obtain sufficient resources in relatively small areas. Other studies have also documented breeding blackpolls using sapling (<5 m) and young (5–11 m) regenerating stands postharvest (Imbeau et al. 1999, Simon et al. 2002). Clearcut harvesting typically occurs on productive sites, thus regenerating stands are predisposed to be productive as well, especially given the large amount of organic material that is left to decay on-site (Tiessen et al. 2002; Corner Brook Pulp and Paper Ltd., pers. comm.). Birds in naturally heterogeneous landscapes, however, had increased space requirements, possibly because they were limited to foraging on trees and scrub found at the shoreline or on the edge of peatlands. These areas were generally less productive than harvested areas, as they did not produce merchantable timber (Corner Brook Pulp and Paper Ltd., pers. comm.).

In conclusion, detailed examination of songbird space use patterns in landscapes with varying levels of natural and anthropogenic gaps in woodland cover suggests that changes to landscape structure have the potential to modify songbird behavior at multiple spatial scales. Our observation that Northern Waterthrushes occupied the largest territories in landscapes having the most extensive harvesting is in agreement with an emerging pattern of songbird territory expansion in response to disturbance. Thus, while forest harvest strongly influences the spatial distribution of resources, passerines may be capable of compensating in areas having (at least) low levels of fragmentation. We observed territorial expansion of values in excess of 800%, but associated costs to individuals remain unknown. The threshold level of disturbance beyond which these songbirds will be unable to successfully alter their spatial requirements is also unclear. Of critical importance is the impact of altered space use patterns on productivity and recruitment. That both specialist and generalist species responded to the broad-scale structure of the landscape indicates that songbird behavior at relatively small spatial scales can be sensitive to broad-scale ecological processes.

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