Songbird response to seismic lines in the western boreal forest: a manipulative experiment

Craig S. Machtans

Abstract: Millions of kilometres of seismic lines have been created for hydrocarbon exploration in the boreal forest and their impact on songbirds is unknown. I conducted a replicated before–after control–impact (BACI) field experiment in southern Northwest Territories to evaluate the impact of 6 m wide seismic lines on songbirds. Territories of all birds on six pairs of 12 ha control and treatment plots were mapped for one year before and one year after seismic lines were cut through the treatment plots. The bird community was not dramatically affected by seismic lines. At the community level, birds did not decline in abundance or move their territories relative to the seismic lines, and they included the seismic lines in their territories. However, ground and shrub nesting species that had territories spanning the seismic lines increased the size of their territories. At the species level, only the ovenbird (Seiurus aurocapilla (L., 1766)) showed a consistent response to seismic lines. Ovenbirds declined in abundance, moved their territories away from seismic lines, and were not observed crossing the lines. Pressure on industry from land managers to reduce the width of seismic lines should continue to minimize the impact of these clearings on all species.

Introduction

Large-scale disturbance of the boreal forest is often associated with forestry practices, but incidental harvest resulting from activities of the oil and gas sector can affect as much or more forest (Schneider 2002). Many phases in the development of oil and gas reserves involve forest clearing, both permanent (roads, pipelines, well sites) and temporary (seismic lines). Seismic lines are linear clearings of forest that are created to allow transmission and recording of vibrations in the ground in a way that allows geological formations to be mapped. These linear clearings are pervasive across landscapes overlaying hydrocarbon deposits such as the western Canadian sedimentary basin. For instance, Alberta had over 1.5 million km of seismic lines in the forested part of the province by the mid 1990s (Alberta Environmental Protection 1998), and tens or hundreds of thousands of new kilometres of lines are approved annually. Seismic lines were 8–10 m wide historically, but now vary between 1 and 6 m depending on the type of equipment used and the investment made for seismic data collection (cost is inversely related to width because of the use of specialized equipment or helicopters). The persistence of seismic lines as non-forested corridors on the landscape depends primarily on a few factors. Seismic lines typically regenerate slowly (MacFarlane 2003; Lee and Boutin 2006) because of all-terrain-vehicle traffic, soil compaction, poor growing conditions (e.g., shading by surrounding forest), and reuse or reclearing of the line. However, seismic lines in the southwestern Northwest Territories often rapidly regenerate to either dense shrub cover or a young seral stage of the surrounding forest, perhaps because of better growing conditions and essentially no traffic during the growing season. There have been no experimental studies of how forest birds are affected by seismic lines, and only recently have any comparative studies been completed (Bayne et al. 2005a, 2005b).

Research on the response of forest birds to linear disturbance has been investigated for many different types of open-
...ings including roads (Reijnen and Foppen 1994 [wide roads]; Rich et al. 1994; Ortega and Capen 1999; King and DeGraaf 2002 [narrow roads]), pipelines (Fleming 2001), power-line corridors (Anderson 1979; Kroodsma 1982), and trails (Miller et al. 1998). Common threads amongst the studies of roads and trails are the presence of traffic, either vehicular or human, and a permanent opening without native ground cover. In several cases it is certainly the direct effect of the traffic (Reijnen and Foppen 1994; Miller et al. 1998) that affects birds. In other cases it appears that birds use the edge as a territory boundary, resulting in habitat loss equal to the area of the disturbance corridor (Rich et al. 1994). Alternatively, evidence exists for some species that edge territories may be of lower quality (Ortega and Capen 1999), extending the effect of the road beyond its physical footprint. Finally, the permanent openings created by power-line and pipeline right-of-ways are wide enough that non-forest species populate the openings, and this invasion of non-forest species influences the integrity of the local system in several ways (Fleming 2001).

It is not clear from previous research on linear openings how seismic lines could affect birds in the boreal forest. Seismic lines are narrower than almost all other disturbances previously studied, they have a total or effective lack of traffic (no noise, dust, or human intrusion), and they do not have a permanently unvegetated surface (such as a gravel road). Modern methods of creating seismic lines mostly or partially preserve the duff layer of the forest floor, and “avoidance” seismic lines (see below) create little apparent break in the canopy heterogeneity of old forests.

The objective of my study was to determine whether seismic lines affect the density of songbirds and (or) the local distribution of their territories. I mapped the locations of songbird territories relative to seismic lines and conducted behavioural observations of individual birds. I also wanted to determine whether birds responded differently to the two types of seismic lines currently created during exploration for hydrocarbon reserves. The first type is a linear clearing that traverses directly through any habitat in its path. The second is termed an “avoidance” line: the path of clearing deviates around any large trees that lie on the seismic line. The line therefore meanders along a generally straight course.

I postulated four a priori outcomes based on the previous research reviewed above. My predictions are all based on the direct assumption that the location of an individual’s territory is directly related to the bird’s assessment of the consequences of including a seismic line in its territory. First, there might be no effect (Fig. 1a), in which case territory locations do not change after seismic lines are cut. Second, birds may choose not to include seismic lines in their territory (Fig. 1b; displacement hypothesis, e.g., Rail et al. 1997). Third, birds may avoid the seismic lines and their immediate edges (Fig. 1c; edge avoidance hypothesis). Last, some birds may be attracted to the disturbed habitat or habitat openings (Figs. 1d and 1e; attraction hypothesis). Within this framework, I also predicted that ground and shrub nesting guilds may be more affected than canopy guilds. This prediction was based on the personal observation that modern 6 m wide seismic lines do not appear to create canopy gaps much larger than those in the existing old forests, but do remove the shrubs and some ground cover.

Methods

Study area

I conducted the study near the community of Fort Liard, Northwest Territories, Canada (60°15′N, 123°30′W). The forests of the region are boreal, subtype upper Mackenzie (relatively highly productive forests along the alluvial plains of the major rivers in the region) (Rowe 1972). Mesic forests are dominated by pure or mixed stands of white spruce (Picea glauca (Moench) Voss), trembling aspen (Populus tremuloides Michx.), balsam poplar (Populus balsamifera L.), and paper birch (Betula papyrifera Marsh.). Hygric sites are dominated by black spruce (Picea mariana (Mill.) BSP) and larch (Larix spp.) with small, topographically constrained occurrences of jack pine (Pinus banksiana Lamb.). Detailed descriptions of the study area and bird community can be found elsewhere (Machtans 2000; Machtans and LaTour 2003).
Study design and field methods

I used a replicated before–after control–impact (BACI) design with six treatment plots and six control plots. Each treatment plot was paired with a control plot in similar habitat in the same immediate area, thereby minimizing confounding habitat and spatial effects. One pair of plots was in mature (closed canopy, 70 years old) aspen that had some areas of dense spruce understory. One pair was in old (open canopy, 120 years old) aspen–poplar forest, and one pair was in old mixedwood forest. Three pairs were in old spruce-dominated forest (150–170 years old) with varying, matched degrees of canopy closure. Each plot was 350 m × 350 m (12.25 ha).

I collected data one year before impact (2002) and one year after (2003). The seismic lines (the “treatment”) were cut through the six treatment plots in late winter prior to the second year of the study. Lines were created by industry-standard techniques: a medium-sized bulldozer simply drove straight through the forest, pushing down trees to create the linear lines. The bulldozer detoured around large trees on the avoidance lines. After a couple of passes by the bulldozer to clear trees and stumps, the fallen material was windrowed along one side of the seismic line, leaving an opening approximately 6 m wide with a drivable surface approximately 4 m wide.

Two intersecting lines were cleared through each treatment plot. Each plot had one linear and one avoidance line cut at right angles, centered on the plot (Fig. 2). Lines were cleared 50 m beyond the study plots. This equates to a line density of 5.7 km per square kilometre of habitat, a moderate coverage of seismic lines. Intersection of two lines in a patch of forest, such as in this experiment, is common even when lower densities of seismic lines are present, as shown in Fig. 1 of Bayne et al. (2005a). There are up to 27 such intersections within any 10 km × 10 km area in my study region, including only historical seismic lines that are marked on topographic maps.

I delineated territories of songbirds on the study plots using the spot mapping protocol of Bibby et al. (2000). Each plot was flagged with transects spaced 50 m apart. The plots were visited 11 or 12 times between 5 and 30 June, in the peak of the migrant breeding season. Daily surveys began 30 min before sunrise and were completed within 6 h after sunrise, with repeat visits separated by 2 or more days.

Individual birds were color-banded after attracting them into a mist net with the songs or calls of a conspecific. Birds whose territories were close to seismic lines were targets for banding (all species), with the expectation that the color-banding would assist with identifying individual birds for behavioural observations. Those observations consisted of keeping an individual bird in sight for 20 min (an “observation bout”) or until it crossed a seismic line and was observed singing on the other side. Birds not singing after they crossed the seismic line were watched until the end of the observation period unless they were lost from sight. The following data were collected: the exact location of the bird, whether it crossed the seismic line, whether it sang on both sides of the seismic line, and a comment on its behaviour.

Data summary and statistical analyses

Territories were hand drawn as minimum-sized polygons according to rules in Bibby et al. (2000). Their recommendations on specific nuances such as drawing edge territories to the approximate size of other conspecific territories (i.e., extending the edge territories off-grid without supporting observations) were followed. Edge territories were flagged in the data set as “partial”. I drew all territories without knowing the identity of the study plot (treatment versus control). Banding and behavioural observation data were particularly useful for verifying typical territory size and location, and especially for verifying that spot mapping observations straddling seismic lines were part of a single territory that included the seismic line.

Spot mapping data sheets were georeferenced in ESRI ArcView 3.2 software. Exact locations of the seismic lines, including all deviations on the avoidance lines, were hand mapped in the field and subsequently digitized. All bird territories were digitized. Analyses were primarily based on the centroid of the territory, since the exact edge of a territory was subjectively demarcated on the spot mapping summary sheets (i.e., a computer was not used to draw minimum convex polygons). Territory centroids were calculated in the geographic information system (GIS) using a modified version of Centroid Ave (http://arcscripts.esri.com). A territory was considered “in” if the centroid was within the plot boundary (e.g., territory 6 in Fig. 2 was “in” for count-
based analyses). The distance from the centroid to the closest point along the edge of both the linear and the avoidance seismic line was then calculated using Nearest Features v3.7 (http://www.jennessent.arcgis.com/arcview/nearest_features.htm).

An index measure of the number of territories overlapping seismic lines was obtained using the GIS. Each cutline was arbitrarily subdivided into 6 m × 6 m squares spaced every 10 m along the line’s length (Fig. 2). The number of territories intersecting each square (“hits”) was counted, by species. Using this technique, rather than simply counting a territory as overlapping or not, prevented bias for the territories that barely contacted the seismic line. Territories centered over the seismic line scored the most hits, and successively fewer hits applied to territories whose centers were farther from the line (Fig. 2). Without this technique, territories that barely touched the seismic lines (likely from chance when they were hand drawn) would have been weighted equally to those actually overlapping the seismic lines. Since I drew territories without foreknowledge of the seismic line location, this happened multiple times. Overlap numbers from a binary “overlapping” or “not overlapping” count were used only as a reference for the patterns seen from the more detailed analysis above. Boreal Chickadee (Poecile hudsonica (Forster, 1772)), Black-capped Chickadee (Poecile atricapillus (L., 1766)), and Gray Jay (Perisoreus canadensis (L., 1766)) were excluded from this analysis and the area analysis below because their breeding territories had enlarged to feeding territories by the fieldwork.

Territory area was calculated with the GIS. A relative comparison of territory areas within the study is valid, but the absolute area of each species’ full territory is probably underestimated by the spot mapping technique, as only the singing territory would have been outlined (e.g., Mazerolle and Hobson 2004). No territories marked as “partial” were used in any area calculations or comparisons (e.g., territory 6 in Fig. 2 would be “partial”).

Digitized cutlines from year two of the study were overlaid back onto the data from year one to obtain pretreatment, within-plot parameters for analyses. Parameters on control plots were similarly generated by duplicating the locations of seismic lines from the corresponding paired treatment plot.

Treatment effects for overall density of territories on plots, territory locations (centroids) relative to seismic lines, and seismic line overlap were assessed with the interaction term (year × treatment) of a repeated-measures analysis of variance (RM-ANOVA) (Gotelli and Ellison 2004). Year was entered as the within-subject factor and treatment type was the between-subjects factor. Box’s M test was used to assess homogeneity of variance between groups. I ran two other analyses to verify that the simpler RM-ANOVA was appropriate. Since treatment and control plots were “blocked” within habitat types, I ran an ANOVA using the block × treatment type interaction as an error term in Proc GLM in SAS (SAS Institute Inc. 1999). Also, since habitat type could also be considered a random effect, I ran a mixed linear model. In both cases there was no appreciable change to the results, so the RM-ANOVA was deemed most parsimonious. Behavioural observation data were analyzed with a χ² test with an expected ratio of 50:50 that therefore assumes birds were equally likely to cross a cutline or stay in the forest on the side where they were first observed. Computations were performed in SPSS release 13.0 (SPSS Inc. 2004), except as noted. Standard error is reported unless otherwise noted.

Statistical results for community-level analyses were considered significant at the 5% level. Results for guilds or individual species were considered significant at the 10% level to avoid type II statistical errors. Given the large number of statistical tests used in my analyses, especially when individual species were considered, spurious results were a concern. Rather than rely on a blind adjustment such as a Bonferroni correction, I instead looked for concordance between several analyses (e.g., abundance change, territory location, territory area, frequency of crossing cutlines) before presenting a result as biologically significant. Several statistically significant results were therefore dismissed as spurious.

**Results**

There were 41 species holding 1504 territories inside the study plots, totalled across both years. There were 32–87 territories per plot (n = 12 plots × 2 years, mean 62.6, SD 15.0). Six woodpecker, two raptor, one owl, one grouse, and 31 passerine species were recorded. Results are reported for passerines (1411 territories) or subgroups of passerines only, as the territories of (the then) excluded species were not reliably mapped by spot mapping. The most common species and their prevalence on plots are listed in Table 1.

**Community and guild results**

Cutting seismic lines through the study plots did not affect the total number of territories. This result was consistent among various parts of the bird community (all passerines, F[1,10] = 2.43, P = 0.15; ground and shrub nesting passerines, F[1,10] = 0.37, P = 0.56; canopy nesting passerines, F[1,10] = 0.89, P = 0.37). There was, however, a strong, negative year effect (F[1,10] = 42.57, P < 0.001) that was directly attributable to a large study-wide decline in Tennessee Warblers (Vermivora peregrina (Wilson, 1811)) (Fig. 3). There was little absolute change (<4%) in the number of territories of passerines in either treatment or control plots between years with Tennessee Warbler records removed (F[1,10] = 0.92, P = 0.36, Fig. 3).

Birds appeared to cross seismic lines as often as would be expected by random chance. Of 211 birds observed during behavioural observation bouts, 113 were observed crossing, whereas 98 did not cross (χ² = 1.06, P = 0.30). There was no difference in the frequency of crossings between linear seismic lines (54% crossed, χ² = 0.627, P = 0.43) and avoidance lines (53% crossed, χ² = 0.45, P = 0.50). There was also no difference in crossing frequency between ground and shrub nesting species (49% crossed, χ²[1] = 0.03, P = 0.87) and canopy nesting species (41% crossed, χ²[1] = 2.315, P = 0.13). For species that were observed more than twice (i.e., there was at least one random chance of crossing), 14 of 15 species were seen crossing at least once. Only Ovenbird (Seiurus aurocapilla (L., 1766)) (with six observation bouts) was not observed crossing seismic lines. The majority of individuals seen crossing cutlines were observed singing on both sides of the line (79 of 113
sang on both sides, \( \chi^2_{(1)} = 17.92, P < 0.001 \). Of the 14 species mentioned above, 12 were seen singing on both sides of the seismic lines. The two not singing were Yellow-bellied Sapsucker (Sphyrapicus varius (L., 1766)) (which would not sing by definition) and White-throated Sparrow (Zonotrichia albicollis (Gmelin, 1789)), which was seen foraging along the lines. American Robin (Turdus migratorius (L., 1766)) and Chipping Sparrow (Spizella passerina (Bechstein, 1798)) were also observed foraging directly on the lines, while Western Tanager (Piranga ludoviciana (Wilson, 1811)) and Swainson’s Thrush (Catharus ustulatus (Wilson, 1840)) were seen foraging on the immediate edges of the seismic lines. Anecdotally, Swainson’s Thrush, Yellow-rumped Warbler (Dendroica coronata (L., 1766)), Ruffed Grouse (Bonasa umbellus (L., 1766)), and Yellow-bellied Sapsucker nests were found within 1 m of the seismic lines, and all hatched successfully.

Passerines did not settle away from newly created seismic lines. The average distance from each territory centroid to the edge of the closest seismic line did not change once seismic lines were cut (controls: 61.0 ± 0.7 m to 59.0 ± 1.9 m; treatments: 64.8 ± 1.2 m to 61.6 ± 2.0 m; \( F_{[1,10]} = 0.12, P = 0.73 \)). The result was similar for the ground and shrub nesting guild (\( F_{[1,10]} = 0.19, P = 0.67 \)) and the canopy guild (\( F_{[1,10]} = 0.75, P = 0.41 \)). Using the type of line as a repeated measure within plots and years, there was no difference between linear and avoidance lines in the above analysis (line type × year × treatment interaction term, treatment plots only, 2003: avoidance = 97.3 ± 2.7 m, linear = 92.3 ± 3.4 m; \( F_{[1,10]} = 0.01, P = 0.94 \)). Only 5 of 126 birds banded before treatment were resighted in the second year. This prevented any type of analysis on individual birds before and after treatment.

More “hits” of passerine territories were recorded above seismic lines (controls: 1088 [2002] to 773 [2003]; treatment: 969 to 1122; \( F_{[1,10]} = 8.04, P = 0.018 \)). When separate RM-ANOVAs were run for high and low guilds, the overall result was more hits for the ground and shrub nesting guild (year × experiment interaction for low, \( F_{[1,10]} = 7.11, P = 0.024 \)) than for the canopy nesting guild (year × experiment interaction for high, \( F_{[1,10]} = 1.01, P = 0.38 \)). Adding line type as a within-subjects term resulted in no difference in the effect observed over linear or avoidance seismic lines (year × line type interaction, for high guild: \( F_{[1,10]} = 0.22, P = 0.65 \); for low guild: \( F_{[1,10]} = 1.82, P = 0.21 \)). Simple counts of territories that overlapped the seismic lines (counted when the edge of the territory touched both edges of the seismic lines as mapped) showed no significant increases resulting from cutting seismic lines (control: 19.2 ± 1.9 in 2002, 16.7 ± 2.0 in 2003; treatment: 18.8 ± 1.6 to 19.5 ± 3.1; \( F_{[1,10]} = 2.26, P = 0.163 \)). The number of territories did not vary by nesting guild (ground and shrub, \( F_{[1,10]} = 0.89, P = 0.37 \); canopy, \( F_{[1,10]} = 1.00, P = 0.34 \)).

Overall, there did not appear to be any change in the aver-
Fig. 4. Average area of the territories of ground and shrub nesting species that overlapped seismic lines on treatment and control plots before and after seismic lines were cut through the treatment plots. Only territories fully on the study plots were included. Bars represent standard error of the mean. Birds had larger territories over seismic lines (repeated-measures ANOVA,  for  = 3.37, )


dage area of territories overlapping seismic lines (  = 1.02,  = 0.337). However, in concordance with the “hits” analysis above, the ground and shrub nesting guild had an increase in territory area of approximately 30% on the treatment plots (Fig. 4; treatment, ± 0.28 ha in 2002 to ± 0.15 ha in 2003; control, ± 0.15 ha;  = 0.096). The area of territories for the canopy nesting guild did not change (treatment, ± 0.28 ha in 2002 to ± 0.14 ha in 2003; control, ± 0.16 ha to ± 0.15 ha;  = 0.06,  = 0.81).

Individual species

Twelve species occurred on at least half of the study plots (Table 1) and were analyzed separately for effects. Ovenbird, Magnolia Warbler (Dendroica magnolia (Wilson, 1811)), and Yellow-rumped Warbler showed a statistically significant change in density attributable to the experiment. The number of Ovenbird territories declined on the treatment plots while their abundance increased on the control plots (treatment, 5.3 ± 1.6 in 2002 to 4.0 ± 1.2 in 2003; control, 4.3 ± 1.7 to 5.7 ± 2.2;  = 5.52,  = 0.041). The number of Magnolia Warbler territories increased on the treatment plots while their abundance decreased on the control plots (treatment, 7.5 ± 2.1 in 2002 to 8.5 ± 1.9 in 2003; control, 7.8 ± 2.5 to 6.3 ± 1.8;  = 5.60,  = 0.040). The number of Yellow-rumped Warbler territories declined more steeply between years on treatment plots (treatment, 4.3 ± 0.6 in 2002 to 2.5 ± 0.2 in 2003; control, 4.0 ± 0.7 to 3.7 ± 0.6;  = 5.55,  = 0.040). To ensure edge territories were not unduly influencing the results, analyses for all 12 species were redone using only territories fully on the spot mapping grid (i.e., not just the centroid on the plot). The statistical results for Ovenbird were strengthened ( = 9.55,  = 0.011), while statistical evidence of a treatment effect disappeared for Magnolia Warbler ( = 1.50,  = 0.249) and was weakened for Yellow-rumped Warbler ( = 3.26,  = 0.10). This additional verification analysis was also done for the community results presented in the preceding section, but there was no change to any of the results.

Six species showed a nonrandom response with regard to crossing cutlines (Table 2). Ovenbird never crossed during six observation bouts. Red-eyed Vireo (Vireo olivaceus (L., 1766)) and Tennessee Warbler tended to stay on the side of the seismic line where first observed. Yellow-rumped Warbler, Western Tanager, and Chipping Sparrow were more likely to cross the seismic lines than to stay on one side.

Two species appeared to move the relative locations of their territories in response to the seismic lines. The average distance from the closest seismic line to the centroid of Ovenbird territories increased after seismic lines were cut (control, 63.4 ± 6.8 m in 2002 to 47.7 ± 8.8 m in 2003; treatment, 49.0 ± 9.6 m to 83.3 ± 9.3 m;  = 4.44,  = 0.080). The average distance decreased slightly for Yellow-rumped Warbler (control, 42.2 ± 9.0 m in 2002 to 67.1 ± 6.1 m in 2003; treatment, 69.3 ± 10.5 m to 56.8 ± 11.3 m;  = 0.072).

Three species showed a change in the count of “hits” used to assess the degree of overlap of territories on seismic lines. The degree of overlap for Ovenbird territories decreased markedly on study plots where seismic lines were cut (control, 14.8 ± 4.8 hits in 2002 to 13.1 ± 3.4 hits in 2003; treatment, 11.0 ± 3.5 hits to 3.3 ± 2.1 hits;  = 3.69,  = 0.084). Chipping Sparrow showed an increase in the degree of overlap on study plots where seismic lines were cut (control, 10.8 ± 4.1 hits in 2002 to 11.0 ± 4.2 hits in 2003; treatment, 8.0 ± 3.3 hits to 21.5 ± 6.0 hits;  = 3.64,  = 0.085). Yellow-rumped Warbler maintained the same degree of overlap on study plots where seismic lines were cut, but this contrasted with a drop in the degree of overlap on control plots (control, 19.8 ± 3.3 hits in 2002 to 8.1 ± 2.4 hits in 2003; treatment, 17.2 ± 3.5 hits to 18.0 ± 2.4 hits;  = 4.96,  = 0.050).

A final analysis was performed using a count of territories that overlapped (or did not overlap) seismic lines. Only Chipping Sparrow, Magnolia Warbler, Ovenbird, Swainson’s Thrush, Tennessee Warbler, and Yellow-rumped Warbler territories overlapped seismic lines on more than half of the study grids with the restrictions for this analysis (see Methods). Ovenbird again showed a significant response, paralleling the result from the “hits”-based analysis above (control, 2.67 ± 1.0 overlap territories per plot in 2002 to 3.33 ± 1.0 in 2003; treatment, 4.33 ± 1.0 to 1.33 ± 0.8;  = 11.41,  = 0.007). The probability of a nonrandom result for other species varied (0.30 ≤  ≤ 1.0).

No statistically significant change in territory area (overlapping seismic lines) was detected for any of the six species described in the previous paragraph (0.12 ≤  ≤ 0.84). There is a reasonable chance of a type II (false negative) statistical error given the missing values apparent when single species are considered.

Discussion

Community response

Seismic lines had subtle, but measurable, effects on the bird community that were evident only when territories di-
rectly over seismic lines were examined. Birds that nest at the ground or shrub level increased the size of their territories over seismic lines by about 30%. A 6 m wide seismic line directly through the center of an average territory (0.82 ha) would represent a direct habitat loss of ~8%, so the observed effect appears larger than the direct loss. However, measuring territory area using only spot mapping data is not accurate enough (e.g., Mazerolle and Hobson 2004) to reliably determine whether the disturbance to response ratio is 1:1 or greater. For example, since I do not have exact boundaries of the territories mapped, it is not appropriate to calculate that the increased area required in the posttreatment territories was almost four times the area lost to the seismic lines. If exact territory delineation was possible, the ratio above could be determined and then used for extrapolation of effects.

Why would birds increase the size of their territories over seismic lines? Interactions with conspecifics (reviewed in Adams 2001) and resource availability (e.g., Wilson 1975; Marshall and Cooper 2004) are two theories commonly used to explain variation in territory size. The former theory posits a complex regulation of territory size from boundary disputes and other exchanges between neighbours. The latter theory uses food abundance or a proxy of food abundance (foliage density or foliage structure) to explain territory size.

A change in territory size due to conspecific regulation does not fit with the results of my study. Two outcomes should have been observed in my experiment if the inverse relationship of territory size to conspecific density of the interaction-based theory held for the observed results. First, the number of territories overlapping seismic lines would have decreased as a means to promote the observed territory expansion. Second, the number of territories on the plot should have declined substantially, as neighbouring territories in all directions should have decreased to allow the same expansion. However, the actual areas of the mapped territories calculated with the GIS and the simple counts of territories above lines clearly showed that larger territories produced the observed effects, negating the first expected result. No plot-wide decreases in abundance were observed for either the entire community or the two guilds used for analyses. This negates the second result expected if neighbour interaction was the primary factor governing territory size in this study.

A specific example of why the conspecific interaction theory may not be appropriate to explain the results of my study is available. Tennessee Warbler density halved in 2003 from a 5-year high in 2002 (C.S. Machtans, unpublished data). Territory size did not change significantly on either the treatment or the control plots (6%–13% larger, respectively, P > 0.23) in spite of the large decrease in the number of neighbouring territories. Tennessee Warbler abundance is closely linked to outbreaks of spruce budworm (Archips fumiferana Clemens) (e.g., Patten and Burger 1998). Spruce budworm density appeared to decline between 2002 and 2003 (annual budworm surveys, B. Decker, Government of Northwest Territories, personal communication), mirroring the change in Tennessee Warbler numbers. Simultaneous with the decline in abundance, the apparent decrease in food resources does not provide strong evidence for either theory of territory size variation. However, the budworms were literally dripping from trees in 2002 (the peak budworm outbreak year), supplying a superabundant food resource that might have eliminated food as a constraint on territory size of Tennessee Warblers. Therefore, perhaps food was not a limiting factor in either year, and territory size did not expand when density of conspecifics was decreased by half.

A decrease in food availability on the seismic lines, perceived directly or by proxy, therefore seems to be a more likely reason territory size increased over seismic lines. I had no direct measures of territory quality. However, other research has shown a strong relationship between territory size and direct food availability (Stenger 1958) or proxies of food availability such as foliage density or structure (Smith and Shugart 1987; Marshall and Cooper 2004; but see Mazerolle and Hobson 2004). This fits well with effects on birds nesting on the ground or in the shrub layer, the part of the forest most directly affected by cutting the seismic lines (see below for a brief discussion on canopy disturbance). As the forb and shrub layer regenerates, one might expect the effect on birds to lessen. The study should be repeated after some regeneration to examine this possibility.

None of the first three predicted effects of cutting seismic lines (see Fig. 1) were evident when the entire community of passerines was considered on all study plots. In response to the experiment, birds did not increase or decrease in abundance on the plots, and the average location and size of their territories did not change. In short, no large-scale effects of cutting seismic lines through the study plots were detected, apparently owing to the ability of most birds to incorporate seismic lines into their territories.

The lack of community response supports threshold widths for seismic lines of 3–8 m; at these widths, birds can adapt to the small openings rather than be displaced by them. Rich et al. (1994) found that openings wider than 8 m functioned as territory boundaries (reducing abundance proportionately). They also noted that “…a 5% reduction in total forest area is below the threshold of forest lost necessary to produce a reduction in the relative abundance

### Table 2. Number of individuals of species seen crossing cutlines out of the total number of individuals observed; only species with nonrandom results are listed.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. observed crossing</th>
<th>( \chi^2 )</th>
<th>P</th>
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<tr>
<td>Ovenbird, Seiurus aurocapilla</td>
<td>0 of 6</td>
<td>6.00</td>
<td>0.014</td>
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<tr>
<td>Red-eyed Vireo, Vireo olivaceus</td>
<td>2 of 10</td>
<td>3.60</td>
<td>0.058</td>
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<td>Tennessee Warbler, Vermivora peregrina</td>
<td>7 of 23</td>
<td>4.167</td>
<td>0.041</td>
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<tr>
<td>Yellow-rumped Warbler, Dendroica coronata</td>
<td>12 of 13</td>
<td>9.308</td>
<td>0.002</td>
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<tr>
<td>Western Tanager, Piranga ludoviciana</td>
<td>13 of 17</td>
<td>4.765</td>
<td>0.029</td>
</tr>
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<td>Chipping Sparrow, Spizella passerina</td>
<td>16 of 23</td>
<td>3.522</td>
<td>0.061</td>
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of forest-interior nesting species..." (Rich et al. 1994, p. 1117). Rail et al. (1997, p. 976) speculated that "...<5 m wide gaps in the canopy are not perceived as habitat discontinuities, even by forest interior species". These assertions agree with the results of my study for 6 m wide seismic lines, the calculation of an 8% forest loss for an average overlapping territory (above), and a plot-wide loss of ~3% (two seismic lines in a 12.25 ha plot). In another study, Ovenbirds incorporated 2–3 m wide seismic lines into their territories (Bayne et al. 2005b), providing evidence that one of the most sensitive species can accommodate some disturbance to its territories. What remains unknown is whether there is a reproductive cost to having larger territories that incorporate linear corridors and whether such a cost would be meaningful on a population scale accounting for the extent (and continued creation) of linear disturbances in the boreal forest.

**Individual species response**

Consistency between various analyses was used as a guiding rule to assess whether statistical outcomes of species-level analyses were biologically meaningful. Only two species appeared to show several consistent responses to various measures analyzed for this study. Yellow-rumped Warblers declined in abundance on treatment plots but apparently moved territories closer to seismic lines, maintained a similar degree of overlap between years, and were seen crossing seismic lines more often than expected by chance. It is unclear what these contradictions mean, but large annual changes in values on the control plots point to sample size or spot mapping issues rather than biologically meaningful effects. Territory boundaries for this species on all plots were scrutinized and reanalyzed for the results noted above.

Ovenbirds, by contrast, responded consistently across all measures. Their abundance declined on plots with seismic lines and they moved their territory centers away from lines, decreased the overlap of territories and seismic lines, and were not observed crossing seismic lines. These results provide strong experimental support for the comparative studies with existing conventional seismic lines published by Bayne et al. (2005a, 2005b), and their discussions are not repeated here. Ovenbird response in this study and Bayne et al.’s studies is consistent with a displacement hypothesis, with ≥6 m seismic lines acting as singing territory boundaries. Bayne and his colleagues did not observe a numerical response (no difference in abundance), perhaps because of the decreased power of a comparative study. Alternatively, the higher densities of Ovenbirds in their study area may be forcing an increased overlap in territories (E. Bayne, personal communication) as opposed to results noted in this study.

Ovenbirds seem to be particularly sensitive to many types of disturbance across their range (summary in Van Horn and Donovan 1994). Results from this study validate those conclusions and provide a biological reason (other than the obvious direct loss of forest) to continue to reduce the width of seismic lines below 6 m.

**Linear versus avoidance seismic lines**

There were no differences in any of the analyses between linear seismic lines and avoidance seismic lines. While this result seems counterintuitive, the overall experimental effect observed for ground and shrub nesting species fits with the similar disturbance to the ground layer for each line type. The removal of the shrub layer and any duff would have been identical between the two types of lines, and therefore any effects would have been general, not line specific.

Canopy nesting species did not appear to be affected by the creation of seismic lines of either type. Interestingly, canopy cover did not differ between the two line types (linear 22%, avoidance 23%). This was because five of the six study plots were in old forests that have aspen with large canopy bowls. The canopy bowls are large enough to provide some cover across the seismic lines. While fewer canopy trees were removed on the avoidance lines, actual remaining canopy cover was nearly identical to that on the linear lines (but half of the original cover; means of 50% in surrounding forest and 22% along lines, P = 0.007). Within the canopy then, there are places along the seismic line where openings are much narrower than 6 m.

It would therefore appear that strictly from a bird management perspective there is little advantage in using avoidance seismic lines. From a practical perspective (and considering other values), it is quite advantageous to use avoidance seismic lines in old forests: they dramatically reduce the total amount of timber harvested and, by extension, substantially reduce the size of the (unnatural) windrowed material along the cutline. There is also a financial incentive for industry, as the cutting of avoidance lines for this study took half as long as the cutting of linear lines and reduced stress on equipment. However, my results suggest that on-the-ground line width would have to be reduced in order to reduce the observed impact of seismic lines on the bird community. Current best practice approaches use lines approximately <1.5 m wide that are serviced by helicopter (in very sensitive habitats or steep terrain) or lines 1–4.5 m wide that are serviced by specially made vehicles (Government of Alberta 2002).

**Other considerations**

A key question regarding this study is whether the immediate effects documented during one year of post-impact surveys are representative of the long-term impact of seismic lines. Several lines of evidence suggest that the study timeline likely revealed the greatest impacts and that these may be constant or decrease over time rather than increase. First, landscape-scale experimental studies of forest fragmentation have found time lag effects (e.g., Schmiegelow et al. 1997). These lag effects are initially evident as crowding of individuals into remaining habitat. The crowding effect disappears 2 years posttreatment, making fragmentation effects more evident. No crowding effects were observed during this study and no species, other than Ovenbird, were displaced by seismic lines. Here, Ovenbird abundance declined immediately rather than showing a delayed (crowding first) effect. One reason to expect a lag response is the presupposition that birds cannot make subtle adjustments to their territory (location or size) upon arrival on the breeding grounds. Since both adjustments were observed here, this supposition seems unwarranted. Also, where birds treated narrow linear features as edges (Rich et al. 1994), the au-
thors found no edge avoidance (prediction three), but rather simple displacement of birds, as posited in the second prediction in this paper.

A final consideration against increasing effects over time is the revegetation of seismic lines. In contrast to lines in Alberta (MacFarlane 2003; Lee and Boutin 2006), seismic lines in the study area have vigorous regeneration of woody species. By ~10 years after creation, the vegetation is dense enough to make it difficult to walk down lines in mesic habitats (xeric habitats are slower to recover) (C.S. Machtans, unpublished data). Off-road vehicle access, a key reason for failed regeneration in Alberta (Lee and Boutin 2006), is not possible along many seismic lines in the study area because of wet conditions. I found that seismic lines affected primarily the ground and shrub nesting bird community, and extensive local experience shows that shrub cover predominates on the old lines in the study area. Therefore, a reasonable expectation (to be tested) would be that the effects of seismic lines would decrease over time as revegetation occurred.

Will nest predation or nest parasitism increase in landscapes with seismic lines, thereby creating long-term effects? Again, several lines of evidence suggest that this is not likely, in contrast to the results of Rich et al. (1994). Studies in extensively forested landscapes have found no increases in nest predation due to either forestry (Bayne and Hobson 1997; Cotterill and Hannon 1999; Ibarzabal and Desrochers 2001; Schmiegelow and Mönkkönen 2002) or narrow roads (Ortega and Capen 2002). There is the possibility that seismic lines will increase the foraging efficiency of predators such as Gray Jays (Ibarzabal and Desrochers 2001). Regarding parasitism, no Brown-headed Cowbirds (Molothrus ater (Boddaert, 1783)) have been observed in the forest during general studies of birds in the Fort Liard area (Machtans and Latour 2003), though a few are regularly seen in the nearby community (C.S. Machtans, unpublished data). In the absence of any major changes in land cover that would allow nest predator communities to change or flourish, or allow Brown-headed Cowbirds to increase, increasing effects from nest parasitism or predation seem unlikely in the study area.

Conclusion

The creation of seismic lines did not have dramatic effects on the songbird community in this study. Other disturbances in the boreal forest such as permanent clearings (roads, pipelines, drilling pads, mining, agriculture, and housing) and forestry have demonstrably larger impacts due to the obvious elimination of suitable habitat: forest songbirds do not nest on gravel roads or in wheat fields. Songbirds, except Ovenbirds, showed a certain amount of plasticity by incorporating the seismic lines into their territories. The territories of shrub and ground nesting species that were directly over seismic lines were larger than territories in undisturbed forest. A likely, but untested, explanation for this is that birds perceive the territories with seismic lines as having poorer food resources and expand their territory area accordingly. Ovenbirds were displaced by 6 m wide seismic lines, showing decreased plot-wide abundance rather than crowding into remaining habitat. There was no difference in response between avoidance and linear lines 6 m wide, so further reduction of the impact of seismic lines on ground and shrub nesting birds, including Ovenbirds, likely requires lines narrower than 6 m.

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