

Articles

Transforming Abandoned Farm Fields to Conifer Plantations Reduces Ruffed Grouse Density

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Abstract

Natural forests likely will be unable to fulfill society's needs sustainably for wood fiber in the near future. In an attempt to meet increasing demands while protecting intact forests, producers have increasingly considered alternative sources of timber, such as intensively managed plantations. In regions that are economically dependent on forest harvesting, abandoned farm fields are often targeted for conversion to intensive coniferous plantations. These sites are generally in an early successional stage that is dominated by deciduous stands, which provide an important habitat type for several game species, including ruffed grouse (*Bonasa umbellus*). Therefore, conversion could represent a loss of habitat for this species and several others that are associated with early successional deciduous stages. We conducted grouse drumming surveys in northwestern Quebec, Canada to evaluate the effects of transforming old fields into conifer plantations on ruffed grouse by comparing densities between two habitat types: abandoned farm fields ($n = 22$) and old fields converted to conifer plantations ($n = 19$). To correct any audibility bias between habitat types, we located all drumming males that were heard at each site. We then analyzed the number of individuals that were detected in the sites with repeated count models. Our results show that overall drumming males avoided plantations. Overhead cover increased drumming male densities in both habitat types, whereas lateral cover increased drumming grouse densities only in plantations. The density of deciduous stems and fruit-bearing stems also had a tendency to increase drumming male densities, but their effects were marginal. Most ruffed grouse in abandoned farm fields used piles of woody debris on the ground as drumming structures rather than large logs or rock outcrops. Our results suggest that plantations do not have the vegetative cover and quantity of food stems necessary to support high ruffed grouse densities during the drumming season and that conversion of abandoned farm fields to coniferous plantations may exert negative cascading effects for reproduction and population growth.

Keywords: abandoned farm fields; *Bonasa umbellus*; drumming surveys; drumming structure; plantations; probability of detection

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Introduction

Ruffed grouse (*Bonasa umbellus*; hereafter grouse), one of the most popular small game birds in eastern North America (Bourret et al. 1991; Knoche and Lupi 2013), occurs mainly in second-growth deciduous and mixed forests (Rusch et al. 2000; Dessecker and McAuley 2001). These shrub-dominated and young forests are characterized by high stem densities. These habitats protect grouse from predators and support higher densities of grouse than in landscapes that are dominated by mature forests (Rusch et al. 2000; Dessecker and McAuley 2001). Dense deciduous stands are especially important for drumming males in the spring (Thompson et al. 1987), whereas young stands with high stem densities or older stands with a well-developed shrub understory are important for brood rearing in the summer (Haulton et al. 2003; Giroux et al. 2007). In northern regions such as in the province of Québec, many farm fields have been abandoned after rural depopulation (Vincent 1995; Hamel et al. 1999; Gachet et al. 2007). These abandoned farm fields have been recolonized by vegetation and have reverted to a shrub-dominated habitat that is thought to be beneficial for grouse (Dessecker and McAuley 2001).

Former agricultural fields are the type of land most frequently converted into high-yield, often monospecific, tree plantations. These lands offer many advantages for wood production: they are generally productive, close to road networks and sawmills, and allow the landowners to benefit financially from otherwise unprofitable fields (Sedjo 1999; Felton et al. 2010). Using abandoned farm fields also has the advantage of being more ecologically and socially acceptable than transforming natural forests into plantations (Seymour and Hunter 1999; Pawson et al. 2013). Plantations that are established on abandoned farm fields could be included in a forest management plan based on a zoning approach under which land is allocated into extensively managed, intensively managed, and conservation zones. In such a framework, gains made from high-yield plantations could relieve the industrial pressure that is placed on natural ecosystems and allow the protection of the last remaining intact forests (Hunter and Calhoun 1995; Potapov et al. 2008). This is particularly true in countries such as Canada, where primary forests are still actively logged (Mackey et al. 2014).

Although plantations offer many benefits, they are often viewed unfavorably both by the public and by biologists with respect to wildlife conservation (Hartley 2002; Hartmann et al. 2010). This perception is partly supported by the available scientific literature. For instance, the avifauna in plantations is frequently reported as being less diverse than in natural forests

and seminatural forests (Gjerde and Saetersdal 1997; Moore and Allen 1999). Negative effects have also been shown for other less-studied taxa, such as amphibians (Waldick et al. 1999), small mammals (Moore and Allen 1999), and arthropods (Magura et al. 2000). Grouse use conifers for roosting or thermal protection during winter (Blanchette et al. 2007), but otherwise avoid pure conifer stands (Rusch et al. 2000; Endrulat et al. 2005). In contrast to plantations, early successional forests or shrub-dominated habitats, like those found on abandoned farm fields, are important for many game species and their predators (Dessecker and McAuley 2001; Litvaitis 2001; Fuller and DeStefano 2003).

In this study, we evaluated the effects of converting abandoned farm fields to conifer plantations on grouse density. Specifically, we quantified differences between the two types of habitat, as the value of the abandoned farm fields had never been estimated for grouse in the region. Grouse use conifer stands for roosting during winter (Thompson and Fritzell 1988; Blanchette et al. 2007), but will generally avoid pure conifer stands during the drumming season because they provide hunting perches and nesting areas for predators (Gullion and Alm 1983). Consequently, we hypothesized that the transformation of old fields with a deciduous and heterogeneous shrub layer into a homogenous habitat dominated by conifer plantations would reduce grouse habitat quality and lead to lower population densities in these habitat types.

Materials and Methods

Study area and sampling design

The study was conducted in the Abitibi Administrative Region of northwestern Quebec, Canada. Deciduous stands are generally uncommon in the Abitibi region and grouse are more closely associated with mixed stands (Dussault et al. 1998). A notable exception is the agricultural part of the region, which is composed mainly of second-growth forests that are dominated by trembling aspen (*Populus tremuloides*) because of overexploitation and repeated uncontrolled slash fires during the colonization of the region in the 1940s (Vincent 1995). These aspen forests are sometimes interspersed with abandoned fields that are dominated by shrub vegetation. Both of these vegetation types are beneficial for grouse (Rusch et al. 2000; Dessecker and McAuley 2001; Zimmerman et al. 2009). However, in the early 1980s, the provincial government started promoting the transformation of abandoned farm fields to plantations by creating a program of subsidies (Hamel et al. 1999; Gachet et al. 2007). After the creation of those programs, many old fields were planted back into conifer plantations in regions that are economically dependent upon resource

exploitation. Although many old fields have already been converted to plantations in Québec, about 100,000 ha of abandoned farm fields are still present in Abitibi Administrative Region. As a result, this region offered an opportunity to study the effects of old farm field conversion to plantations on grouse.

The study area is located at the southern limit of the boreal forest. Regional climate is continental with a mean annual temperature of 0.6°C. Annual precipitation is 823 mm, of which 639 mm falls as rain from April to November. The mean frost-free period is 64 d (Environment Canada 1982). Vegetation is characterized by mixed wood dominated by balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and paper birch (*Betula papyrifera*), with white spruce (*Picea glauca*) and trembling aspen as codominants (Brandt 2009). We conducted the study in the agroforested landscape of Abitibi, where human disturbances (agriculture and logging) have altered the original forest cover. Here, the landscape mainly consisted of agricultural fields, early successional habitats, and second-growth forest tracts that originated from overexploitation and burning in the 1940s (Vincent 1995).

The two types of habitats were old fields that had been abandoned ($n = 22$; hereafter abandoned fields) and old fields that had been planted with conifers ($n = 19$; hereafter plantation fields). All study sites had to have at least one side in contact with a forested edge. Plantations consisted of jack pine (*Pinus banksiana*; $n = 14$) or white spruce ($n = 5$). Sites varied between 6.73 and 42.88 ha (mean = 15.34; SD = 6.89). We selected the sites from a set of potential survey locations that had been identified during the previous years, with the constraint of also maximizing the spatial distribution in the survey region (Figure 1). However, because of the constraints imposed by auditory surveys we also tried to minimize travel distance by pairing plantation fields with an abandoned field whenever it was possible. Each site was separated by ≥ 1 km from the nearest neighboring site, to maintain statistical independence.

We wanted to investigate the effect of different stages of vegetation development in both abandoned fields and plantation fields. However, it was impossible to include age as a stratification variable for abandoned fields, because their colonization by grasses (i.e., Gramineae) induced patterns of succession by woody vegetation that were inconsistent over time. A similar issue occurred for plantation fields, as growth varied greatly among species and soil types. Instead of directly incorporating age, we developed an index that was based on development of the woody vegetation to represent the evolution of abandoned fields through time. We defined the three stages of abandoned fields as follows: stage 1 of abandoned fields ($n = 8$) had between 25% and 50% of the ground covered by woody vegetation (herbaceous-dominated abandoned farm fields); stage 2 ($n = 8$) had $> 50\%$ of the ground covered by woody vegetation (shrub-dominated abandoned farm fields); and stage 3 ($n = 5$) had young shade-intolerant trees that had established on most ($> 50\%$) of the area (young forest-dominated abandoned farm

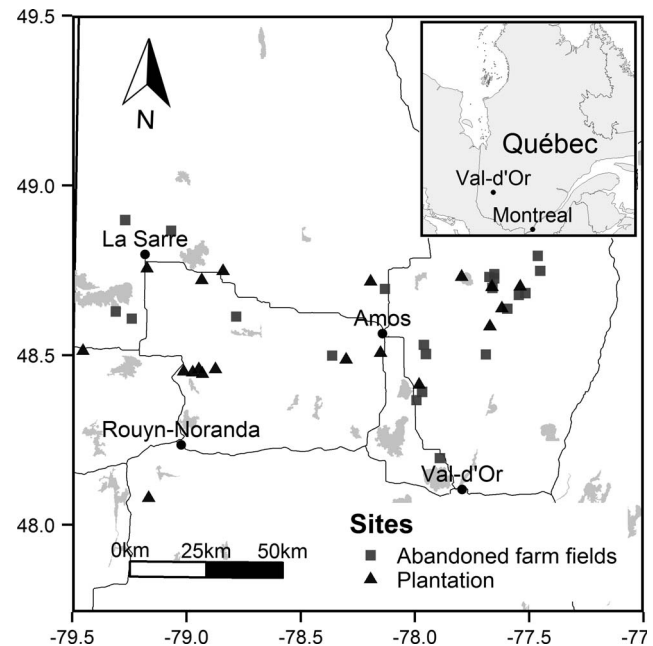


Figure 1. Study area with the locations of the sampling sites of drumming ruffed grouse (*Bonasa umbellus*) in Abitibi, Québec, Canada during the spring breeding season of 2006. Gray squares represent abandoned farm fields, dark triangle represent coniferous plantations, and black lines represent the major roads in the study area.

fields). In plantation fields, stage 1 ($n = 4$) had trees that were 1 to 3 m high, stage 2 ($n = 7$) consisted of trees 3–7 m high, and stage 3 ($n = 8$) was composed of trees > 7 m high.

Vegetation inventories

Seven permanent sampling stations were established along a transect that was situated in the middle of each site, perpendicular to the forested edge. The first station was placed 10 m from the edge and subsequent stations were spaced 10 m apart. Each station was identified with a permanent marker. We counted all available tree and shrub stems (> 0.3 m from the ground) present in a 1-m plot around each station. Lateral cover was estimated visually by estimating the percentage of obstruction for each 0.5-m section of a 30 cm \times 2 m profile board placed at 15 m on each side of the station (Nudds 1977). The overhead canopy closure of trees (> 4 m high) and shrubs (1.5–4 m) was evaluated visually at five interception points (3-m spacing) on each side of the station (Bertrand and Potvin 2003). Vegetation measurements were made once at each site either in 2004 or 2005, when we established the stations for a companion study on hare habitat use (Roy et al. 2010). We also measured vegetation cover outside the sites by extending the transect 10 and 20 m into the neighboring forested edge.

Grouse surveys

During the spring mating season, male grouse use a breeding and territorial display that is called drumming, by beating their wings back and forth in rapid

succession while standing on a display structure (Rusch et al. 2000; Garcia et al. 2012). Males are faithful to their drumming site and the habitat surrounding these sites is important to the grouse throughout the year and for most life-history stages (Gullion 1984). Females also spend part of their lifetime in these habitats and the sex ratio is 1:1 for the species during the breeding season (Rusch and Keith 1971a). Because males are faithful to their drumming sites and because their drumming displays are easily detected, drumming surveys are often used to survey grouse populations (Dussault et al. 1998; Zimmerman and Gutiérrez 2007). For this study, we conducted a drumming survey at each site between April 25 and May 15 of 2006. Temperatures averaged 4.5°C (SD = 7.9°C) during this survey period.

A previous study in the region determined that the audibility range for grouse was generally < 100 m (Dussault et al. 1998). Because we wanted to evaluate the use of abandoned fields and plantation fields, we placed a listening station 150 m from the closest forested edge in each site. We began surveys once snow had melted and birds had started drumming (Dussault et al. 1995). Each survey was conducted by two observers during a period between 30 min before dawn and 6 h after dawn. Observers listened for 5 min, noting each bird that they heard (Dussault et al. 1998), together with the azimuth of the drumming individual. Observations were recorded only if both observers heard the drumming bird and if they agreed upon its general direction. Observers were screened before the survey to ensure they could detect grouse drumming at long distances (≥ 100 m). We tallied the number of individuals that were detected at a station at the end of each survey. Date, time of day, and air temperature were also recorded. No surveys were conducted if wind speed exceeded 3 on the Beaufort scale (i.e., > 12 km/h) or during rainy days (Gullion 1989; Hansen et al. 2011a). The order in which the surveys were conducted was constrained by travel distance, and sites close to each other were surveyed on the same day as much as possible. We repeated surveys twice at each site during the breeding season and alternated the time of day of the surveys within each site. We also alternated the surveys between plantation fields and abandoned fields to avoid any potential bias in detection probability through time (Data S1, *Supplemental Material*).

A preliminary study during 2005 indicated that the audibility range in plantation fields was greater than expected because we had regularly detected grouse that used drumming structures in adjacent forested stands (Roy 2008). We checked the origin of the drumming male immediately after each drumming survey in 2006. To do so, an observer walked until he encountered either the drumming male or a drumming structure with obvious signs of utilization (i.e., fecal droppings). If the observer reached the edge of the site and the drumming male could still be heard in the adjacent forest, we assumed that the bird was not associated with the study site. In such cases, individuals were not used in the following analyses that specifically compared habitat use of plantation fields and abandoned fields. Once a used drumming structure was found, it was classified into one

of four classes: pile of debris on the ground; rock outcrop; small fallen tree < 10 cm in diameter; or large fallen tree > 10 cm (Data S2, *Supplemental Material*).

Statistical analyses

Vegetation cover. We calculated average lateral and overhead cover for each site. For overhead cover, we summed the canopy closure of trees and shrubs into a single index. We compared vegetation cover metrics between groups of treatments and vegetation stage using beta regression (Ferrari and Cribari-Neto 2004). In beta regression, the response variable (a proportion) is assumed to follow a beta distribution over the interval (0, 1) and the interpretation of the results is similar to that of a logistic regression (Ferrari and Cribari-Neto 2004). The distribution has a highly flexible shape and can be defined by two parameters: the mean (μ) and the overdispersion parameter (Φ), such that:

$$\text{Lateral cover}_i \sim \text{Beta}(\mu_i \phi, \phi[1 - \mu_i]) \quad (1)$$

$$\text{logit}(\mu_i) = \beta_{\text{Type}_i} + \beta_{\text{Stage}_i} + \beta_{\text{Type}_i, \text{Stage}_i} \quad (2)$$

$$\phi \sim \text{Gamma}(a, b) \quad (3)$$

where β_{Type} is the block level effect for the habitat type, β_{Stage} is the block effect for the stage of vegetation and $\beta_{\text{Type, Stage}}$ is the interaction term between the two classes. Contrast between the block levels, habitat type, and interactions were derived directly within the model (Kéry 2010; Kruschke 2010). We estimated the parameters of the beta regressions using a Bayesian framework that was implemented in JAGS (Text S1, *Supplemental Material*; Plummer 2003) from R using the R2jags package (Yu-Sung and Yajima 2012; R Core Team 2013). We used normal priors with a mean of zero and a standard deviation of 100 for the β parameters, whereas we used a Gamma distribution with a shape and rate of 0.01 for the overdispersion parameter. We ran six Markov chain Monte Carlo chains with randomized starting values. After a burn-in of 5,000 samples, we saved every 20th iteration of 20,000 samples from the posterior distribution to reduce correlations. We assessed model convergence using the R-hat diagnostic (Gelman et al. 2013).

Food stem abundance. We combined possible food items into two categories. Stems from alder (*Alnus* sp.), aspen (*Populus* sp.), and willows (*Salix* sp.) were grouped together, as the buds and catkins of these deciduous plants can be consumed by the grouse during winter and the spring (Svoboda and Gullion 1972; Doerr et al. 1974). The stems from dogwood (*Cornus* sp.), rose (*Rosa* sp.), northern bush honeysuckle (*Diervilla lonicera*), and *Ribes* sp. were grouped together since these plants bear soft fruits that are consumed by grouse during late summer and fall (Stafford and Dimmick 1979; Burger 1987; Rusch et al. 2000). We discarded stems from coniferous species as they are generally not consumed by grouse. We pooled the stems counted in our seven vegetation plots in each site and compared the

abundance of each stem class between groups of treatments and vegetation stages using a Poisson regression.

$$\text{Deciduous stems}_i \sim \text{Poisson}(\lambda_i) \quad (3)$$

$$\log(\lambda_i) = \beta_{\text{Type}_i} + \beta_{\text{Stage}_i} + \beta_{\text{Type}_i, \text{Stage}_i} + \varepsilon_i \quad (4)$$

$$\varepsilon_i \sim \text{Normal}(0, \sigma) \quad (5)$$

where β_{Type} is the block level effect for the habitat type, β_{Stage} is the block effect for the stage of vegetation, and $\beta_{\text{TypeStage}}$ is the interaction term between the two classes. Both data sets were overdispersed and we included an overdispersion parameter, ε_i , in the analysis. Contrasts between the habitat type, vegetation stage, and interaction were derived directly within the model. We fitted the models to data in a Bayesian framework (Text S2, *Supplemental Material*). We used normal priors with a mean of zero and half-Cauchy priors for the standard deviation (Gelman 2006). We ran six chains of 20,000 iterations following a burn-in of 5,000 iterations. We saved every 20th iteration from the posterior distribution and assessed model convergence using the R-hat diagnostic.

Grouse density. Imperfect detectability is a component of animal sampling and not accounting for this problem in wildlife studies can lead to spurious conclusions (Anderson 2001; Mazerolle et al. 2007). Thus, we analyzed the numbers of individuals that were detected in the survey sites with repeated count models, which enable the estimation of abundance in the presence of imperfect detection probability (Royle 2004). The model assumes demographic closure (i.e., no birth, death, emigration, or immigration) during the sampling period. Given the short period of the survey and our encounter history (see Results section), we are confident that we met this assumption during the survey.

As above, we fit the repeated count models to data in a Bayesian framework (Text S3, *Supplemental Material*). We conducted Bayesian model selection using the Kuo and Mallick (1998) indicator variable, as described by Royle and Dorazio (2008). Specifically, all variables are multiplied by an indicator term that uses a Bernoulli prior distribution. A variable is included in the model when the indicator is equal to one and it is excluded from the model when the indicator equals zero (Royle and Dorazio 2008). The proportion of iterations in which a particular variable is selected can be monitored and used to provide an estimate of the Bayes factor (i.e., the odds ratio) that the variable will be included in the model (Smith et al. 2011; Converse et al. 2013). We identified the most important variable by calculating the odds ratio of a variable or of an interaction being included in the models by using the prior mean assigned to each variable and the posterior mean estimated by the model. Jeffreys (1961) suggested interpreting the weight of evidence in favor of a model as negative (Bayes factor < 1), marginal (1 < Bayes factor < 3.16), substantial (3.16 < Bayes factor < 10), strong (10 < Bayes factor < 31.62),

very strong (31.62 < Bayes factor < 100), or decisive (Bayes factor > 100). To avoid influencing model selection, we selected the prior parameters for these Bernoulli variables to produce equal prior probabilities for each of the possible models (Smith et al. 2011).

We considered the effects of temperature and Julian day (Gullion 1966; Zimmerman and Gutiérrez 2007), together with their quadratic terms, as explanatory variables on the probability of detection (p). To model grouse abundance (λ), we included the effect of habitat types, lateral and overhead cover (Rusch et al. 2000), the mean density of soft fruit stems and deciduous stems present at the sites, and the quadratic effect of lateral and overhead cover. To account for the possibility that the effects of lateral cover, overhead cover, soft fruit stem density, and deciduous stem density would change between habitat type we included an interaction term between each of these explanatory variables and habitat type. However, to avoid needlessly complicated interaction terms (Guthery 2008) and to avoid overfitting, we imposed constraints on the variable indicators included in the model to limit the number of interactions to one in any given model (see Text S4, *Supplemental Material*). We included the size of the site as an offset on abundance, to express the counts as densities (Kéry 2010). The general model was defined as:

$$Y_{i,j} \sim \text{Binomial}(p_{i,j}, N_i) \quad (6)$$

$$\text{logit}(p_{i,j}) = \alpha_0 + \sum_k \gamma_k \alpha_k Z_{i,j} \quad (7)$$

$$N_i \sim \text{Poisson}(\lambda_i) \quad (8)$$

$$\log(\lambda_i) = \beta_0 + \sum_j \omega_j \beta_j X_{j,i} + \log(\text{Area}_i) \quad (9)$$

where Y_{ij} is the number of grouse observed in site i during visit j , N_i is the true abundance of grouse in site i , ω and γ are the respective indicator variables for the abundance and detection components, β and α are estimates of the respective predictors for the abundance and detection, and X and Z are the respective explanatory variables for the abundance and detection models. The explanatory variables were standardized to zero mean and unit variance before analysis to ease the interpretation and convergence of the models (Kéry 2010).

We gave each of the α and β parameters a mean zero normal prior, and we scaled the variance prior distributions as a function of the numbers of parameters entering the model, as recommended by Link and Barker (2009). We used independent priors for abundance and the detection variance parameter. We also avoided putting the interactions terms under the same prior distribution as the individual component coefficient as they are conceptually a different class of variables (Kruschke 2010). For the detection component of the model, we used a Gamma prior with a shape of 3.29 and a rate of 7.8 for the precision parameter. This prior results in a marginal distribution that is approximately uniform

on the logit scale (Link and Barker 2009). For the abundance component of the model, we used a half-Cauchy prior for the standard deviation, as suggested by Gelman (2006). For the repeated count model, we ran six chains with randomized initial values for 340,000 iterations, with the first 5,000 iterations used as a burn-in and saved every 20th iteration. We assessed model convergence using the R-hat diagnostic and we used the sums of the squared Pearson residuals to assess the model fit via posterior predictive checks (Kéry 2010). We subsequently calculated Bayes factors to assess the relative support for each variable (Smith et al. 2011) and we used Jeffreys Bayes factor classification to assess the strength of evidence for the inclusion of each variable in the model. We also derived the regression coefficient for parameters with a Bayes factor > 1 . The estimates of the regression parameters were conditional on their inclusion in the model and we also avoided averaging across interactions and polynomial terms.

Drumming structure survey. We analyzed the frequency of each type of drumming structure across vegetation stage with a log-linear model for contingency tables (Text S5, *Supplemental Material*; Kruschke 2010). We used normal priors with a mean of zero and half-Cauchy priors for the standard deviation (Gelman 2006). We ran six chains of 20,000 iterations following a burn-in of 5,000 iterations. We saved every 20th iteration from the posterior distribution and assessed model convergence using the R-hat diagnostic.

Results

Vegetation cover changes and food stem abundance

The effect of vegetation stage on lateral cover varied across habitat types. Specifically, lateral cover gradually increased between stages 1 and 2, and between stages 1 and 3 for abandoned fields ($\hat{\beta}_{1,2} = 0.606$, 90% Bayesian credible interval [BCI] [0.005, 1.184]; $\hat{\beta}_{1,3} = 0.847$, 90% BCI [0.101, 1.59]). Lateral cover in plantation fields increased between stages 1 and 2 ($\hat{\beta}_{1,2} = 1.034$, 0.90% BCI [0.234, 1.91]), but remained similar between stages 1 and 3 ($\hat{\beta}_{1,3} = 0.099$, 90% BCI [-0.634, 0.837]). Overhead cover increased with vegetation stage in both abandoned fields and plantation fields ($\hat{\beta}_{1,2} = 0.899$, 90% BCI [0.389, 1.384]; $\hat{\beta}_{1,3} = 1.954$, 90% BCI [1.464, 2.445]), but overhead cover was less developed in plantation fields than in abandoned fields ($\hat{\beta}_{\text{Type}} = -0.826$, 90% BCI [-1.203, -0.448]). Forest stands adjacent to the survey sites were generally dominated by aspen (36 sites of 41). Most of these stands were deciduous ($n = 23$) or mixed deciduous ($n = 16$), whereas only two stands were coniferous. Consequently, adjacent forest stands had a low overhead canopy closure (mean \pm SD = 63% \pm 28%) compared with the survey sites. Understory vegetation in the adjacent forest stands was also sparse, which resulted in a lower lateral cover (mean \pm SD = 67% \pm 14%) compared with the survey sites. Deciduous stem abundance was significantly lower in plantations than in abandoned fields ($\hat{\beta}_{\text{Type}} = -2.231$, 90% BCI [-3.135, -1.334]), but remained similar between stages 1 and 2 ($\hat{\beta}_{1,2} = 0.440$, 90% BCI [-0.727, 1.522]) and

stages 1 and 3 ($\hat{\beta}_{1,3} = 1.023$, 90% BCI [-0.104, 2.16]). Soft fruit stem abundance was not influenced by the habitat type ($\hat{\beta}_{\text{Type}} = -1.083$, 90% BCI [-2.707, 0.44]) or the vegetation stage ($\hat{\beta}_{1,2} = -0.178$, 90% BCI [-2.043, 1.888]; $\hat{\beta}_{1,3} = 1.392$, 90% BCI [-0.647, 3.327]).

Grouse density

We conducted surveys between April 25 and May 15 of 2006 and surveyed on average 4.21 sites per day (SD = 1.13). On average 10 d (SD = 3.24) elapsed between the surveys within each site. Overall, we detected a total of 55 drumming males (mean = 1.08 drumming males per visit; SD = 1.45), 44 grouse in abandoned fields, and 14 grouse in plantation fields during the auditory surveys. The majority (72.7%; $n = 32$) of grouse that were detected in abandoned fields occupied the site, whereas few (14.3%; $n = 2$) of the grouse that were heard in plantation fields were actually on the site. All the other grouse were in the adjacent forest stands.

The posterior predictive check for the global model did not indicate a lack of fit (Bayesian P -value = 0.482) and the mixing of chains was adequate for all parameters (all R-hat values = 1.1). Of all the variables considered, only the interaction between habitat type and the quadratic effect of lateral cover was strongly supported (Bayes factor > 10 ; Table 1). Grouse density was lower in plantation fields than in abandoned fields and grouse density increased with lateral cover until it reached an optimum at about 65%, but subsequently declined in plantation fields (Table 2; Figure 2). However, there was no discernible effect of lateral cover on grouse densities in abandoned farm fields. The effect of overhead cover, the density of deciduous stems, and the density of soft fruit stems also garnered some weak support ($1 < \text{Bayes factor} < 3.2$; Table 1). Following multimodel inference, grouse density increased with overhead cover, the density of deciduous stems, and the density of soft fruit stems (Table 2; Figure 2); however, the effects of both classes of stems were marginal and included zero in the 90% BCI (Table 2). For the detection models, the effect of Julian day and temperature garnered weak support ($1 < \text{Bayes factor} < 3$; Table 1), whereas the quadratic expressions of each variable were rejected (Bayes factor < 1 ; Table 1). Model-averaged predictions for Julian day and air temperature suggested a weak negative effect on detection, but both parameters included zero in the 90% BCI (Table 2).

Drumming structure use

We identified 34 distinct drumming structures during our surveys, of which only two were found in plantation fields. Most drumming structures consisted of small piles of debris on the ground ($n = 19$), followed by small fallen trees (< 10 cm; $n = 9$), large fallen trees (> 10 cm; $n = 4$), and rock outcrops ($n = 2$). Because there were only two grouse detected in plantations, we restricted our contingency analysis to abandoned fields. Grouse tended to use stage 1 abandoned fields less than average ($\hat{\beta} = -0.393$, 90% BCI [-0.999, 0.017]; Figure 3), but the effects were not significant at the 90% level. Grouse used piles of debris on the ground more often

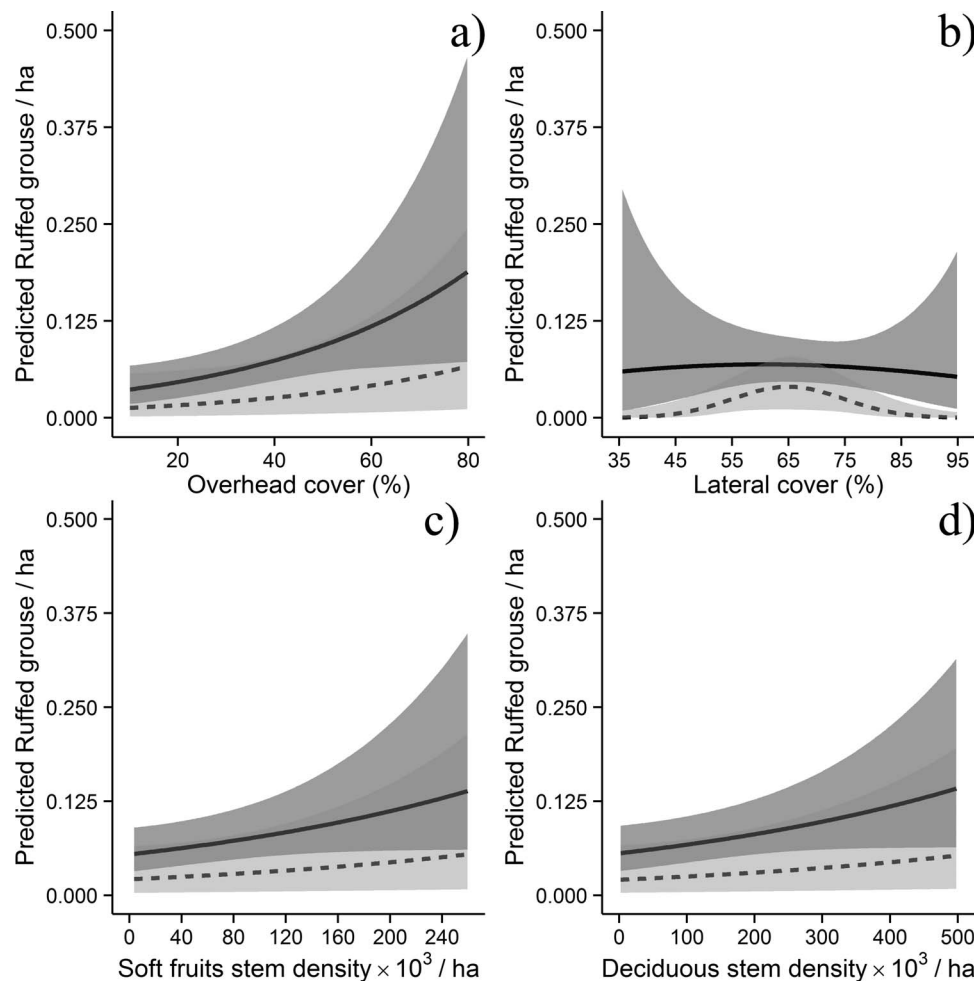


Figure 2. Predicted density of drumming ruffed grouse (*Bonasa umbellus*) in abandoned farm fields (solid line; dark gray) and plantations (dotted line; light gray) sampled in 2006 in Abitibi, Québec, Canada according to model-averaged predictions as a function of lateral cover (a) and vertical cover (b). Predicted detection probabilities according to model-averaged predictions are shown as a function of Julian day (c) and temperature (d) during the spring breeding season of 2006. For all panels, the solid or dotted line represents the mean and the shaded area represents the 90% Bayesian credible intervals (BCI).

than average ($\hat{\beta} = 1.094$, 90% BCI [0.517, 1.679]), but tended to use less often both large fallen logs ($\hat{\beta} = -0.707$, 90% BCI [-1.515, -0.051]) and rock outcrops ($\hat{\beta} = -0.713$, 90% BCI [-1.534, -0.061]). There were no significant interactions between the type of drumming structure and the abandoned field vegetation stage

Discussion

Grouse habitat use

Abandoned fields represent attractive habitat for drumming grouse if the overhead cover is sufficiently developed. Abandoned farmlands at stage 1 had low grouse counts, most likely because of the absence of overstory vegetation, whereas abandoned fields stages 2 and 3 had high grouse counts because of their well-developed overhead cover (Rusch and Keith 1971a; Dussault et al. 1998; Rusch et al. 2000). The predicted grouse densities in abandoned fields stage 2 (mean \pm SD: 0.110 ± 0.095 male/ha) and stage 3 (mean \pm SD: 0.230 ± 0.164 male/ha) are comparable with the 0.08 male/ha

reported by Rusch et al. (2000) for good grouse habitat. Observational studies suggest that during the drumming season, grouse choose a drumming habitat with well-developed overhead cover, which increases protection from avian predators, and a less developed lateral cover for facilitating the detection of ground predators (Rusch and Keith 1971b; Hale et al. 1982; Hansen et al. 2011b).

The abundance of both types of food stems also tended to increase grouse densities and the effects of stem types were comparable in magnitude. However, their effect was not as marked as the effect of overhead cover. Not surprisingly, deciduous stems were more abundant in abandoned fields than in plantations, which explains in part why grouse were more abundant in abandoned farm fields. The distribution of stems bearing soft fruits could not be explained, however, by the type of habitat or the stage of vegetation and was apparently random in our study. This is likely explained by the colonization of the sites by grasses since their presence precluded the establishment of shrubs and herbaceous species that typically bear fruits.

Table 1. Model selection results for the explanatory variable used in estimating density and detection probability of ruffed grouse (*Bonasa umbellus*) during drumming surveys conducted in abandoned farm fields and plantations in Abitibi, Québec, Canada during the spring breeding season of 2006. The posterior inclusion probability is the probability that the variable or the interaction between the variables should be included in the model, and the Bayes factor is the posterior odds ratio in favor of the set of models including the variable vs. the set of models not including the variable.

Variable	Posterior inclusion probability	Bayes factor
Density		
Type	0.424	0.735
Lateral cover	0.150	0.177
Overhead cover	0.751	3.019
Type × lateral cover	0.190	0.234
Type × overhead cover	0.495	0.979
Lateral cover + lateral cover ²	0.477	0.914
Overhead cover + overhead cover ²	0.467	0.875
Type × lateral cover + type × lateral cover ²	0.916	10.885
Type × overhead cover + type × overhead cover ²	0.448	0.811
Soft fruit stems	0.590	1.436
Deciduous stems	0.568	1.313
Type × soft fruit stems	0.434	0.768
Type × deciduous stems	0.352	0.543
Detection		
Julian day	0.549	1.216
Temperature	0.604	1.527
Julian day + Julian day ²	0.331	0.494
Temperature + temperature ²	0.382	0.618

Most of the structures that were used by grouse in abandoned fields consisted of small piles of debris on the ground. These results oppose most of the literature published on grouse drumming structures, where large logs are usually preferred (Gullion 1967; Zimmerman and Gutiérrez 2008; Hansen et al. 2011b). This discrepancy could reflect the availability of such structures rather than active selection. Indeed, our sites were former agricultural fields and offered few large fallen logs and

rock outcrops. However, our results show that the quantity of drumming structures does not appear to limit drumming grouse male distribution.

In contrast, only two plantation fields were used for drumming and, in both cases, the drumming structure was a large fallen log on the edge of the plantation (< 12 m). Such a low level of use suggests that grouse avoid plantation fields during the drumming season. This is consistent with previous studies where grouse avoid pure

Table 2. Model-averaged parameter estimates for the most likely variables explaining the density and detection of ruffed grouse (*Bonasa umbellus*) during drumming surveys conducted in abandoned farm fields and plantations in Abitibi, Québec, Canada during the spring breeding season of 2006. The *F* statistic represents the proportion of the posterior distribution that is the same direction of the mean effect.

Variable	Mean	90% Credible interval	<i>F</i>	
Density		Lower	Upper	
Type	0.268	−0.120	0.964	0.818
Lateral cover	−0.013	−0.414	0.362	0.511
Lateral cover ²	−0.794	−1.685	−0.119	0.985
Type × lateral cover	−0.02	−0.555	0.482	0.517
Type × lateral cover ²	0.727	0.074	1.584	0.979
Overhead cover	0.475	0.075	0.851	0.984
Soft fruit stems	0.281	−0.006	0.620	0.932
Deciduous stems	0.219	0.000	0.456	0.941
Detection				
Julian day	−0.386	−0.918	0.116	0.896
Temperature	−0.502	−1.166	0.228	0.885

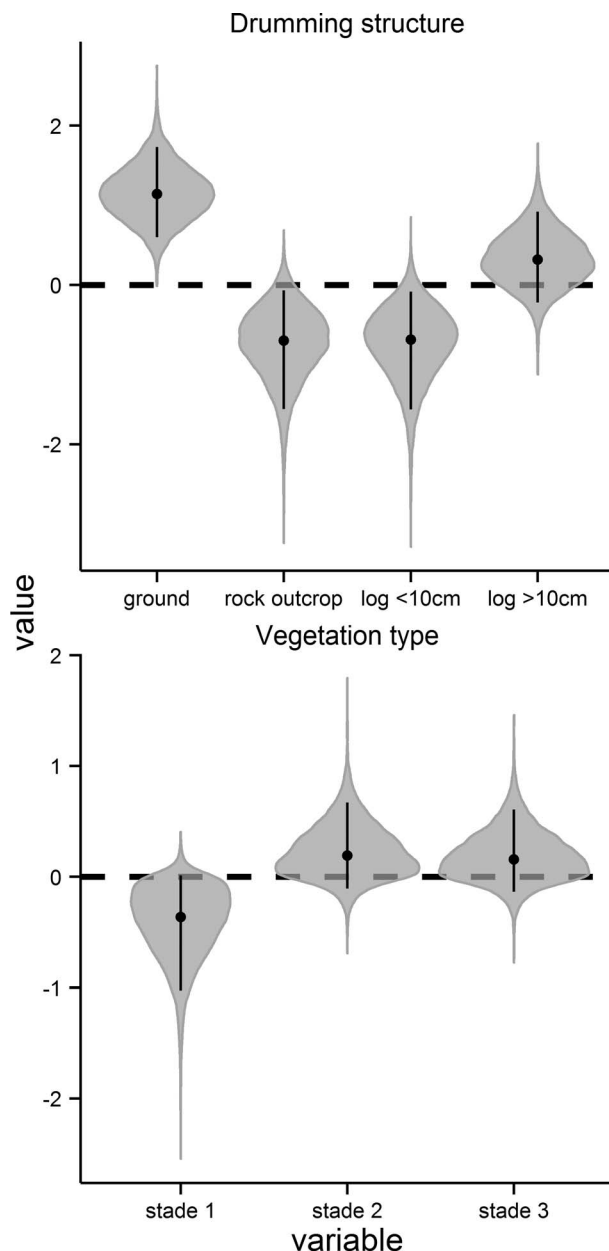


Figure 3. Estimated coefficients (on log scale) for the effect of drumming structure and vegetation stage on the drumming structures used by ruffed grouse (*Bonasa umbellus*) in abandoned farm fields in Abitibi, Québec, Canada during the spring breeding season of 2006. The dots represent the mean effect, the bars are the 90% Bayesian credible intervals (BCI), and the gray areas represent the full posterior distribution.

conifer stands during the drumming season (Rusch and Keith 1971a; Gullion and Alm 1983; Thompson and Fritzell 1989). Previous studies on conifer plantations in Michigan and in Minnesota also reported lower grouse abundance in coniferous plantations compared with aspen forest (Gysel 1966; Gullion 1984; Kouffeld et al. 2013). However, Gullion (1990) hypothesized that grouse could use plantations and attain relatively high densities if aspen were dispersed in small stands on about 10% of the plantations, because it would increase both food and

cover. Unfortunately, the term “plantation” is broad and without a universal definition (Hartley 2002), and can mean anything from replanting commercially harvested natural forests after harvesting (i.e., reforestation) to establishing regularly spaced monocultures on land that had not been occupied by forest (i.e., afforestation). The sites in our study had been cleared for agriculture 60–85 y ago. Thus, our study relates to the results of afforestation on grouse density, whereas previous studies have been more concerned with the effect of reforestation. The avoidance of coniferous plantations by grouse in our study can be explained in part by the low vegetative cover and the low quantity of deciduous food. Given that plantations are mechanically tended to control the growth of understory vegetation at later stages, which reduces lateral cover and the abundance of deciduous food stems, these sites are unlikely to support high grouse densities. Although yearly variation undoubtedly plays a role in grouse density, it is doubtful that the 16:1 grouse ratio in favor of abandoned fields would change drastically in the short term as a function of years. In essence, the conversion of abandoned fields into plantation fields is the conversion of a prime drumming habitat into a habitat that is avoided.

Conclusions

Previous studies have demonstrated a limited effect of afforestation on understory vegetation and snowshoe hare habitat use in Abitibi (Gachet et al. 2007; Roy et al. 2010). However, our study suggests that transforming abandoned farm fields into plantations will reduce grouse density. Monitoring the effects of intensive silviculture is often species specific, and it is important to monitor the scale and the speed at which these conversions are undertaken (Hartley 2002). For the grouse, planning at the landscape scale would be important for minimizing the negative effect of abandoned farm field conversion to plantations (Hartley 2002), especially since decision makers have bolstered investments in intensive plantations (Coulombe et al. 2004). Improving the quality of the aspen stands that are present in the agricultural landscape could also alleviate some of the negative impacts, as would interspersing some aspen stands between the plantations to maintain some protective cover for the grouse (Gullion 1990). However, even if such conversions increase the protection of remaining intact forests, a local decline in grouse populations could be negatively perceived by hunters and conservationists. Indeed, grouse hunting is popular in the region and is often done on private lands rather than in remote intact forests, where ecological services such as hunting are not accessible for human use (Cimon-Morin et al. 2014).

Supplemental Material

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Text S1. JAGS Code for the Analysis of Vegetation Cover in Abandoned Farm Fields and Plantations Sampled for Drumming Ruffed Grouse (*Bonasa umbellus*) During the 2006 Spring Breeding Season in Abitibi, Québec, Canada. (1 KB TXT).

Found at DOI: <http://dx.doi.org/10.3996/022015-JFWM-021.S1>.

Text S2. JAGS Code for the Analysis of Available Food Stems in Abandoned Farm Fields and Plantations Sampled for Drumming Ruffed Grouse (*Bonasa umbellus*) During the 2006 Spring Breeding Season in Abitibi, Québec, Canada.

Found at DOI: <http://dx.doi.org/10.3996/022015-JFWM-021.S2> (2 KB TXT).

Text S3. JAGS Code for the Repeated Count Analysis of Drumming Ruffed Grouse (*Bonasa umbellus*) Sampled in Abandoned Farm Fields and Plantations During the 2006 Spring Breeding Season in Abitibi, Québec, Canada.

Found at DOI: <http://dx.doi.org/10.3996/022015-JFWM-021.S3> (22 KB TXT).

Text S4. Appendix—Calculating Prior Probabilities for the Inclusion Parameters.

Found at DOI: <http://dx.doi.org/10.3996/022015-JFWM-021.S4> (1 KB TXT).

Text S5. JAGS Code for the Analysis of Drumming Structure Used by Ruffed Grouse (*Bonasa umbellus*) in Abandoned Farm Fields During the 2006 Spring Breeding Season in Abitibi, Québec, Canada.

Found at DOI: <http://dx.doi.org/10.3996/022015-JFWM-021.S5> (1 KB TXT).

Data S1. Vegetation variables and grouse counts associated with each site. Variable are site identification, habitat type, vegetation stage, area (ha) of the sampling site, lateral cover, overhead cover, deciduous stem abundance, soft fruit stem abundance, total number of grouse heard during the first visit, total number of grouse heard during the second visit, number of grouse in the site during the first visit, number of grouse during the second visit, Julian day for the first visit, temperature (°C) during the first visit, Julian day for the second visit, temperature (°C) during the second visit.

Found at DOI: <http://dx.doi.org/10.3996/022015-JFWM-021.S6> (2 KB TXT)

Data S2. Drumming structure used by grouse in each site. Variable are site identification, habitat type, vegetation stage, number of grouse using small logs as a drumming structure, number of grouse using rock outcrops as a drumming structure, number of grouse drumming directly on the ground or on a pile of debris, number of grouse using a large log as a drumming structure.

Found at DOI: <http://dx.doi.org/10.3996/022015-JFWM-021.S7> (1 KB TXT).

Reference S1. Bertrand N, Potvin F. 2003. Caractérisation des habitats fauniques: méthodologie et résultats observés. Direction de l'environnement forestier, Ministère des ressources naturelles, de la faune et des parcs du Québec, Québec.

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Found at DOI: <http://dx.doi.org/10.3996/022015-JFWM-021.S11> (1440 KB PDF).

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