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Habitat Occupancy by Spruce Grouse (*Canachites canadensis*) in the south of its range, Québec, Canada

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Abstract

Studying habitat occupancy at the margins of species' distributions can be helpful in clarifying species' requirements and planning management measures. Spruce grouse (*Canachites canadensis* Linnaeus, 1758), a bird species associated with northern short-needle coniferous forests in North America, has its southeastern range limit where coniferous forests are mixed with temperate deciduous forests and agricultural lands. Some isolated populations are found in these habitats. Using a single-season occupancy modelling approach, we investigated habitat use by spruce grouse, accounting for imperfect detection, in the lowlands of the St. Lawrence River in southern Québec, Canada. We conducted call-response spruce over three years at 279 sites (59 sites in 2007, 100 sites in 2008 and 120 sites in 2009). At the site level, the probability of occupancy was 21% (IC: 10.7% - 37.9%) and probability of detection was 54% (IC: 34.7% - 73.0%). Based on the covariates in the models, occurrence increased with higher cover of coniferous trees and low deciduous shrubs, and decreased with higher cover of deciduous trees. Finally, detection probability was highest at the beginning of the survey (50% in late April) and was influenced by year.

Keywords: Spruce grouse, *Canachites canadensis*, occupancy model, detection probability

Introduction

Species' geographic distributions are limited by species' tolerances imposed by abiotic and biotic factors (Parmesan et al. 2005). Species decline in abundance toward the extremes of their range, where habitat fragmentation allows the species to persist in isolated patches but where the probability of extinction is higher due to lower abundance (Guo et al. 2005). Studying habitat use at species' range margins may be particularly important to understand species' requirements. This is the case of the Spruce Grouse (*Canachites canadensis* Linnaeus, 1758) (Gill and Rasmussen 2021), a conifer-dependent species with a geographic range that coincides with the North American boreal forest (Schroeder et al. 2018), with some residual populations found in the transition zone between the boreal and temperate deciduous forests.

Spruce grouse use a variety of coniferous forest types throughout their range, generally with at least one short-needled conifer (Boag and Schroeder 1992). In eastern Canada, this species is mainly found in the spruce-moss forest with red spruce (*Picea rubens* Sarg.), black spruce (*Picea mariana* (Mill.)), white spruce (*Picea glauca* (Moench)), and balsam fir (*Abies balsamea* (L.)), and sometimes with a component of larch (*Larix* sp.) (Williamson et al. 2008). The southeastern extent of the geographic range in Québec coincides with the northern edge of the sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis*, Britton), and American linden (*Tilia americana* L.) bioclimatic domain, where coniferous habitats are found around large peat bogs or other poorly drained sites (Williamson et al. 2008), and are surrounded by mixed and deciduous forest and agricultural lands.

Populations of spruce grouse are roughly stable continentally (Schroeder et al. 2018), where their abundance varies by habitat and year. Based on point estimates occasionally conducted during studies on the species, spring density can vary from 3 to 15 males/km²

(Turcotte et al. 2000; Potvin and Courtois 2006). Thus, given the extent of the range of the species and the presence of favourable habitat throughout most of Québec, the spruce grouse population is estimated to be between 1.1 and 3.5 million individuals (Williamson et al. 2008). However, recent studies have shown that spruce grouse populations are declining in the southeastern portions of the species' range (Anich et al. 2013; Ross et al. 2016; Gilbert and Blomberg 2019) and there are concerns about the situation of residual populations in southeastern Québec, where coniferous habitat patches are limited and surrounded by a matrix of deciduous forests and agriculture. Studying habitat use can be particularly important to understand the local distribution of the species and implement management measures. Spruce grouse are expected to experience a range contraction due to climate change-induced habitat loss at the southern edge of their range, and may therefore have a more northerly distribution limit in the future (Roy et al. 2020).

Our goal was to study the presence of residual populations of spruce grouse found near large peat bogs of the southern St. Lawrence, where mixed, deciduous and coniferous forest are found within agriculture lands. We used a single-season occupancy analysis (Mackenzie et al. 2002) to account for imperfect detection and studied habitat use during the breeding period. We hypothesized that the composition of forest stands will have an effect on occupancy probabilities, with sites with high coniferous cover being more likely to be selected and sites with high deciduous cover likely to be avoided. Boag and Schroeder (1992) found that spruce grouse appear to select relatively dense stands with a well-developed shrub layer. We also hypothesized that a higher cover of mid-sized and low shrubs will increase the occupancy probability of spruce grouse.

Materials and methods

Study area

Our study area was in the lowlands of the Saint Lawrence River in southern Québec, Canada (Figure 1). We surveyed a landscape of 184 km² of private woodlots composed of semi-forested ombrotrophic peatlands, forested lands, agricultural lands, and small towns. The forest mosaic consisted of 38% forests less than 4 m tall and 24% black, white, or Norwegian spruce stands over 4 m tall (Blanchette 2019). The dominant forest cover was coniferous, composed essentially of black spruce mixed with tamarack (*Larix laricina* (Du Roi)), balsam fir, and eastern white cedar (*Thuja occidentalis* L.). There were also deciduous species, such as red maple (*Acer rubrum* L.), bigtooth aspen (*Populus grandidentata* Michx.), gray birch (*Betula populifolia* Marsh.), yellow birch and paper birch (*Betula papyrifera* Marsh.). The understory was characterized by ericaceous shrubs such as blueberries (*Vaccinium* spp.), Labrador tea (*Rhododendron groenlandicum* (Oeder)), leatherleaf (*Chamaedaphne calyculata* (L.)), and sheep laurel (*Kalmia angustifolia* L.).

Spruce Grouse Surveys

We conducted spruce grouse surveys in 2007, 2008 and 2009. We surveyed 59 sites in 2007, 100 sites in 2008 and 120 sites in 2009. Some sites were visited in two different years; for a total of 279 unique site-years for the study. We selected forest types that may support spruce grouse based on dominant species (spruce, fir, eastern larch, and eastern white cedar), and height class (> 7 m) from a map of the forest inventory (scale: 1:20 000) of the *Ministère des Forêts, de la Faune et des Parcs du Québec*, updated in the study area. Sampling sites, generated using ArcGIS10.0 (ESRI2010), were spaced > 200 m with two constraints: > 50 m from stand edges and < 200 m from the access road. Sites that were not accessible were discarded. Species composition and vegetal structure in the sites was similar within the years (Table 1), with a little more coniferous cover of coniferous trees (> 4 m) in 2007 than in the other two years.

Two observers conducted call-response surveys (Turcotte et al. 2000; Boag and McKinnon 1982; Potvin and Courtois 2006). The observers broadcast a recording of female territorial calls for 15 minutes, using 5 W portable amplifiers (model No 7–100; Pignose Industries, Las Vegas, USA). Spruce grouse is an easily identified species and calls are diagnostic (Turcotte et al. 2000; Potvin and Courtois 2006). All spruce grouse seen or heard within a 100 m-radius were recorded according to sex (Schroeder and Boag 1989). This survey was approved by the Animal Welfare Committee of the Ministère des Forêts, de la Faune et des Parcs du Québec (CPA-08-00-05). During the survey, the observers recorded the time of sampling, the temperature, the wind speed using Beaufort scale, and the Julian day (starting April 23), variables that we hypothesize could affect detection probability based on previous studies (Robinson 1980; Conway and Gibbs 2001; Schroeder et al. 2018). Sampled sites were visited one to three times between late April and early June.

Landscape Characteristics

Vegetation characteristics were sampled in a 11.28 m radius circular plot (0.04 ha) placed at the centre of each sampling site. We measured habitat variables: mean canopy height (m), basal area (BA; m²/ha) of trees (DBH ≥ 9 cm) per species using a 2-factor BAF prism, percent cover of trees (> 4 m high), percent cover of the mid-story layer, percent cover of “high shrubs” (1–4 m high) and percent cover of understorey “low shrubs” (< 1 m high). We measured mean canopy height with a clinometer, and we visually estimated percent cover of coniferous and deciduous mid-story and understorey layers within the plot using the following scale (%): 0, 1–20, 20–40, 40–60, 60–80, 80–100. Sites had an average tree cover of 40–60%, and were dominated by coniferous species (Table 1). Black spruce was the dominant species at the sites, followed by balsam fir and tamarack. The percent cover

of high and low shrubs was variable ($\sim 0\text{--}40\%$) with a similar proportion of deciduous and coniferous species.

Statistical models

We used single-season occupancy analysis (Mackenzie et al. 2002) to estimate the occupancy and detection probabilities of spruce grouse. To limit the number of models considered, we use a hierarchical approach using a two-step model selection procedure (Franklin et al. 2000; Olson et al. 2005). First, we compared models which evaluated the influence of observation variables, including temperature, wind speed, time since sunrise (minutes), Julian day, and year on detection probability, while we held explanatory variables for occupancy constant using the “*unmarked*” package in program R (Fiske and Chandler 2011; R Core Team 2013). We included year as a factor because some sites were visited in multiple years. We also included models with a quadratic effect for the Julian day, temperature, and time since sunrise. We based model selection on Akaike’s Information Criterion adjusted for small samples (AICc) and Akaike weights using the “*AICmodavg*” package (Burnham and Anderson 2002; Mazerolle 2017).

Second, we build a set of 12 models with the explanatory variables most likely to explain the occupancy probability of spruce grouse (Table 1) using the detection variables from the most supported model selected by AICc from step 1 (All habitat models are in Table 4). We contrasted the structure of these models against a null model (intercept only on both occupancy and detection). We ranked each model using the Akaike information criterion (AICc), and used ΔAICc to determine the strength of evidence for each model (Burnham and Anderson 2002), using a criterion of $\Delta\text{AICc} < 2.0$. We tested the goodness-of-fit of the global model in each stage of the AICc model selection MacKenzie and Bailey (2004) using a parametric bootstrap approach with 10000 bootstrap samples. Predictor variables used in analyses were transformed to standardize means and variances, and correlated

variables ($r > 0.6$) were not included in the same model. We estimated parameter averages and 95% confidence limits using a multimodel inference with the *modavgShrink()* function in the “*unmarked*” package (Fiske and Chandler 2011).

Results

A total of 279 sites were visited between 2007 and 2009. The mean number of visits per sites was 2.72 with a maximum of three visits per year (Table 2). During the three years of surveys, spruce grouse were found at least once in 49 sites, giving us a naïve occupancy estimate of 19%.

In the first step of our analysis, we created nine models including the observation variables and their quadratic effects to explain detection probability. As the global model indicated some overdispersion ($X^2 = 11.94$, $P = 0.12$, $\hat{c} = 1.5$) in the goodness-of-fit test (MacKenzie and Bailey 2004) we used the $\hat{c}$ value to correct the AICc selection. The top-ranked model (AICcWt = 0.63) included the variables Julian day and year and was the only competitive model (< 2.0 Delta-AICc) (Table 3). The variables of this model were used to predict detection probability in the occupancy models built in the second step of our analyses.

In the second step, we built a set of 13 models with explanatory variables most likely to explain the occupancy probability of the spruce grouse (Table 4). As the global occupancy model indicated low overdispersion in the goodness-of-fit test ($X^2 = 12.53$, $P = 0.09$, $\hat{c} = 1.64$) we used the $\hat{c}$ value to correct the AICc selection. Two models were competitive based on Delta-AICc, with 0.54 and 0.46 AICcWt (Table 4). The top-ranked models indicated that occupancy was affected by: (i) vegetation structural stage (percent cover of trees and percent cover of high and low shrubs of coniferous and deciduous species) and (ii) percent black spruce, tamarack and balsam fir BA (variables included only in the second top-ranked model). Occupancy probability during a single survey was 21% (IC:

10.7% - 37.9%) and the average detection probability was 54% (IC: 34.7% - 73.0%). The percent cover of coniferous trees and low deciduous shrubs had a positive effect on occupancy, while the cover of deciduous trees had a negative effect (Table 5). For example, spruce grouse occupancy probability exceeded 50% when conifer cover was > 60%, low deciduous shrub cover > 20%, and deciduous tree cover was <20% (Figures 2, 3, 4). However, the confidence interval of the other of variables overlapped zero, which indicates substantial uncertainty in their support (Table 5).

Finally, detection probability decreased with the Julian day, with 50% detection probability at the beginning of the survey (April 23), and < 25% detection probability after May 18 (Table 5, Figure 5). It also decreased within year, without an effect in 2007 (zero was included in 95% IC) and a negative effect in 2008 and 2009 with 24% and 17% detection probability respectively (Figure 6).

Discussion

We successfully modelled the occupancy of the spruce grouse, accounting for imperfect detection, in a low-density population situated in the south of its range, where mixed deciduous and coniferous forests are in a matrix of agricultural lands. As we hypothesized, spruce grouse occupancy increased with coniferous tree and low deciduous shrub cover, and decreased with higher cover of deciduous trees.

The spruce grouse is a specialist of coniferous forests (Boag et Schroeder 1992; Potvin et Courtois 2006). Indeed, studies have found that spruce grouse occupy habitats based on the presence of particular conifer species, for example, black spruce in Wisconsin (Anich et al. 2013) and northern Minnesota (Hass 1974), jack pine in Michigan and Ontario (Robison 1980, Naylor 1988) or lodgepole pine and white spruce in Alberta (Keppie and Herzog 1978). However, in our study we did not find black spruce, tamarack, or balsam fir to be close to significant individually, whereas overall coniferous cover was significant.

This may be because of the small sample size for some species, as the majority of conifer cover in our sites consisted of black spruce, tamarack and balsam fir. Also, the three species are considered an important food source for spruce grouse in winter when their diet is almost exclusively based on conifer needles (Allan 1985; Anich et al. 2013; Zlonis et al. 2017). Increased coniferous tree cover is also associated with decreased vulnerability to avian predators (Szuba 1989) because it increases access to higher perches, which may allow individuals to see predators from a distance (Fernández-Juricic et al. 2004). Dense habitat is another of the main characteristics selected by spruce grouse, mainly during the breeding season (Allan 1985; Ross 2015); a dense deciduous cover < 1 m of height could provide protection against ground predators that prey mostly on eggs (Boag and Schroeder 1992). As our model predicted, an increase in deciduous tree cover has a negative influence on the occurrence of the species. The presence of deciduous trees can be a real problem for the persistence of grouse populations (Blanchette 2019), and several studies have reported that the occurrence of coniferous trees within a deciduous forest matrix can subdivide spruce grouse populations, making them more prone to local extinction (Boag and Schroeder 1992; Potvin and Courtois 2006; Ross et al. 2016).

Our approach allowed us to estimate the occupancy of spruce grouse while explicitly accounting for heterogeneity in detection probabilities. Detection of spruce grouse indicated that detection probability was strongly influenced by the year of sampling and the Julian day. The mean detection probability was estimated to be 54%, similar to results from Ross et al. (2016). The detection probability was not influenced by the year in 2007 whereas the following years (2008 and 2009) had a negative effect, decreasing the detection probabilities to 24% and 17% respectively. This heterogeneity in detection probability could be explained by the increased number of sites visited during 2008 and 2009; when we explored a greater variety of habitats. The sampling sites in 2008 and 2009

represented a greater variety of habitats including less coniferous cover than the 2007 sites, and the daily movements or temporary emigration of species to search for resources could result in lower detection. In addition, during the study period we marked several grouse and did continuous telemetry monitoring over the following months, until spring 2010. This monitoring may have disturbed the grouse and made them more fearful and therefore less detectable. As observed in the results of the telemetry monitoring study (Desrochers et al. 2021), 42% of the grouse captured and fitted with a transmitter moved away from the observer during the calls survey, reducing detection of the grouse (Desrochers et al. 2021). We expected detection probability to be influenced by Julian day because, as prior research had shown, males tend to respond more to call-backs during peak breeding season (late April and early May) but are less likely to respond to such stimuli later in the season (Robinson 1980). The other observational variables that we considered, such as time since sunrise and wind speed, were discarded in the second stage of model selection because they did not have an effect on detection probability. As Lycke et al. (2011) found, and unlike other bird species that are more active during the morning (Drapeau et al. 1999), timing of calls (between sunrise and noon) did not seem to have an effect on the response of spruce grouse. However, others have found that spruce grouse males tend to be more active during the early morning hours, and the frequency of calls and displays decreases as noon approaches (Schroeder and Boag 1989; Schroeder et al. 2018). It is unclear whether there is an effect of time since sunrise on the detection probability of this species, so we suggest including this variable in future analyses.

Roy et al. (2020) suggests that where spruce grouse occur at low density, as is the case in our study area, pellet surveys could offer a complimentary and sensitive alternative to the call-survey method. In addition, long-term population monitoring data would be ideal to understand how populations will be impacted by climate change and habitat loss. Indeed,

Gilbert and Blomberg (2019) found a > 80% reduction in the apparent abundance of spruce grouse on Mount Desert Island, ME, based on a 25-y resurvey, and similar results have been observed in the Adirondack Mountains of New York where 40-y resurvey work found that occupied patches declined by 25% (Ross et al. 2016). We recommend further monitoring of this southern Québec population to confirm or refute the long-term declines observed in other regions, and to assess the future viability of the population.

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Table captions

Table 1. Differences in observed in habitat variables (mean and standard deviation “SD”) used to predict occupancy within the years from sites sampled in 2007, 2008 and 2009 for spruce grouse (*Canachites canadensis*) in southern Québec, Canada.

			Mean ± SD		
Type	Variable Acronym	Description	2007 (n = 59)	2008 (n = 100)	2009 (n = 120)
Species composition	% BA Black spruce	Percent of black spruce (<i>Picea mariana</i>) basal area (DBH > 9cm) in the site	54% ± 35%	52% ± 33 %	46% ± 34%
	% BA Tamarack	Percent of tamarack (<i>Larix laricina</i>) basal area (DBH > 9cm) in the site	13% ± 26%	16 %± 23%	18% ± 24%
	% BA Balsam fir	Percent of balsam fir (<i>Abies balsamea</i>) basal area (DBH > 9cm) in the site	15% ± 14%	12% ± 23%	11% ± 22%
Vegetal structure (class 0 = 0%, 1 = 1% - 20%, 2 = 21% - 40%, 3 = 41% - 60%, 4 = 61% - 80%, 5 = 81 - 100%)	% CT	Percent cover of trees (> 4 m)	3.25 ± 1.20	3.18 ± 1.05	3.24 ± 1.05
	% Coniferous CT	Percent cover of coniferous trees (> 4 m)	3.10 ± 1.27	2.88 ± 1.13	2.77 ± 1.11
	% Deciduous CT	Percent cover of deciduous trees (> 4 m)	0.54 ± 0.57	0.60 ± 0.57	0.81 ± 0.75
	% SCH	Percent of mid_story layer cover “high shrubs” (1-4 m high)	1.49 ± 0.84	1.75 ± 0.96	1.67 ± 0.93
	% Coniferous SCH	Percent cover of mid_story layer (1-4 m high) of coniferous species	1.15 ± 0.58	1.36 ± 0.72	1.33 ± 0.73
	% Deciduous SCH	Percent cover of mid_story layer (1-4 m high) of deciduous species	0.85 ± 0.94	0.80 ± 0.88	0.80 ± 0.84
	% SCL	Percent cover of lower layer “low shrubs” (<1 m high)	1.86 ± 1.25	1.96 ± 1.22	1.80 ± 1.14
	% Coniferous SCL	Percent cover of lower-story layer (<1 m high) of coniferous species	1.27 ± 0.83	1.25 ± 0.85	1.21 ± 0.79
	% Deciduous SCL	Percent cover of lower-story layer (<1 high) of deciduous species	1.24 ± 1.02	1.27 ± 1.11	1.23 ± 0.98

366 Table 2. Detection histories of spruce grouse (*Canachites canadensis*) on three consecutive
 367 visits, southern Québec, Canada, springs 2007, 2008 and 2009. Presence = 1, absence =
 368 0, “.” = NA.

Détection histories	Number of sites
0 – 0 – 0	182
0 – 0 – 1	5
0 – 0 – .	39
0 – 1 – 0	2
0 – 1 – .	4
0 – . – .	9
1 – 0 – 0	15
1 – 0 – .	9
1 – 1 – 0	5
1 – 1 – 1	2
1 – 1 – .	6
1 – . – .	1

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Table 3. Ranking of model selection for different scenarios on detection probability (p) of the spruce grouse (*Canachites canadensis*) based on Akaike's information criterion corrected for small samples (AICc). Detection variables included *year*, *Julian day*, *wind*, *minutes after sunrise* and *temperature*. Table shows the number of estimated parameters (K), difference in AICc relative to top model (Δ AICc) and Akaike weights (AICc Wt). Based on data obtained from callback surveys conducted during April and May 2007, 2008 and 2009 in southern Québec, Canada.

Model	K	AICc	Δ AICc	AICc Wt
$\Psi (.) p$ (year + Julian day)	4	391,18	0	0,63
$\Psi (.) p$ (year + Julian day + Julian day ²)	5	393,25	2,07	0,22
$\Psi (.) p$ (year + Julian day + Julian day ² + wind + minutes after sunrise + minutes after sunrise ²)	10	394,85	3,67	0,1
$\Psi (.) p$ (year + Julian day + wind + minutes after sunrise)	7	397,94	6,75	0,02
$\Psi (.) p$ (year + minutes after sunrise + minutes after sunrise ²)	5	399,97	8,79	0,01
$\Psi (.) p$ (year)	3	400,15	8,97	0,01
$\Psi (.) p$ (year + minutes after sunrise)	4	401,98	10,8	0
$\Psi (.) p$ (year +temperature)	4	402,09	10,91	0
$\Psi (.) p$ (year +temperature + temperature ²)	5	402,97	11,79	0
$\Psi (.) p (.)$	2	414,29	23,1	0

Table 4. Ranking of all occupancy model selection for different scenarios on occupancy probability (ψ) of the spruce grouse (*Canachites canadensis*) based on Akaike's information criterion corrected for small samples ($AICc$). Detection probability variables were the same for every model ($p(i) = p(\text{year} + \text{Julian day})$). The table shows the number of estimated parameters (K), difference in $AICc$ relative to top model ($\Delta AICc$) and Akaike weights ($AICcWt$). Based on data obtained from callback surveys conducted during April and May 2007, 2008 and 2009 in southern Québec, Canada.

Models	K	$AICc$	$\Delta AICc$	$AICc Wt$
Ψ (Vegetation structure)* $p(i)$	10	346,24	0	0,54
Ψ (Global)* $p(i)$	13	346,59	0,36	0,46
Ψ (% BA ^a Black spruce + % BA Tamarack) $p(i)$	6	368,09	21,85	0
Ψ (% Coniferous CT ^b + % Deciduous CT) $p(i)$	6	369,13	22,9	0
Ψ (% BA Black spruce + % BA Tamarack + % BA Balsam fir) $p(i)$	7	369,67	23,43	0
Ψ (% Coniferous SCL ^c + % Deciduous SCL) $p(i)$	6	371,79	25,55	0
Ψ (%SCL) $p(i)$	5	374,91	28,67	0
Ψ (% BA coniferous) $p(i)$	5	383	36,77	0
Ψ (% BA Tamarack + % BA Balsam fir) $p(i)$	6	385,26	39,02	0
Ψ (% SCH ^d) $p(i)$	5	387,37	41,14	0
Ψ (% Coniferous SCH + % Deciduous SCH) $p(i)$	6	388,35	42,11	0
Ψ (% CT) $p(i)$	5	390,89	44,66	0
Ψ (.) $p(i)$	4	391,18	44,95	0

^a Percent of basal area (DBH > 9cm) in the site

^b Percent tree cover (> 4 m)

^c Percent low shrub cover (> 1 m)

^d Percent high shrub cover (1 – 4 m)

* Vegetation structure = % Coniferous SCL + % Coniferous SCH + % Coniferous CT + % Deciduous SCL + % Deciduous SCH + % Deciduous CT

* Global = % BA Black spruce + % BA Tamarack + % BA Balsam fir % Coniferous SCL + % Coniferous SCH + % Coniferous CT + % Deciduous SCL + % Deciduous SCH + % Deciduous CT

Table 5. Estimation of model-average of parameters coefficients (β), unconditional SE, and 95% unconditional confidence intervals on logit scale for the occupancy probability (ψ) parameters and detection probability (p) from the spruce grouse (*Canachites canadensis*) AIC model selection, calculated using *modavgShrink()* function from ‘unmarked’ R package (Fiske and Chandler 2011). Based on data obtained from callback surveys conducted during April and May 2007, 2008 and 2009 in southern Québec, Canada.

Variable	Estimate model-average (β)	Unconditional SE	95% Unconditional confidence interval	
			Lower	Upper
ψ (% BA ^a Black spruce)	0.21	0.56	-0.88	1.30
ψ (% BA Tamarack)	0.13	0.38	-0.62	0.88
ψ (% BA Balsam fir)	0.05	0.36	-0.64	0.75
ψ (% Coniferous SCL ^b)	0.26	0.38	-0.49	1.01
ψ (% Coniferous SCH ^c)	0.45	0.39	-0.31	1.22
ψ (% Coniferous CT^d)	1.21	0.44	0.35	2.07
ψ (% Deciduous CT)	-1.13	0.52	-2.15	-0.1
ψ (% Deciduous SCL)	1.53	0.56	0.42	2.63
ψ (% Deciduous SCH)	0.28	0.32	-0.34	0.93
p (Julian day)	-0.55	0.21	-0.95	- 0.19
p(year2007)	0.18	0.41	-0.63	0.99
p(year2008)	-1.11	0.37	-1.84	-0.38
p(year2009)	-0.52	0.21	-0.93	-0.11

^a Percent of basal area (DBH > 9cm) in the site

^b Percent low shrub cover (> 1 m)

^c Percent high shrub cover (1 – 4 m)

^d Percent tree cover (> 4 m)

Figure captions

Figure 1. Distribution of sites sampled for spruce grouse (*Canachites canadensis*) in southern Québec, Canada, in April and May 2007, 2008 and 2009. The images of North America and Quebec are from the USGS, ScienceBase-Catalog. The upper right corner image uses the Coordinate Reference Systems NAD83 (EPSG:4269). The lower right corner image with habitat types is from the "*Troisième inventaire écoforestier du Québec méridional*" (MFFP).

Figure 2. Variations of spruce grouse (*Canachites canadensis*) occupancy probability according to the cover of coniferous trees in the occupancy models based on surveys in southern Québec, Canada (2007–2009), using the multi-inference model. Error bars denote 95% confidence intervals around predictions.

Figure 3. Variations of spruce grouse (*Canachites canadensis*) occupancy probability according to the cover of the low deciduous shrub (< 2 m high) in the occupancy models based on surveys in southern Québec, Canada, (2007–2009), using the multi-inference model. Error bars denote 95% confidence intervals around predictions.

Figure 4. Variations of spruce grouse (*Canachites canadensis*) occupancy probability according to the cover of deciduous trees in the occupancy models based on surveys in southern Québec, Canada, (2007–2009), using the multi-inference model. Error bars denote 95% confidence intervals around predictions.

Figure 5. Variations of spruce grouse (*Canachites canadensis*) detection probability according to the Julian day in the occupancy models based on surveys in southern Québec, Canada, (2007–2009) using the multi-inference model. Error bars denote 95% confidence intervals around predictions.

Figure 6. Variations of spruce grouse (*Canachites canadensis*) detection probability according to the year in the models based on surveys in southern Québec, Canada,

430 (2007–2009) using the multi-inference model approach. Error bars denote 95% confidence
431 intervals around predictions.

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Figure 1. Distribution of sites sampled for spruce grouse (*Canachites canadensis*) in southern Québec, Canada, in April and May 2007, 2008 and 2009. The images of North America and Quebec are from the USGS, ScienceBase-Catalog. The upper right corner image uses the Coordinate Reference Systems NAD83 (EPSG:4269). The lower right corner image with habitat types is from the "Quatrième inventaire écoforestier du Québec méridional" (Berger and Leboeuf 2013).

215x190mm (300 x 300 DPI)

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245x142mm (300 x 300 DPI)

Figure 3. Variations of spruce grouse (*Canachites canadensis*) occupancy probability according to the cover of the low deciduous shrub (< 2 m high) in the occupancy models based on surveys in southern Québec, Canada, (2007–2009), using the multi-inference model. Error bars denote 95% confidence intervals around predictions.

245x142mm (300 x 300 DPI)

Figure 4. Variations of spruce grouse (*Canachites canadensis*) occupancy probability according to the cover of deciduous trees in the occupancy models based on surveys in southern Québec, Canada, (2007–2009), using the multi-inference model. Error bars denote 95% confidence intervals around predictions.

245x142mm (300 x 300 DPI)

Figure 5. Variations of spruce grouse (*Canachites canadensis*) detection probability according to the Julian day in the occupancy models based on surveys in southern Québec, Canada, (2007–2009) using the multi-inference model. Error bars denote 95% confidence intervals around predictions.

338x190mm (300 x 300 DPI)

Figure 6. Variations of spruce grouse (*Canachites canadensis*) detection probability according to the year in the models based on surveys in southern Québec, Canada, (2007–2009) using the multi-inference model approach. Error bars denote 95% confidence intervals around predictions.

245x142mm (300 x 300 DPI)