



Original investigation

Comparative evaluation of three sampling methods to estimate detection probability of American red squirrels (*Tamiasciurus hudsonicus*)

Emilie E. Chavel^{a,*}, Marc J. Mazerolle^b, Louis Imbeau^a, Pierre Drapeau^c

^a Centre d'étude de la forêt (CEF), Institut de Recherche sur les Forêts (IRF), Université du Québec en Abitibi-Témiscamingue (UQAT), 445 boulevard de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada

^b Centre d'étude de la forêt (CEF), Département des sciences du bois et de la forêt, Université Laval, 2405 rue de la Terrasse, Québec, QC G1V 0A6, Canada

^c Centre d'étude de la forêt (CEF), Département des sciences biologiques, Université du Québec à Montréal (UQAM), 141 Avenue Président-Kennedy, Montréal, Québec, H2X 1Y4, Canada

ARTICLE INFO

Article history:

Received 2 August 2016

Accepted 5 November 2016

Handled by Danilo Russo

Available online 9 November 2016

Keywords:

Detectability

Live-trapping

Playback count

Point count

Site occupancy

Sciurids

ABSTRACT

Measuring changes in species distribution and understanding factors influencing site occupancy are recurring goals in wildlife studies. Imperfect detection of species hinders such studies, resulting in the underestimation of the number of sites occupied by the species of interest. American red squirrels (*Tamiasciurus hudsonicus*) are sampled traditionally with live-traps that require substantial resources to deploy and monitor. Here, we assessed whether auditory methods yield similar detection probabilities. We compared the detection probability of American red squirrels in boreal forest using point counts, playback counts, and live-trapping. Over the summer of 2014, we conducted three trapping sessions in 60 sites within black spruce forests of northwestern Quebec, Canada. We also conducted 10 min point counts in the same sites, together with playback counts using recordings of American red squirrel alarm and territorial calls. Using dynamic occupancy models to analyse three primary periods, all composed of three secondary periods, we found that the detection probability of squirrels from point counts was as high as with live-trapping. Our results thus highlight the value of the point count method in measuring American red squirrel occupancy.

© 2016 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Introduction

Studies on wildlife populations are often designed to understand patterns of species distribution to inform management strategies. Site occupancy, i.e. the probability of a landscape unit to be occupied by a species of interest (MacKenzie et al., 2006), can help determine the factors that influence species presence at a given location (e.g., habitat modelling – Scott et al., 2002; Pearce and Boyce, 2006; Richmond et al., 2010), as well as understand metapopulation dynamics (Sjögren-Gulve and Hanski, 2000). Over the last decade, occupancy models have been developed to cope with the underestimation of site occupancy due to the imperfect detectability of the species of interest (MacKenzie et al., 2002, 2006). Detection probability may vary with site characteristics (e.g.,

lateral cover, tree density), sampling periods (e.g., weather conditions), and sampling methods, which lead to heterogeneity in detection probabilities across sites and surveys (MacKenzie et al., 2006; Otto and Roloff, 2011). When the variation in detection probability explained by covariates remains low, investigators should use sampling protocols with high detection probability (Pollock et al., 2002).

American red squirrels (*Tamiasciurus hudsonicus*) are widespread across North America and are often studied to understand population dynamics in relation to their territorial behaviour. Individuals are promiscuous, defend long-term territories, and adapt their territorial behaviour according to gender, reproductive status, and identity of squirrel competitors (Larsen, 1993; Price et al., 1990). Territory size, covering on average 65 m² (Larsen and Boutin, 1994), mainly depends on food availability and quality, which also influence density (Klenner and Krebs, 1991; Larsen and Boutin, 1995; Boutin et al., 2006). Like most small mammals, red squirrels are usually sampled using live-trapping techniques. However, auditory surveys are commonly carried out as this species is highly vocal, marking and defending territories

* Corresponding author.

E-mail addresses: emilie.chavel@uqat.ca

(E.E. Chavel), marc.mazerolle@sf.ulaval.ca (M.J. Mazerolle), louis.imbeau@uqat.ca (L. Imbeau), drapeau.pierre@uqam.ca (P. Drapeau).

using loud and distinctive alarm calls (Smith, 1978; Larsen and Boutin, 1994; Green and Meagher, 1998). Several studies have relied on this behaviour to either understand associations and competition among individuals (Price et al., 1990; Dantzer et al., 2012; Wilson et al., 2015) or to estimate the relative abundance of this species in an area (Buchanan et al., 1990; Sieving and Willson, 1998; Bayne and Hobson, 2000; Russell et al., 2010). Likewise, site occupancy could be studied using auditory methods. To our knowledge, the reliability of passive point counts and playback surveys in detecting individuals as compared to live-trapping has yet to be assessed for American red squirrels.

Our first objective was to compare the detection probability of squirrels with these two auditory methods relative to live-trapping. Live-trapping and auditory methods rely on different individual behaviours for detection. Whereas auditory methods depend on territorial or vocal animals during short observation periods, live-trapping detects animals moving in the vicinity of traps that have been captured. Because live-trapping targets individuals in the site over extended hours regardless of territorial behaviour and life stage, we hypothesised that live-trapping would yield the highest detection probability, followed by playback counts, and passive point counts. For our second objective, we combined the two auditory methods (point and playback counts) to increase species detection, and compared the resulting detection probability against the detection probability of American red squirrels obtained from live-trapping. We hypothesised that we would observe an increase in detection probability when combining the two auditory methods compared to when used on their own. We also hypothesised that if these auditory methods were initially associated to lower detection probabilities than live-trapping, combined together, they would allow the detection of American red squirrel with similar probabilities to those of live-trapping.

Material and methods

Study area

The study area covered a total of 8325 km² (79°29' W, 49°00' N–75°39' W, 50°22' N) and was located in black spruce forests of northwestern Quebec, Canada (Fig. 1). This boreal region is characterised by a subpolar continental climate with mean monthly temperatures ranging from –16°C to 20°C and 850 mm of annual precipitation (Blouin and Berger, 2002; Bergeron et al., 2004). The forest canopy is dominated by black spruce (*Picea mariana*, Mill.). Jack pine (*Pinus banksiana*, Lamb.) and balsam fir (*Abies balsamea*, Mill.) also occur, along with deciduous species such as paper birch (*Betula papyrifera*, Marshall) and trembling aspen (*Populus tremuloides*, Michx.). The understory is mainly composed of dwarf ericaceous shrubs. Feather mosses form a dense carpet, which is slowly replaced by *Sphagnum* species as drainage conditions deteriorate or in the absence of wildfire (Fenton and Bergeron, 2006). The region is characterised by recurrent and severe wildfires over vast areas (Bergeron et al., 2004), although this major disturbance is being increasingly replaced by various forest management and harvesting strategies (Imbeau et al., 2015).

Using a stratified sampling design, we selected a total of 60 forested sites that were equally distributed among old undisturbed forest (CTRL – continuous forest over 100-years-old), post-fire remnant patches (PFRP – 3.1 ha [range: 0.2–11.1]) left after wildfires that occurred over 20 years ago, green tree retention patches (GTRP – 0.8 ha [range: 0.1–1.6]) left after recent clear-cutting (<10 years), and linear cutblock separators (LCBS – 60–100 m large, connected to old-growth forests) that separate clearcut areas. Sites were at least 500 m apart. Based on the average movement distance of American red squirrels (Larsen and Boutin, 1994), the distance

between any two sites was sufficiently large to ensure independence among sites. Sites were characterised by a density of large trees ranging from 0 to 2444 trees ha⁻¹ (first quartile = 333 ha; median = 756 ha, third quartile = 1400 ha). GTRP were mostly composed of small trees with a dbh less than 10 cm, with a resulting average density of large trees of 584 trees ha⁻¹ [range: 44–2133]. The average density of large trees found in CTRL and PFRP was 839 trees ha⁻¹ [range: 0–2089] and 827 trees ha⁻¹ [range: 0–1644], respectively. LCBS were densely packed with large trees, with an average density of 1407 large trees ha⁻¹ [range: 311–2444].

Squirrel surveys

Live-trapping was conducted from 1 June 2014 to 21 August 2014, using Tomahawk (Tomahawk Live Trap llc®) live-traps baited with peanut butter and apple pieces. No pre-baiting was carried out. Based on 17 recent studies that used live-trapping with various squirrel species and under different sampling regimes, only 53% of these used pre-baiting (see Appendix A of Supplementary material). We established one transect line of six live-traps per site with a distance of 10 m between traps. Transects were 50 m long to accommodate our smallest sites. Traps were set late in the afternoon and left on site for three consecutive days. Traps were checked twice a day (early morning and late afternoon). Each site was monitored with this trapping regime of three consecutive days during three sessions over the summer 2014 (three days in June, three days in July, and three days in August). Trapping sessions in a given site were separated by 27 days. Captured squirrels were pit-tagged, identified to sex and age, weighed, and assessed for health and reproductive conditions for a concurrent study. All individuals were subsequently released. All manipulations adhered to the Canadian Council on Animal Care Guidelines and were approved by the Institutional Animal Care Review Committee, Université du Québec en Abitibi-Témiscamingue (UQAT, permit no. 2013-04-02).

Point and playback counts were both conducted during the same period as live-trapping in a given site, from sunrise to mid-morning when squirrels are the most active. Once all traps on site were checked and potentially captured individuals were released, we waited 10 min before starting the auditory sampling. We listened for squirrels for 10 consecutive minutes and noted all detections within this period. Following the point count, we played squirrel calls using portable players plugged into amplifiers. Squirrel calls were extracted from the audio book “Le son de nos forêts” (Elliot and Mack, 1994), and they were played back three times over a period of 10 min. For both playback and point counts, and for each site, we recorded whether individuals were detected or not. Point counts were carried out over two consecutive days, three times over the summer (two days in June, July, and August). We encountered technical problems in June that prevented us from using playback counts on more than 12 occasions over that month. However, playback was carried out over three consecutive days, on the two last trapping sessions at each site (three days in both July and August). When a playback or point count was not conducted on a given day due to unfavourable weather conditions or to technical problems, we considered it as a missing value in the analyses.

Environmental data

We did not expect understory strata to impede the hearing of listeners. Rather, we expected large live tree density to influence the listeners' ability to detect calling squirrels. Therefore, we characterised tree density by counting the number of trees that were equal to or larger than 10 cm in diameter at breast height (dbh), within a 15 × 15 m quadrat. All values were expressed as a number of stems per hectare.

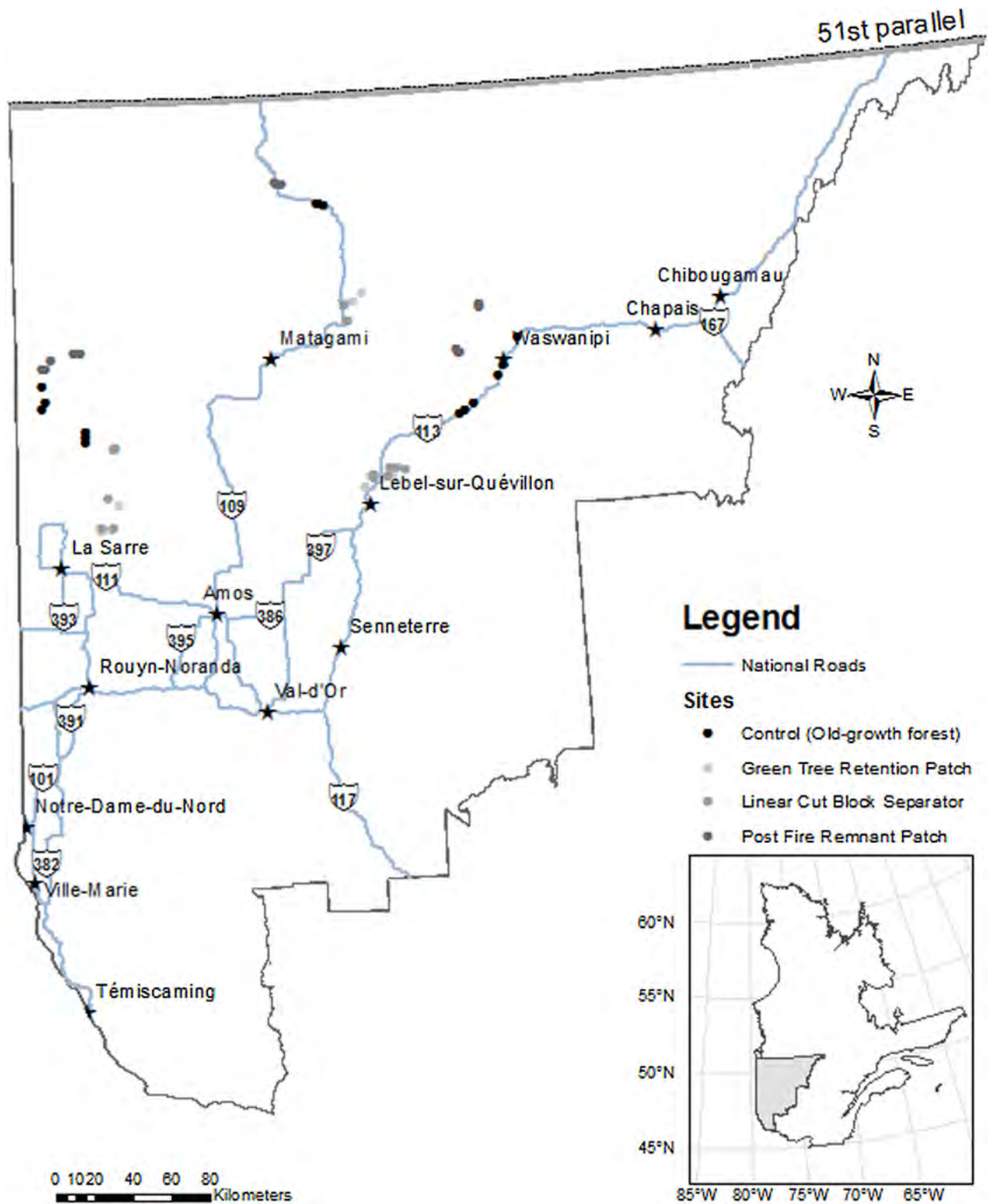


Fig. 1. Location of the study sites in black spruce forest of northwestern Quebec, Canada.

Cost analysis of each methods

We calculated costs of each sampling method based on the effort required to survey 60 sites during one sampling session (i.e., 3 consecutive nights). We considered four types of expenditures: equipment, personnel, lodging and travel. Equipment costs were

based on 2014 purchase prices. Personnel costs were calculated for a team of four people based on institutional salary for a research assistant in 2014 (\$17.25/h plus taxes). Travel costs included the rental of a vehicle of two King-cab 4 × 4 trucks, insurance, and fuel. Lodging costs were of \$16 per night per person, based on the price paid to stay overnight in the institutional research station.

As sites were sampled by groups of 12 at a time, a total of 20 days were required to sample 60 sites using live-trapping [5 groups of sites \times (1 day for travelling towards a given group of sites and setting traps + 3 days of sampling)]. A total of 16 days were required to conduct playback counts [1 day for travelling towards the first group of sites + 5 groups of sites \times (2 mornings of sampling + 1 day of sampling and travelling towards the next group of sites)]. A total of 11 days were required to conduct point counts [1 day for travelling towards the first group of sites + 5 groups of sites \times (1 morning of sampling + 1 day of sampling and travelling towards the next group of sites)].

Statistical analyses

Our data frame was composed of detections and non detections during three primary periods (i.e. sampling sessions) for each of the three sampling methods. Each primary period consisted of three secondary periods (i.e. sampling days). We used dynamic occupancy models to estimate the detection probability (p) of squirrels, as well as the probabilities of initial occupancy (ψ), extinction (ε), and colonisation (γ) (MacKenzie et al., 2003). The dynamic occupancy model allows potential changes in squirrel occupancy among trapping sessions. We opted for this approach because juveniles begin dispersing within the first month after leaving the family den (Larsen and Boutin, 1994). Considering that American red squirrels defend territories of about 65 m² (Larsen and Boutin, 1994), they probably never travel outside hearing distances of our sites using auditory methods, and seldom use areas not crossed by our trapping transects.

All analyses were conducted using the *unmarked* package (Fiske and Chandler, 2011) in R (version 3.0.1, R Development Core Team, 2015). All hypotheses and corresponding model structures are listed in Table 1.

Effect of sampling method

We compared the detection probability of different sampling methods by considering a categorical variable (Method) that consisted of three levels (live-trapping, playback counts, and point counts). We predicted that live-trapping would yield a higher detection probability than the auditory methods because live-trapping targets individuals of different life stages over a longer period of time than auditory methods.

Effect of live-trapping on auditory methods

Trap-induced stress may cause squirrels to change their behaviour, including vocalisation (Bosson et al., 2012). Because playback and point counts were always conducted after having checked traps, we quantified the influence of a trapping or handling effect on the detection probability during auditory methods with a second categorical variable (Method⁺). The latter variable consisted of five levels: live-trapping, playback count following a capture, playback count following no capture, point count following a capture, and point count following no capture. Method and Method⁺ were never included together in the same candidate model. We predicted that live-trapping a squirrel would increase the detection probability of playback and point counts, given that territorial individuals would likely vocalise a few minutes after having been released at a site.

Primary period and pre-baiting effects

Two time categorical variables were considered in our candidate models, viz., the primary sampling period (Session) with three levels and the sampling visit during a primary sampling period (Visit) with three levels. We allowed the detection probability to vary with Session as we predicted that detection probability would increase

Table 1

List of hypotheses tested with dynamic occupancy models to primarily assess the effects of covariates on detection probability of American red squirrels (*Tamiasciurus hudsonicus*) sampled in black spruce forest of northwestern Quebec with three different sampling methods, viz., live-trapping, playback counts, and point counts. All following hypotheses were tested when analysing detection probabilities associated to each sampling method. We excluded the two hypotheses that proposed changes in site colonisation and local extinction over the summer of 2014 from the analyses of combined auditory methods, because the latter only included two primary sampling sessions. Note that models containing interactions also include main effects.

Model parameter	Model structure	Hypotheses
Detection (p)	$p(\cdot)$	Detection probabilities are constant among visits and sites, regardless of sampling and environmental variables
Detection (p)	$p(\text{Method})$	Detection probabilities associated with live-trapping are higher than auditory methods (hypothesis 1)
Detection (p)	$p(\text{Method}^+)$	Detection probabilities associated with auditory methods are negatively impacted by the prior successful trapping of squirrel individuals (hypothesis 2)
Detection (p)	$p(\text{Session})$	Detection probabilities increase throughout the summer of 2014 (hypothesis 3)
Detection (p)	$p(\text{Visit})$	Detection probability in a given primary period is higher on later sampling visits than first sampling visits, regardless of the sampling method (hypothesis 4)
Detection (p)	$p(\text{Session} + \text{Method})$	Hypotheses 1 + 3
Detection (p)	$p(\text{Session} + \text{Method}^+)$	Hypotheses 2 + 3
Detection (p)	$p(\text{Session} + \text{Visit})$	Hypotheses 3 + 4
Detection (p)	$p(\text{Method}: \text{Tree Density})$	Detection probabilities associated with auditory methods are negatively impacted by the density of large live trees due to sound obstruction.
Detection (p)	$p(\text{Visit}: \text{Method})$	Detection probability in a given primary period from live-trapping is higher on later sampling visits than first sampling visit ("pre-baiting" effect for live-trapping only)
Occupancy (ψ)	$\psi(\text{Tree Density})$	Probabilities of initial site occupancy increase with the density of large live trees
Colonisation (γ)	$\gamma(\cdot)$	Colonisation probabilities are constant throughout the study and independent from any environmental variable
Colonisation (γ)	$\gamma(\text{Session})$	Colonisation probabilities increase from June to August 2014
Local extinction (ε)	$\varepsilon(\cdot)$	Local extinction probabilities are constant throughout the study and independent from any environmental variable
Local extinction (ε)	$\varepsilon(\text{Session})$	Local extinction probabilities decrease from June to August 2014

Note: Covariate acronyms: Method, sampling method (live-trapping, playback count, or point count); Method⁺, sampling method that takes into account whether an individual squirrel was trapped before conducting the two auditory methods (live-trapping, playback count after at least one capture, playback count after no capture, point count after at least one capture, or point count after no capture); Tree Density, number of live trees with a diameter larger than 10 cm; Session, sampling session (i.e. primary period – 3 in total); Visit, sampling visits (i.e. secondary period – 3 in total) within a sampling session. Parameters followed by (·) indicate that they are constant.

over the summer due to changes in density following juvenile dispersal. We introduced the categorical variable *Visit* to test for a possible “pre-baiting” effect, caused by individuals getting accustomed to traps. The *Visit* × *Method* interaction formally tests the pre-baiting effect for live-trapping.

Effect of tree density

Finally, we introduced a variable reporting the density of live trees greater than 10 cm in dbh per hectare (*Tree Density*-numerical variable standardised to zero mean and unit variance). We predicted that detection probability would decrease with *Tree Density* when using point and playback counts due to hearing impediment.

We contrasted the different detection scenarios above to a null model with constant detection probability, for a total of 10 detection probability scenarios. Our study focused on detection probability, but we included a single variable on occupancy to account for potential heterogeneity in occupancy in all models. Specifically, we allowed occupancy to vary with *Tree Density* as large trees provide good habitat for American red squirrels (Carey, 2000). We predicted that more juveniles would disperse between the last two periods rather than between the first two. We considered three different scenarios involving colonisation probability (γ) and extinction probability (ε) (1) probabilities of extinction and colonisation constant across primary periods, (2) probability of extinction varying among primary periods (*Session*), but constant colonisation probability, (3) constant probability of extinction, but colonisation probability varying among primary periods. Thus, we considered a total of 30 *a priori* models (10 scenarios of detection probability × three scenarios of colonisation and extinction probabilities, Appendix B of Supplementary material).

We used an information-theoretic approach based on Akaike's Information Criterion for small samples (AIC_c) to compare candidate models (Burnham and Anderson, 2002). We assessed the goodness-of-fit of the most complex model using an extension of the MacKenzie and Bailey (2004) goodness-of-fit test with 10 000 bootstraps implemented in the *AICcmodavg* package (Mazerolle, 2015). The goodness-of-fit test did not suggest overdispersion ($\hat{c} < 1$). We identified variables appearing in the top-ranked models ($\Delta AIC_c < 4$) and computed model-averaged predictions and 95% unconditional confidence intervals using the entire set of candidate models.

Pooled auditory methods

The analyses described above were also conducted on a second data set consisting of pooled detections from point and playback counts at each visit. Here, we compared detection probabilities from combining two low-cost sampling methods relative to live-trapping. As previously mentioned, playback counts were not entirely conducted over the first sampling session due to technical problems. Thus, the models considered in the second analysis only included two sampling sessions (i.e. primary periods) of three consecutive days each (i.e. secondary periods) in July and August. In this analysis, *Method* became a two-level categorical variable (live-trapping vs combined auditory methods) and *Method*⁺ became a three-level categorical variable (live-trapping, combined auditory methods following no capture, and combined auditory methods following a capture). A total of 10 *a priori* models were explored (Appendix C of Supplementary material). We expected a higher detection probability when combining playback and point counts together than when considering them on their own, because the complementary information on detection patterns among visits should result in a greater number of detections than either method alone. The most complex model did not suggest overdispersion ($\hat{c} < 1$).

Results

Squirrel surveys

We live-trapped a total of 65 American red squirrels over the summer of 2014, with a total effort of 3131 trap nights ($n_{\text{live-trapping}} = 1061, 1057, 1013$ for sessions 1–3, respectively). We recorded the presence of 22 individuals with a total effort of 372 playback calls ($n_{\text{playback.count}} = 12, 180, 180$ for sessions 1–3, respectively), whereas 36 individuals were detected with 360 point counts ($n_{\text{point.count}} = 120$ for each session).

The number of sites where squirrels were detected varied with sampling methods and sampling sessions (Table 2). The total number of sites where squirrels were detected at least once over the summer of 2014 was higher when using point counts (22 sites) than with the two other methods (18 sites each). When combining point and playback counts, a total of 26 sites had at least one detection of American red squirrel over the summer of 2014. A total of 13 sites were apparently colonised between the first and second session, whereas 11 sites were colonised between the second and third session. Likewise, apparent local extinction was observed at four sites between the first and second session, and at 11 sites between the second and third session.

Comparison of sampling methods

All models converged. The top-ranked model consisted of the interactive term between *Method* and *Tree Density* on the detection probability (Table 3). This model had 26% of the Akaike weight and was closely followed by the model allowing the detection probability to vary with the sampling method. Taken together, these two models accounted for 45% of the weight (Table 3). For the two covariates that had some support, multimodel inference indicated that live-trapping had the highest detection probability across all sampling sessions (model-averaged prediction ± unconditional SE: 0.269 ± 0.071), followed by point counts (0.231 ± 0.059), whereas playback counts had the lowest detection probability (0.139 ± 0.057 , Fig. 2). There was neither a difference between live-trapping and point counts (model-averaged effect size on logit scale, [95% CI], i.e. $\text{modavgEffect}_{\text{logit[CI]}}: -0.19, [-1.10, 0.71]$), nor between live-trapping and playback counts ($\text{modavgEffect}_{\text{logit[CI]}}: -0.81, [-1.89, 0.28]$). Increasing density of live large trees from 0 to 2444 trees ha⁻¹ had no effect on the detection probability of any sampling method, i.e. live-trapping ($\text{modavgEffect}_{\text{logit[CI]}}: 1.14, [-1.63, 3.9]$), point count ($\text{modavgEffect}_{\text{logit[CI]}}: -0.48, [-2.02, 1.06]$), and playback count ($\text{modavgEffect}_{\text{logit[CI]}}: -0.68, [-2.57, 1.21]$).

Considering the other variables, there was no evidence of a trapping or handling effect on the detection probability of auditory methods, as the models including (*Method*⁺) had no support (Table 3). Detection probability did not vary with the sampling session and we found no evidence for a pre-baiting effect, because models including this hypothesis on detection probability had no support relative to the other candidate models (sum of Akaike weights = 0.04, Table 3). Finally, there was no support for models allowing local extinction and colonisation probabilities to vary with primary sampling sessions (Table 3).

For the analysis of the detection data pooled among auditory methods, all models also converged. The top-ranked model allowed the detection probability to vary with the interaction between the sampling visit (*Visit*) and the sampling method (*Method*) (Akaike weight = 0.33, Table 4). This model was followed closely by the model allowing the detection probability to vary with the sampling session. Taken together, these two models accounted for 49% of the Akaike weight (Table 4).

Table 2
Number of sites where American red squirrels (*Tamiasciurus hudsonicus*) were detected for each sampling session and each sampling method, with the corresponding percentage in brackets. A total of 60 sites were sampled each session in black spruce forests of northwestern Quebec.

Method	Number of sites where squirrels were detected			Total number of sites where squirrels were detected during the summer of 2014
	Session 1	Session 2	Session 3	
Live-trapping	2 (3)	9 (15)	15 (25)	18 (30)
Point count	12 (20)	12 (20)	7 (12)	22 (37)
Playback count	NA	7 (12)	13 (22)	18 (30)
Combined auditory methods	NA	16 (27)	16 (27)	26 (43)
All methods	12 (20)	21 (35)	21 (35)	34 (57)

Table 3
Ranking of dynamic occupancy models comparing the three sampling methods used to detect American red squirrels (*Tamiasciurus hudsonicus*), based on their relative support (Akaike weight, ω_i). The top-ranked model scored an AICc of 535.36. Models with weights adding up to 0.95 are displayed.

Candidate model	Δ AICc	ω_i	K
$\psi(\text{Tree Density}) p(\text{Tree Density: Method}) \gamma(\cdot) \varepsilon(\cdot)$	0.00	0.26	10
$\psi(\text{Tree Density}) p(\text{Method}) \gamma(\cdot) \varepsilon(\cdot)$	0.75	0.19	7
$\psi(\text{Tree Density}) p(\text{Tree Density: Method}) \gamma(\text{Session}) \varepsilon(\cdot)$	1.51	0.12	11
$\psi(\text{Tree Density}) p(\text{Method}) \gamma(\text{Session}) \varepsilon(\cdot)$	2.57	0.07	8
$\psi(\text{Tree Density}) p(\text{Session + Method}) \gamma(\cdot) \varepsilon(\cdot)$	2.89	0.06	9
$\psi(\text{Tree Density}) p(\text{Tree Density: Method}) \gamma(\cdot) \varepsilon(\text{Session})$	3.00	0.06	11
$\psi(\text{Tree Density}) p(\text{Method}) \gamma(\cdot) \varepsilon(\text{Session})$	3.27	0.05	8
$\psi(\text{Tree Density}) p(\text{Visit}) \gamma(\cdot) \varepsilon(\cdot)$	3.67	0.04	7
$\psi(\text{Tree Density}) p(\text{Visit}) \gamma(\text{Session}) \varepsilon(\cdot)$	5.52	0.03	8
$\psi(\text{Tree Density}) p(\text{Session + Method}) \gamma(\cdot) \varepsilon(\text{Session})$	5.62	0.02	10
$\psi(\text{Tree Density}) p(\cdot) \gamma(\cdot) \varepsilon(\cdot)$	5.77	0.02	5
$\psi(\text{Tree Density}) p(\text{Session + Method}) \gamma(\text{Session}) \varepsilon(\cdot)$	5.78	0.01	10
$\psi(\text{Tree Density}) p(\text{Method}^*) \gamma(\cdot) \varepsilon(\cdot)$	5.80	0.01	9
$\psi(\text{Tree Density}) p(\text{Visit}) \gamma(\cdot) \varepsilon(\text{Session})$	6.17	0.01	8

Although combining the two auditory sampling methods (point and playback counts) increased detection probabilities of American red squirrels compared when using each separately, we found no difference between the combined auditory methods and live-trapping (Fig. 3, $\text{modavgEffect}_{\logit[CI]}: 0.14 [-0.89, 1.17]$). Moreover, there was no effect of the sampling day on the detection probability associated to either sampling method, as confidence intervals around model-averaged differences between visits largely included 0 for all methods. Similarly, detection probability did not vary with the sampling session ($\text{modavgEffect}_{\logit[CI]}: -0.24 [-1.25, 0.77]$). There was no support for models that included the effect of tree density or a live-trapping effect on detection probability (Table 4).

Costs of sampling methods

Total costs differed by several thousands of Canadian dollars between live-trapping (\$40 004.81) and the two other sampling methods used in the present study (\$31 364.48 and \$14 050.50 for playback count and point count respectively, Appendix D of Supplementary material). This was not surprising as the number of hours spent in the field was between 1.1 and 3.3 times greater for live-trapping compared to either passive point counts or playback, respectively.

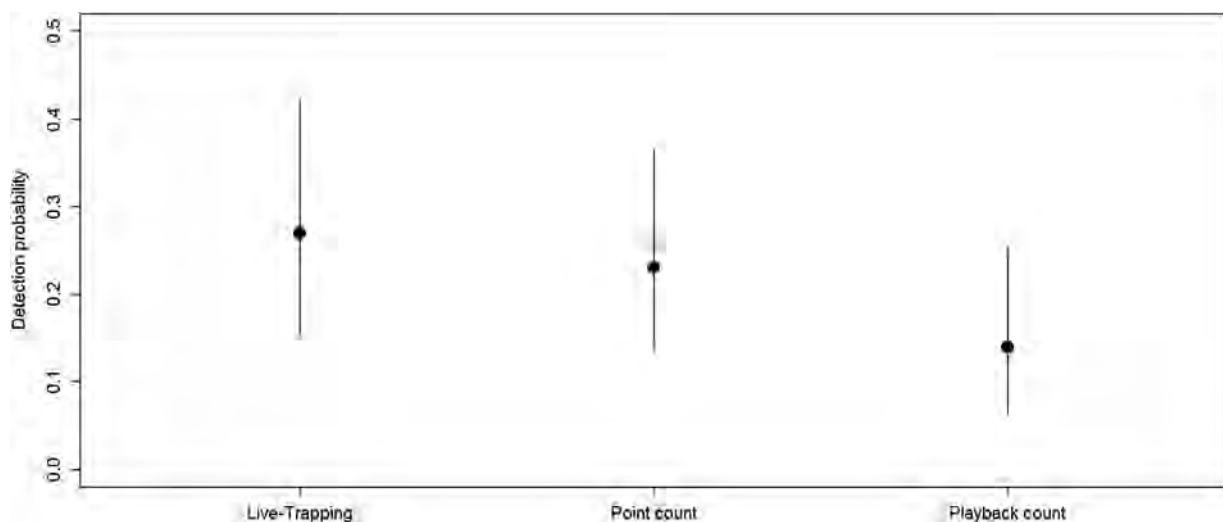


Fig. 2. Predicted detection probabilities for three methods used to sample American red squirrel (*Tamiasciurus hudsonicus*). Error bars denote 95% unconditional confidence intervals.

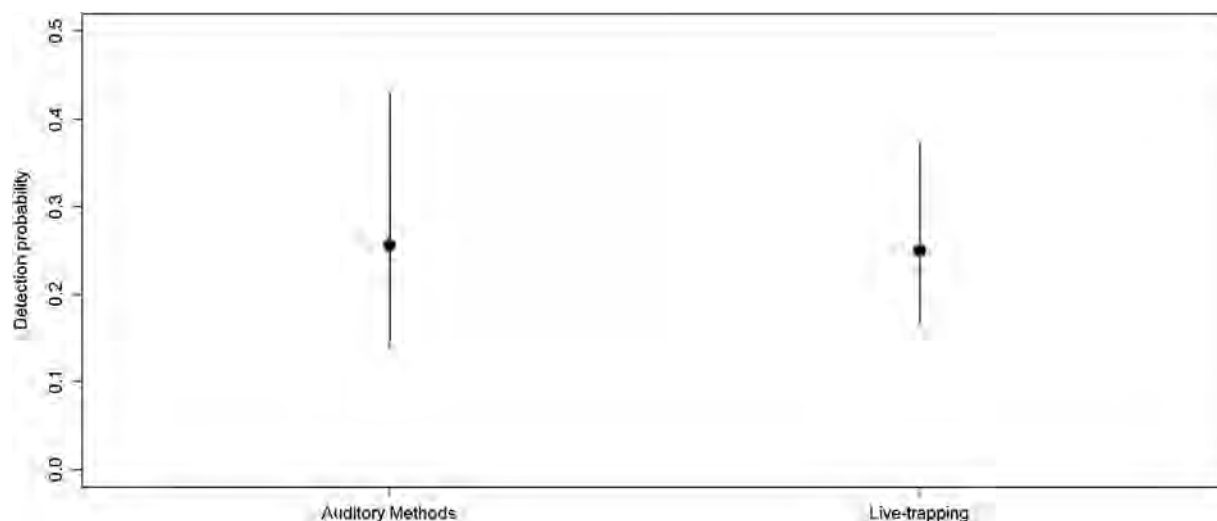


Fig. 3. Predicted detection probabilities of American red squirrels (*Tamiasciurus hudsonicus*) using either live-trapping or point counts combined with playback count. Error bars denote 95% unconditional confidence intervals.

Table 4

Ranking of dynamic occupancy models comparing live-trapping vs auditory methods combined (point and playback counts) in detecting American red squirrels (*Tamiasciurus hudsonicus*), based on their relative support (Akaike weight, ω_i). The top-ranked model scored an AICc of 470.94. Models with weights adding up to 0.95 are displayed.

Candidate model	Δ AICc	ω_i	K
$\psi(\text{Tree Density}) p(\text{Visit: Method}) \gamma(\cdot) \varepsilon(\cdot)$	0.00	0.33	10
$\psi(\text{Tree Density}) p(\text{Session}) \gamma(\cdot) \varepsilon(\cdot)$	1.47	0.16	6
$\psi(\text{Tree Density}) p(\text{Session + Visit}) \gamma(\cdot) \varepsilon(\cdot)$	2.05	0.12	8
$\psi(\text{Tree Density}) p(\text{Obstruction: Method}) \gamma(\cdot) \varepsilon(\cdot)$	2.44	0.10	8
$\psi(\text{Tree Density}) p(\cdot) \gamma(\cdot) \varepsilon(\cdot)$	2.60	0.09	5
$\psi(\text{Tree Density}) p(\text{Visit}) \gamma(\cdot) \varepsilon(\cdot)$	3.00	0.08	7
$\psi(\text{Tree Density}) p(\text{Session + Method}) \gamma(\cdot) \varepsilon(\cdot)$	3.21	0.07	7

Discussion

There is a growing body of literature that focuses on the importance of accounting for imperfect detection probability when studying patterns of species distribution and population parameters (e.g., MacKenzie et al., 2003; Mazerolle et al., 2007; Smith et al., 2007; Kéry and Schmidt, 2008; Kellner and Swihart, 2014). As detection can be greatly affected by the sampling protocol, studies have emphasised the importance of carefully defining the sampling period, allocating sufficient effort, and using appropriate sampling techniques (Drapeau et al., 1999; Otto and Roloff, 2011). Squirrel occupancy has been studied using several sampling methods other than live-trapping (e.g. Buchanan et al., 1990; Fisher et al., 2005; Mortelliti and Boitani, 2008; Gurnell et al., 2011; Allard-Duchêne et al., 2014), but to our knowledge, no one specifically compared the detection probability of alternative methods to live-trapping. In the present study, we quantified the detection probability of three different sampling methods, namely live-trapping, playback, and point counts. Given the sampling effort that was defined for all three sampling methods, live-trapping and point counts had the highest probability of detection compared to playback counts (Fig. 2). However, we found no difference between live-trapping and point count methods. This indicates that point counts could be considered as an effective sampling method when focusing on squirrel site occupancy, which could often be conducted simultaneously to auditory ornithological surveys. Indeed, American red squirrels are opportunistic predators of bird nests in boreal forests, despite being mostly granivorous (Reitsma et al., 1990; Bayne and Hobson, 2002). The abundance of nesting birds and nest densities decline in

the presence of American red squirrels (Darveau et al., 1997; Martin and Joron, 2003; Willson et al., 2003), potentially reducing the local distribution of some bird species (Siepielki, 2006). Reliance upon point counts to investigate co-occurrence patterns of American red squirrels and nesting birds agrees with the view of Richmond et al. (2010), who recommend the use of a unique sampling technique for measuring occupancy of all species of interest.

Live-trapping has been traditionally used for sampling small mammals in mark-recapture studies (e.g., Harris et al., 1990; Pradel, 1996) and as such, live-trapping enables the estimation of several population parameters that cannot be obtained by alternative methods. Nevertheless, our results suggest that using point counts to study site occupancy by American red squirrels presents several benefits. Point counts are non-invasive (Ralph et al., 1995) and easy to implement over a large number of sites. In our study, we estimate that point counts cost half as much than live-trapping, due to halving the travel time to sites. Besides, for similar effectiveness in detecting individuals, less invasive methods should always be preferred over invasive methods (Hubbard, 2008; Gompper et al., 2006).

Although playback counts had slightly lower detection probabilities than the two other sampling techniques (Fig. 2), there was no real difference according to multimodel inference. Live-trapping and territorial calls stem from different behaviours, but detection probability from live-trapping and auditory methods was surprisingly similar. These results emphasise that the playback count technique is worth considering when monitoring squirrel occupancy. Like point counts, the biological process behind playback counts is well suited to study occupancy (Burton et al., 2015). Both auditory methods rely on territorial behaviours displayed by squirrels. Unlike live-trapping which could sample either resident squirrels or dispersing individuals, auditory methods mainly focus on individuals holding a territory. Nonetheless, the choice of recorded calls during playback counts may influence the intensity of territorial behaviour of squirrels. Responses to playback calls varies with the local density of squirrels (Shonfield et al., 2012), sex, and breeding status (Price et al., 1990). American red squirrels are also more likely to respond to territorial calls from an unknown individual than to those of neighbours (Price et al., 1990). It would thus be interesting to test whether detection probabilities vary with the type of call being used during playback counts.

Sampling techniques must be adapted to the species of interest, but also to the environment in which sampling will be conducted.

Site characteristics can influence the effectiveness of sampling techniques to detect species. Surprisingly, the density of large trees did not negatively affect the two auditory methods that we used, which disagrees with the conclusions of several studies (e.g., Richards, 1981; Pacifici et al., 2008) and with our own prediction. The detection probability of American red squirrels seemed to slightly increase with the density of large live trees regardless of the sampling method used to detect individuals. An increase in large trees (both dead and alive) may enable a denser population of red squirrels to establish territories or favour females sharing territories with their juveniles (Wheatley et al., 2002; Patterson and Malcolm, 2010), because large trees represent important attributes in boreal forests, providing shelter and food for a number of animal species (Gauthier et al., 2008). However, we found no relationship between squirrel occupancy and the number of large live trees in our study.

Sampling period is another factor that could influence the detection of species with different sampling techniques. In this study, the detection probability of American red squirrels did not vary with sampling session, although we expected squirrels to vocalise more frequently in late summer, i.e., when juveniles begin dispersing to find territories and when territory boundaries must be clearly advertised (Larsen and Boutin, 1994). Juvenile dispersal potentially did not occur by the end of our study, and this would explain the lack of change in the probabilities of colonisation and local extinction when allowed to vary with the sampling session. Squirrels are active year-round, modifying their social behaviour at different periods of the year (e.g., peak in juvenile dispersal, food-hoarding – Steele, 1998; Larsen and Boutin, 1994; Wauters and Dhondt, 1993). Likewise, changes in their environment (such as masting events) may alter their likelihood to enter live-traps (Selonen et al., 2015). Our study focused exclusively on the summer period, but extending the sampling to other times of the year might reveal different patterns.

Some studies advocate combining several techniques to increase the probability of detecting a species of interest (Garden et al., 2007; Haigh et al., 2012; Petitot et al., 2014). Live-trapping and point counts are comparable in terms of detection probability. Pooling detection data that were obtained by playback and point counts did not increase substantially detection probability. However, the probability of detection (predicted average probability and SE) from the combined methods matched that obtained with our live-trapping effort. Our results emphasise the complementarity of point and playback count methods when studying occupancy by American red squirrels.

In this study, we showed that auditory methods are reliable in detecting American red squirrels. These results show promise for site occupancy studies of other vocal mammalian species such as eastern chipmunks (*Tamias striatus*) and Douglas squirrels (*Tamiasciurus douglasii*) (Smith, 1978; Snyder, 1982; Burke Da Silva et al., 1994). To a lesser extent, eastern gray squirrels (*Sciurus carolinensis*) and Eurasian red squirrels (*Sciurus vulgaris*) also occasionally vocalise (Lishak, 1984; Randler, 2006; Getschow et al., 2013). The sciurid species mentioned above are also nest predators (Reitsma et al., 1990; Callahan, 1993; Newson et al., 2010; Mori et al., 2013). Formally estimating the detection probability of point and playback counts on *Tamiasciurus* and *Tamias* species would be valuable where individuals might influence the nesting success of birds. Likewise, similar studies should be conducted for both *Sciurus* species, after adapting the protocol to these two quieter species. Obtaining valid occupancy data of sciurid nest predators and breeding birds at the same sites is essential to investigate the co-occurrence of the two groups as well as examine their shared responses to habitat disturbance.

Acknowledgements

This study was funded by fellowships from the Fonds de Recherche du Québec – Nature et Technologies (FRQNT), the Natural Sciences and Engineering Research Council of Canada (NSERC), and the University of Quebec in Abitibi-Témiscamingue (UQAT). The authors thank field assistants, especially A. Juigner, H. Dion-Phénix and F. Bordeleau-Martin, who provided invaluable assistance. Special thanks to W. Parsons for reviewing the English grammar, style, and syntax of this manuscript. Two anonymous reviewers also provided helpful comments on an earlier version of this manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2016.11.003>.

References

- Allard-Duchêne, A., Pothier, D., Dupuch, A., Fortin, D., 2014. Temporal changes in habitat use by snowshoe hares and red squirrels during post-fire and post-logging forest succession. *For. Ecol. Manag.* 313, 17–25.
- Bayne, E.M., Hobson, K.A., 2000. Relative use of contiguous and fragmented boreal forest by red squirrels (*Tamiasciurus hudsonicus*). *Can. J. Zool.* 78, 359–365.
- Bayne, E.M., Hobson, K.A., 2002. Effects of red squirrel (*Tamiasciurus hudsonicus*) removal on survival of artificial songbird nests in boreal forest fragments. *Am. Midl. Nat.* 147, 72–79.
- Bergeron, Y., Gauthier, S., Flannigan, M., Kafka, V., 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology* 85, 1916–1932.
- Blouin, J., Berger, J.P., 2002. Guide de reconnaissance des types écologiques-Région écologique 5a Plaines de l'Abitibi. Ministère des Ressources Naturelles et de la Faune, Direction des Inventaires Forestiers, Division de la classification écologique et productivité des stations, Québec. Rep. n° 2002–3072, Québec, Canada, pp. 1–180.
- Bosson, C.O., Islam, Z., Boonstra, R., 2012. The impact of live trapping and trap model on the stress profiles of North American red squirrels. *J. Zool.* 288, 159–169.
- Boutin, S., Wauters, L.A., McAdam, A.G., Humphries, M.M., Tosi, G., Dhondt, A.A., 2006. Anticipatory reproduction and population growth in seed predators. *Science* 314, 1928–1930.
- Buchanan, J.B., Lundquist, R.W., Aubry, K.B., 1990. Winter populations of Douglas' squirrels in different-aged Douglas-fir forests. *J. Wildl. Manage.* 54, 577–581.
- Burke Da Silva, K., Kramer, D.L., Weary, D.M., 1994. Context-specific alarm calls of the eastern chipmunk, *Tamias striatus*. *Can. J. Zool.* 72, 1087–1092.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach, 2nd ed. Springer-Verlag, New York.
- Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., Boutin, S., 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol.* 52, 675–685.
- Callahan, J.R., 1993. Squirrels as predators. *Great Basin Nat.* 1, 137–144.
- Carey, A.B., 2000. Effects of new forest management strategies on squirrel populations. *Ecol. Appl.* 10, 248–257.
- Dantzer, B., Boutin, S., Humphries, M., McAdam, A.G., 2012. Behavioral responses of territorial red squirrels to natural and experimental variation in population density. *Behav. Ecol. Sociobiol.* 66, 865–878.
- Darveau, M., Bélanger, L., Huot, J., Mélançon, E., DeBellefeuille, S., 1997. Forestry practices and the risk of bird nest predation in a boreal coniferous forest. *Ecol. Appl.* 7, 572–580.
- Drapeau, P., Leduc, A., McNeil, R., 1999. Refining the use of point counts at the scale of individual points in studies of bird-habitat relationships. *J. Avian Biol.* 30, 367–382.
- Elliot, L., Mack, T., 1994. *Le Son De Nos Forêts*. Centre de conservation de la faune aîlée de Montréal, Canada.
- Fenton, N.J., Bergeron, Y., 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. *J. Veg. Sci.* 17, 65–76.
- Fisher, J.T., Boutin, S., Hannon, S.J., 2005. The protean relationship between boreal forest landscape structure and red squirrel distribution at multiple spatial scales. *Land. Ecol.* 20, 73–82.
- Fiske, I., Chandler, R., 2011. Unmarked: an R package for the fitting hierarchical models of wildlife occurrence and abundance. *J. Stat. Softw.* 43, 1–23.
- Garden, J.G., McAlpine, C.A., Possingham, H.P., Jones, D.N., 2007. Using multiple survey methods to detect terrestrial reptiles and mammals: what are the most successful and cost-efficient combinations? *Wildl. Res.* 34, 218–227.
- Gauthier, S., Vaillancourt, M.A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P., Bergeron, Y., 2008. *L'aménagement écosystémique en forêt boréale*, 1st ed. Presses de l'Université du Québec, Québec, Canada.

- Getschow, C.M., Rivers, P., Sterman, S., Lumpkin, D.C., Tarvin, K.A., 2013. Does gray squirrel (*Sciurus carolinensis*) response to heterospecific alarm calls depend on familiarity or acoustic similarity? *Ethology* 119, 983–992.
- Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A., Cryan, J.R., 2006. A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. *Wildl. Soc. Bull.* 34, 1142–1151.
- Green, E., Meagher, T., 1998. Red squirrels, *Tamiasciurus hudsonicus*, produce predator-class specific alarm calls. *Anim. Behav.* 55, 511–518.
- Gurnell, J., McDonald, R., Lurz, P.W.W., 2011. Making red squirrels more visible: the use of baited visual counts to monitor populations. *Mammal Rev.* 41, 244–250.
- Haigh, A., Butler, F., O'Riordan, R.M., 2012. An investigation into the techniques for detecting hedgehogs in a rural landscape. *J. Negat. Results* 9, 15–26.
- Harris, S., Cresswell, W.J., Forde, P.G., Trehwella, W.J., Woodlard, T., Wray, S., 1990. Home range analysis using radiotracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev.* 20, 97–123.
- Hubbard, C.R., 2008. A Comparison of Invasive and Non-invasive Techniques for Measuring Fiddler Crab Density in a Salt Marsh. (M.Sc. Dissertation), Georgia Southern University, Statesboro, USA.
- Imbeau, L., St-Laurent, M.H., Marzell, L., Brodeur, V., 2015. Current capacity to conduct ecologically sustainable forest management in northeastern Canada reveals challenges for conservation of biodiversity. *Can. J. For. Res.* 45, 567–578.
- Kéry, M., Schmidt, B.R., 2008. Imperfect detection and its consequences for monitoring in conservation. *Community Ecol.* 9, 207–216.
- Kellner, K.F., Swihart, R.K., 2014. Accounting for imperfect detection in ecology: a quantitative review. *PLoS One* 9, e111436.
- Klenner, W., Charles, J., Krebs, C.J., 1991. Red squirrel population dynamics I. The effect of supplemental food on demography. *J. Anim. Ecol.* 60, 961–978.
- Larsen, K.W., Boutin, S., 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. *Ecology* 75, 214–223.
- Larsen, K.W., Boutin, S., 1995. Exploring territory quality in the North American red squirrel through removal experiments. *Can. J. Zool.* 73, 1115–1122.
- Larsen, K.W., 1993. Female Reproductive Success in the North American Red Squirrel (*Tamiasciurus hudsonicus*). Ph. D. Thesis. Department of Zoology, University of Alberta, Edmonton.
- Lishak, R.S., 1984. Alarm vocalizations of adult gray squirrels. *J. Mammal.* 65, 681–684.
- MacKenzie, D.I., Bailey, L.L., 2004. Assessing the fit of site-occupancy models. *J. Agric. Biol. Environ. Stat.* 9, 300–318.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. *Ecology* 84, 2200–2207.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. *Occupancy Estimation and Modelling*. Academic Press Burlington, USA.
- Martin, J.L., Joron, J., 2003. Nest predation in forest birds: influence of predator type and predator's habitat quality. *Oikos* 102, 641–653.
- Mazerolle, M.J., Bailey, L.L., Kendall, W.L., Royle, J.A., Converse, S.J., Nichols, J.D., 2007. Making great leaps forward: accounting for detectability in herpetological field studies. *J. Herpetol.* 41, 672–689.
- Mazerolle, M.J., 2015. AICcmovavg: Model Selection and Multimodel Inference Based on (Q)AIC(c). R Package Version 2.0-3.
- Mori, E., Ancillotto, L., Menchetti, M., Romeo, C., Ferrari, N., 2013. Italian red squirrels and introduced parakeets: victims or perpetrators? *Hystrix* 24, 195–196.
- Mortelliti, A., Boitani, L., 2008. Inferring red squirrel (*Sciurus vulgaris*) absence with hair tubes surveys: a sampling protocol. *Eur. J. Wildl. Res.* 54, 353–356.
- Newson, S.E., Rexstad, E.A., Baillie, S.R., Buckland, S.T., Aebischer, N.J., 2010. Population change of avian predators and grey squirrels in England: is there evidence for an impact on avian prey populations? *J. Appl. Ecol.* 47, 244–252.
- Otto, C.R.V., Roloff, G.J., 2011. Using multiple methods to assess detection probabilities of forest-floor wildlife. *J. Wildl. Manag.* 75, 423–431.
- Pacifici, K., Simons, T.R., Pollock, K.H., 2008. Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. *Auk* 125, 600–607.
- Patterson, J.E., Malcolm, J.R., 2010. Landscape structure and local habitat characteristics as correlates of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus* occurrence. *J. Mammal.* 91, 642–653.
- Pearce, J.L., Boyce, M.S., 2006. Modelling distribution and abundance with presence-only data. *J. Appl. Ecol.* 43, 405–412.
- Petitot, M., Manceau, N., Geniez, P., Besnard, A., 2014. Optimizing occupancy surveys by maximizing detection probability: application to amphibian monitoring in the Mediterranean region. *Ecol. Evol.* 4, 3538–3549.
- Pollock, K.H., Nichols, J.D., Simons, T.R., Farnworth, G.L., Bailey, L.L., Sauer, J.R., 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13, 1–15.
- Pradel, R., 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52, 703–709.
- Price, K., Boutin, S., Ydenberg, R., 1990. Intensity of territorial defense in red squirrels: an experimental test of the asymmetric war of attrition. *Behav. Ecol. Sociobiol.* 27, 217–222.
- R Development Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ralph, C.J., Sauer, J.R., Droege, S., 1995. Monitoring bird populations by point counts. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-GTR-149, Albany, USA.
- Randler, C., 2006. Red squirrels (*Sciurus vulgaris*) respond to alarm calls of Eurasian jays (*Garrulus glandarius*). *Ethology* 112, 411–416.
- Reitsma, L.R., Holmes, R.T., Sherry, T.W., 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and Eastern chipmunks, *Tamias striatus*, on nest predation in a Northern hardwood forest: an artificial nest experiment. *Oikos* 57, 375–380.
- Richards, D.G., 1981. Environmental acoustics and censuses of singing birds. *Stud. Avian Biol.* 6, 297–300.
- Richmond, O.M.W., Hines, J.E., Beissinger, S.R., 2010. Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. *Ecol. Appl.* 20, 2036–2046.
- Russell, R.E., Lehmkühl, J.F., Buckland, S.T., Saab, V.A., 2010. Short-term responses of red squirrels to prescribed burning in the Interior Pacific Northwest, USA. *J. Wildl. Manag.* 74, 12–17.
- Scott, J.M., Heglund, P.J., Morrison, M.L., Hauffer, J.B., Raphael, M.G., Wall, W.A., Samson, F.B., 2002. *Predicting Species Occurrences: Issues of Scale and Accuracy*, 1st ed. Island Press, Washington, USA.
- Selonen, V., Varjonen, R., Korpimäki, E., 2015. Immediate or lagged responses of a red squirrel population to pulsed resources. *Oecologia* 177, 401–411.
- Shonfield, J., Taylor, R.W., Boutin, S., Humphries, M.M., McAdam, A.G., 2012. Territorial defence behaviour in red squirrels is influenced by local density. *Behaviour* 149, 369–390.
- Siepielki, A.M., 2006. A possible role for red squirrels in structuring breeding bird communities in lodgepole pine forests. *Condor* 108, 232–238.
- Sieving, K.E., Willson, M.F., 1998. Nest predation and avian species diversity in northwestern forest understory. *Ecology* 79, 2391–2402.
- Sjögren-Gulve, P., Hanski, I., 2000. Metapopulation viability analysis using occupancy models. *Ecol. Bull.* 48, 53–71.
- Smith, J.B., Jenks, A.J., Klaver, R.W., 2007. Evaluating detection probabilities for American marten in the Black Hill, South Dakota. *J. Wildl. Manag.* 71, 2412–2416.
- Smith, C.C., 1978. Structure and function of the vocalizations of tree squirrels (*Tamiasciurus*). *J. Mammal.* 59, 793–808.
- Snyder, D.P., 1982. *Tamias striatus*. *Mamm. Species* 168, 1–8.
- Steele, M.A., 1998. *Tamiasciurus hudsonicus*. *Mamm. Species* 586, 1–9.
- Wauters, L., Dhondt, A.A., 1993. Immigration pattern and success in red squirrels. *Behav. Ecol. Sociobiol.* 33, 159–167.
- Wheatley, M., Larsen, K.W., Boutin, S., 2002. Does density reflect habitat quality for North American red squirrels during a spruce-cone failure? *J. Mammal.* 83, 716–727.
- Willson, M.F., De Santo, T.L., Sieving, K.E., 2003. Red squirrels and predation risk to bird nests in northern forests. *Can. J. Zool.* 81, 1202–1208.
- Wilson, D.R., Goble, A.R., Boutin, S., Humphries, M.M., Coltman, D.W., Gorrell, J.C., Shonfield, J., McAdam, A.G., 2015. Red squirrels use territorial vocalizations for kin discrimination. *Anim. Behav.* 107, 79–85.