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À mes parents, à mes ami(e)s et à tous les passionnés
que j'ai rencontrés tout au long de ces années.

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# Avant-propos

Cette thèse est constituée de trois chapitres présentés sous la forme d'articles scientifiques rédigés en anglais. Je suis l'auteur principal de chacun des articles et André Desrochers, mon directeur de recherche et Gilles Seutin, mon co-directeur, sont co-auteurs. Ces derniers ont contribué de façon variable à la formulation des objectifs, aux analyses des données, à l'interprétation des résultats et à la révision des articles. L'introduction générale de la thèse présente brièvement les objectifs et les méthodes pour chacun des chapitres. Les chapitres 1 et 2 sont présentés tels que publiés. L'article constituant le chapitre 3 est encore en révision, je présente donc la version du 16 mars 2018, telle que soumise pour publication.

## Chapitre 1

Le premier chapitre a été publié en 2011 : Aubry, Y., A. Desrochers, and G. Seutin. 2011. Response of Bicknell's Thrush (*Catharus bicknelli*) to boreal silviculture and forest edges: a radio-tracking study. *Canadian Journal of Zoology* 89(6):474-482. doi:10.1139/z11-011.

## Chapitre 2

Le second chapitre a été publié en 2016: Aubry, Y., A. Desrochers, and G. Seutin. 2016. Regional patterns of habitat use by a Threatened forest bird, the Bicknell'sThrush, in Quebec. *Canadian Journal of Zoology* 94(4):301-309. doi: 10.1139/cjz-2015-0209.

## Chapitre 3

Le troisième article s'intitule « Aubry, Y., A. Desrochers, and G. Seutin. Not enough habitat or not enough birds? Low habitat occupancy by Bicknell's Thrush (*Catharus bicknelli*) in Québec's Laurentian Highlands. ». Celui-ci est actuellement en révision au magazine: *Avian Conservation and Ecology-Écologie et Conservation des Oiseaux (ACE-ECO)*.

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# Introduction générale

## Gestion forestière et conservation de la biodiversité

Depuis la signature de la Convention sur la biodiversité en 1992, le monde de la foresterie n'a cessé d'être sollicité pour intégrer la conservation de la biodiversité dans son modèle d'affaire et dans ses pratiques d'exploitation de la ressource (Sharma et Henriques 2005). Les exploitants de cette ressource étaient et sont toujours sous la surveillance tant des groupes de citoyens, d'environnementalistes, d'actionnaires que de consommateurs. De plus, les différents modes de certification des produits forestiers ont été déterminants dans l'intégration des valeurs et des principes de cette convention dans la culture entrepreneuriale de l'industrie forestière canadienne (Sharma et Henriques 2005). La gestion des ressources forestières évolue pour faire face, entre autres, aux changements climatiques et aux enjeux sociaux en reconnaissant la nature complexe de cette ressource (Messier et al. 2016). Le Canada détient plus de 30 % des forêts mondiales dites primaires (peu ou pas modifiées par des actions anthropiques ; Mackey et al. 2015). Dans le contexte où la demande pour la matière ligneuse demeure croissante, il y a un intérêt à repousser les limites septentrionales de la forêt commerciale vers le nord ce qui affecterait la destinée de ces forêts et de la faune qui s'y retrouve (Imbeau et al. 2015). Plusieurs chercheurs canadiens sont alarmés par le sort appréhendé des oiseaux de l'écosystème boréal et proposent la protection de vastes étendues et le développement durable des ressources qui y sont exploitées (Wells et al. 2014). À l'échelle mondiale, le mouvement *Nature needs half* fait la promotion d'une vision basée sur la science priorisant une saine relation entre la nature et les gens garantissant qu'une quantité suffisante d'espaces naturels soient protégés et inter-reliés pour assurer une protection et le maintien des écosystèmes et de la biodiversité (Locke 2013; Noss et al. 2012; site web : http://natureneedshalf.org/). Par contre, ce mouvement ne fait pas unanimité dans la communauté scientifique (Kopnina 2016) et les collectivités qui dépendent de la ressource forestière (Rotherham et Armson 2016).

L'évaluation de la conservation de la biodiversité demeure un défi de taille pour les aménagistes tant par la définition d'objectifs mesurables que par sa complexité (Tear et al. 2005). Pour plusieurs, l'usage d'indicateurs (*single species umbrella sensu* Roberge et Angelstam 2004) simplifie cette tâche et permet d'estimer une partie des objectifs de conservation de la biodiversité. Par contre, dans bien des cas ces indicateurs apportaient peu d'information et n'étaient pas représentatifs des autres organismes qui n'avaient pas été mesurés (Hagan et Whitman 2006 : Roberge et Angelstam 2006).

Au Québec, la conservation de la diversité biologique est inscrite dans les critères d'aménagement durable des forêts (MFFP 2015). Jusqu'à récemment, les pratiques sylvicoles sur le territoire québécois étaient largement dominées par les coupes totales créant de grandes ouvertures et de vastes peuplements équiens (Boucher et al. 2015). Cette situation représentait une divergence importante de la variabilité des peuplements selon un régime de perturbations naturelles (Cyr et al.2009). Avec la venue de l'aménagement écosystémique, ces pratiques ont été modulées pour que les résultats se rapprochent des régimes de perturbations naturelles (Kuuluvainen et al. 2015; Bergeron et al. 1999) sans compromettre les fonctions biologiques et les propriétés socio-économiques des écosystèmes forestiers (MFFP 2015).

## Concept d'habitat

La mise en application des différentes mesures de protection de la biodiversité du milieu forestier doit reposer sur de bonnes connaissances des habitats utilisés et de l'écologie des différents organismes considérés. L'ensemble des attributs environnementaux physiques et des ressources nécessaires à une espèce animale pour sa survie et sa reproduction représentent la définition de base de l'habitat (Block et Brennan 1993). Les processus interactifs entre les facteurs biotiques et abiotiques, intrinsèques ou non à un habitat (Jones 2001) déterminent la qualité de l'habitat et les paramètres démographiques qui en découlent pour une espèce donnée (Ruskin et al. 2017).

Il est essentiel d'identifier quelles informations un oiseau utilise pour s'établir dans un habitat particulier. Une ou plusieurs informations peuvent être considérées dans le processus de sélection : la ressource alimentaire (Rolstad et al. 2000), la structure et la composition végétale de l'habitat, la disponibilité de bons sites de nidification (Martin et Roper 1988), la présence de congénères/conspécifiques (Ward et Schlossberg 2004; Etterson 2003; Lane et al. 2001; Muller et al. 1997; Smith et Peacock 1990; Stamps 1988) ou d'une autre espèce (e.g.: attraction hétérospécifiques; Krebs 2001; Forsman et al. 1998), le succès reproducteur des années antérieures (Desrochers et Magrath 1996) ou même celui des voisins, obtenu par l'accès à « l'information publique » (*sensu* Doligez et al. 1999; 2002; 2003; 2004; Switzer 1997; Wagner et Danchin 2003). L'échelle spatiale peut également moduler le choix de l'habitat. La sélection de l'habitat suivrait un processus spatial hiérarchique (Jones 2001; Rolstad et al. 2000; Johnson 1980; Hildén 1965). Cody (1981) mentionne que la structure de végétation, la compétition et la productivité en ressource alimentaire sont corrélés avec la qualité d'un habitat et son taux d'occupation.

Dans un contexte démographique, Fretwell et Lucas (1970) décrivent la répartition des individus selon deux modèles : le modèle de distribution-idéale-libre et le modèle de distribution-idéale-despotique. Dans le premier cas, en situation de trop forte densité dans les habitats de première qualité, les individus s'établissent librement dans des habitats qualifiés de sous-optimaux alors que dans le second, les individus territoriaux occupant les habitats de bonne qualité contraignent les congénères aux habitats sous-optimaux. Dans les deux cas, on est en présence d'un mécanisme de sélection de l'habitat de densité –dépendance (Rosenzweig 1991).

Par ailleurs, la répartition d'un habitat pour une espèce n'est pas toujours continue, elle peut être fragmentée. Cette fragmentation affecte les oiseaux de différentes façons (Taylor 2017; Smith et al. 2011; Fisher et Lindenmayer 2007; Fahrig 2002; Villard et al. 1995). Deux des conséquences sont le niveau d'isolement des habitats et la création de bordures (Faaborg et al. 1993) ce qui peut altérer la dynamique interactive des communautés ou organismes associés (Ries et al. 2004; Desrochers et Fortin 2000; Donovan et al. 1997; Murcia 1995; Yahner 1988). D'autres facteurs tels qu'une faible densité de l'espèce, un ratio des sexes biaisé, un faible taux de recrutement et de dispersion de l'espèce peuvent également avoir des effets négatifs sur la démographie locale de l'espèce (Greene 2003).

## Foresterie et structure de l'habitat

Au-delà des coupes qui ont façonné le paysage de la forêt québécoise (Boucher et al. 2015), les traitements sylvicoles ont également contribué à modifier la structure des forêts exploitées (Homyack et al. 2004) tant au niveau de la densité que de la composition des peuplements. Plus particulièrement, l'éclaircie précommerciale, un traitement qui a connu son essor dans les années '80, a pour objectif de stimuler la croissance en diamètre/radiale des arbres conservés et à réduire la vulnérabilité des peuplements de sapins baumiers aux dommages générés par la tordeuse des bourgeons de l'épinette (Barrette et al. 2016). Les jeunes peuplements conifériens de succession (stade gaulis), généralement très denses sont éclaircies pour ne conserver que des arbres/tiges d'avenir distantes de 1-2 m, pour une densité finale de 1500-3125 tiges*ha$^{-1}$ (MRNFP 2004). En présence de sapin et d'épinette, l'épinette est favorisée. Les interventions sont pratiquées dans des peuplements de 15-20 ans ou d'environ 2-3 m de hauteur. Ces traitements représentent une source importante de revenue pour plusieurs communautés rurales du Québec. Les résultats de l'éclaircie précommerciale semblent varier selon plusieurs facteurs tels que la densité et l'âge initiale des tiges, la qualité des sols, les objectifs de production du traitement (p.ex. : bois de sciage *vs* copeaux) et du temps de rotation des coupes (Schneider et al. 2013; Pitt et Lanteigne 2008; Pothier 2002) et la vulnérabilité des peuplements aux épidémies.

Après un tel traitement, le changement dans la densité, la structure et la composition des peuplements peuvent affecter plusieurs espèces fauniques (Homyak et al. 2004, 2007; Griffin et Mills 2007; Bujold 2004). Pa exemple, la réduction de la densité de tiges réduit la protection des nids de plusieurs espèces contre la prédation (Martin et Joron, 2003). Lorsque la densité des tiges et la composition des peuplements traités par une éclaircie de peuplements forestiers est comparée aux peuplements adjacents, non-traités, le contraste est tel que ce type d'éclaircie peut constituer une forme de fragmentation de l'habitat.

## L'application des « filtres fin et brut » dans le contexte forestier

Au Québec, on applique le principe de filtre brut pour identifier des territoires uniques menant à la création d'aires protégées (Girardin et al. 2002). Le filtre brut est un moyen de protéger certains écosystèmes et la biodiversité qui s'y trouve (Hunter 1990; Noss 1987). L'aménagement écosystémique, tel que favorisé au Québec, procède par filtre brut (Rompré et al. 2010). Par contre, certaines espèces spécialistes ou plus sensibles aux changements d'habitatnécessitent une approche par filtre fin (Rompré et al. 2010). Ces espèces échappent au concept de filtre brut puisqu'elles dépendent souvent d'éléments ou de processus écologiques spécifiques : le Pic à face blanche (*Picoides borealis*) dépend du feu contrôlant la végétation au sol et de la présence de pins d'un certain diamètre pour nicher (James et al. 2001), le Garrot d'Islande niche dans des cavités creusées par certains pics près de plans d'eau sans poisson où il s'alimente (Gouvernement du Québec 2013).

## Conservation d'une espèce rare : la Grive de Bicknell

Depuis sa découverte en 1881, la Grive de Bicknell (*Catharus minimus bicknelli*), un passereau forestier de la même famille que le Merle d'Amérique

(*Turdus migratorius*) n'avait d'intérêt que pour certains naturalistes et biologistes, les conservateurs de musées et les taxinomistes puisqu'elle ne représentait qu'une sous-espèce de la Grive à joues grises (*Catharus minimus*). Avec les travaux de Ouellet (1993) et les analyses génétiques initiales (G. Seutin, communication personnelle), et ses recommandations auprès de l'*American Ornithologists' Union* (maintenant l'*American Ornithological Society*), la Grive de Bicknell fut élevée au rang d'espèce (*Catharus bicknelli*; AOU 1995). Cette décision a été appuyée par de récentes études moléculaires (Ellison 2001; Seutin et al. 2001; Outlaw et al. 2003; Wilson et al. 2004; Winker et Pruett 2006; FitzGerald et al. 2017).

La littérature sur cette espèce est relativement récente. Si ce n'est les premiers documents publiés par Brewster (1883) et Wallace (1939) qui relatent une somme d'information importante sur son habitat et son écologie, c'est à la fin des années '90, après la publication de Ouellet (1993) que la communauté scientifique du Vermont, du Québec et du Nouveau-Brunswick a commencé à s'intéresser à cette espèce. Voici une brève revue des travaux les plus importants. Afin d'identifier la répartition de l'espèce, des travaux d'inventaires ont été amorcés en Nouvelle-Angleterre (Atwood et al. 1996), au Nouveau-Brunswick (Nixon et al. 2001) et au Québec (YA données inédites). Mais ce sont les travaux de l'équipe du Vermont, en 1997, qui ont révélé les particularités du système social de l'espèce (Goetz et al. 2003; Strong et al. 2004) en observant la présence de plusieurs mâles nourrisseurs à certains nids. Cette situation a été documentée l'année suivante, au Québec, par l'équipe que je dirigeais en Gaspésie. Cette multi-paternité comportementale est également accompagnée d'une multi-paternité génétique (Goetz et al. 2003; YA données inédites). Par ailleurs, les efforts de baguage, tant au Vermont qu'au Québec, ont démontré que le ratio des sexes était biaisé en faveur des mâles, c'est-à-dire 2 à 3 mâles par femelle (Rimmer et al. 2001). Ball (2000) a même observé que les femelles pouvaient chanter, situation plutôt inusitée pour un passereau de région septentrionale. De plus, l'espèce ne défend pas de territoire proprement dit. Ces dernières informations étaient d'une grande importance relativement au dénombrement de l'espèce, ainsi on ne pouvait plus estimer le nombre d'oiseaux à partir des méthodes généralement utilisées pour de nombreux autres passereaux. Aussi, on a rapidement constaté qu'il y avait des enjeux de conservation pour cette nouvelle espèce tant sur les aires de nidification que d'hivernage. Un premier rapport de situation pour le comité sur la situation des espèces en péril au Canada a été publié (Nixon 1999) suivi d'un second (COSEPAC 2009), menant à son statut d'espèce menacée de disparition (Gouvernement du Canada 2012). Plusieurs projets ont démarré afin de mieux décrire l'habitat utilisé par l'espèce et les enjeux de conservation sur les aires de nidification (Connoly 2000; Nixon et al. 2001; Hale 2001, 2006; Connolly et al. 2002; Chisholm 2005; Lambert et al. 2005; Chisholm et Leonard 2008; Frey 2008, 2011; Studd et al. 2012; Parrish 2013; McKinnon et al. 2014) et sur les aires d'hivernage (Rompré et al. 2000; McFarland 2013) où le Vermont Center for Ecostudies a investie beaucoup d'énergie. Depuis les années '90, outre certaines autorités fédérales et provinciales, quelques organismes se préoccupent de la Grive de Bicknell et contribuent aux connaissances qui permettent de mieux orienter les efforts de conservations de l'espèce tant au Canada (p. ex. : Études d'oiseaux Canada et le Regroupement QuébecOiseaux) qu'aux États-Unis (p. ex. : *Vermont Center for Ecostudies*). Depuis, la littérature n'a cessé de s'enrichir pour le bénéfice de la conservation de cette espèce menacée.

L'élévation de la Grive de Bicknell au rang d'espèce a des conséquences importantes en matière de conservation. En effet, celle-ci, plus méridionale et entièrement allopatrique par rapport à sa proche parente, la Grive à joues grises, niche surtout dans les forêts en altitude dominées par le Sapin baumier (FitzGerald 2017). On la retrouve donc dans les Appalaches ; depuis les Catskill dans l'état de New York jusqu'en Gaspésie et sporadiquement en marge du bouclier canadien entre le mont Sir-Wilfrid, près de Mont-Laurier, et Havre-Saint-Pierre, au Québec ainsi que localement au Nouveau-Brunswick et au Cap-Breton en Nouvelle-Écosse. Pour sa part, la Grive à joues grises niche principalement dans les forêts boréales d'épinettes noires (*Picea mariana*; FitzGerald 2017) depuis Terre-Neuve et la Labrador jusqu'en Sibérie orientale.

La Grive de Bicknell représente une priorité de la conservation de la biodiversité en Amérique du Nord (Downes et al. 2000; Pashley et al. 2000). Cette grive est endémique à la partie nord-est du continent nord-américain et son aire de nidification, discontinue, en fait l’une des espèces de passereau dont la répartition est la plus restreinte au nord du Mexique (Townsend et al. 2015). Son succès de reproduction semble être fortement limité par la prédation et les conditions météorologiques extrêmes (C. Rimmer communication personnelle, YA données inédites). L’effectif de cette espèce est relativement faible, on estime que la population canadienne de Grives de Bicknell compte entre 40 500 et 49 000 individus (COSEPAC 2009). Le Québec abriterait la majorité de cette population. Aux États-Unis l’estimation est de 56 000–90 000 individus (Hill et Lloyd 2017).

La majorité des passereaux forestiers démontrent un comportement social monogame (Ehrlich et al. 1988). On a longtemps associé à ce type de comportement un modèle selon lequel les territoires individuels ne se chevauchent pas et sont répartis plutôt uniformément dans les habitats propices (concept de disques élastiques, Huxley 1934; Nice 1937). Ce modèle est souvent implicite dans la pratique de l’aménagement et de la conservation de la faune. Le système social de la Grive de Bicknell ne correspond pas au modèle classique de la monogamie et sa répartition à l’intérieur de son habitat n’est pas uniforme (Goetz et al. 2003). Des observations réalisées en Gaspésie et en Estrie entre 1997 et 2007 (YA données inédites) ont démontré que cette grive ne défend pas de territoire à proprement dit, mais occupe des domaines vitaux qui se chevauchent. Dans les nids, on observe une paternité multiple et plusieurs mâles peuvent participer à l’alimentation d’une même nichée (Goetz et al. 2003; YA données inédites). Les travaux récents ont indiqué que le ratio des sexes est biaisé en faveur des mâles (Townsend et al. 2015) ce qui peut placer certaines populations locales, particulièrement les petites, en situation de précarité (stochasticité démographique) si une mortalité excessive affecte les femelles. On pourrait alors observer la disparition de certaines populations sous un effet de Allee (Stephens

1999). Des informations détaillées sur ce sujet sont fondamentales afin de bien comprendre la répartition spatiale de l'espèce dans son habitat et de bien orienter les actions de conservation.

Enfin, sur les aires de nidification, l'intégrité écologique de son habitat pourrait être compromise par certaines pratiques sylvicoles (telles que l'éclaircie précommerciale), le développement de complexes récréo-touristiques en montagne, l'implantation d'infrastructures de communication et d'éoliennes, la pollution atmosphérique (Rimmer et al. 2001; 2004) et les changements climatiques (Hughes 2000; Lambert et al. 2004). Au Canada seulement 5 % de l'habitat potentiel de l'espèce est protégé (COSEPAC 2009) alors qu'aux États-Unis, 76,6 % de son habitat bénéficie de protection (Hill et Lloyd 2017).

La Grive de Bicknell passe la saison hivernale principalement dans les Grandes Antilles. Par conséquent, la conservation de l'espèce requiert une approche internationale. À l'instar des aires de nidification, sa répartition y est fragmentée et limitée à quelques endroits sur quelques îles de cette région (Townsend et al. 2015). Le plus grand enjeu de conservation consiste à la perte d'habitat par la conversion de la forêt en zone de culture. Cette situation est surtout critique à basse et moyenne altitude où se retrouvent les principales concentrations de femelles, segment le plus important de la population de l'espèce (McFarland et al. 2013). Plus de 90 % des forêts ont disparue sur l'île d'Hispaniola (Townsend et al. 2015). Les enjeux sur les aires d'hivernage représentent probablement les plus importants facteurs limitant pour la conservation de l'espèce.

## Objectif et organisation de la thèse

Pour bien articuler les efforts de conservation d'une espèce, les connaissances sur l'écologie et l'habitat que la Grive de Bicknell utilise sont essentielles. J'examine les différents paramètres écologiques reliés à la présence de la Grive de Bicknell dans un environnement forestier québécois dominé par l'exploitation de la matière ligneuse. J'essaie de comprendre comment l'espèce se répartit sur le territoire en fonction des différents traitements sylvicoles et si l'espèce bénéficie d'assez d'habitat pour se reproduire. L'ensemble des résultats présentés dans cette thèse devraient pouvoir se traduire en recommandations et seront applicables à des approches de gestion du territoire prenant en compte la conservation de la Grive de Bicknell.

### Chapitre 1

Ce chapitre, *Response of Bicknell's Thrush (Catharus bicknelli) to boreal silviculture and forest stand edges: a radio-tracking study* (Aubry et al. 2011), présente des données de radio-télémétrie récoltées au mont Gosford, en Estrie. Ces données ont servi à estimer la taille des domaines vitaux dans un environnement modifié par les différentes coupes totales et les traitements d'éclaircies précommerciales. La sensibilité de l'espèce aux bordures et à l'hétérogénéité du paysage est également examinée.

### Chapitre 2

L'objectif du chapitre 2, *Regional patterns of habitat use by a threatened forest bird, the Bicknell's Thrush (Catharus bicknelli), in Quebec* (Aubry et al. 2016), est de vérifier comment l'abondance de l'espèce varie en présence d'éclaircie, en fonction de l'altitude et de la topographie et en relation avec l'abondance de la Grive à dos olive, une espèce possiblement compétitrice. Ici j'ai utilisé des points d'écoutes réalisés sur une période de plusieurs années à deux sites géographiquement distincts, au mont Gosford en Estrie et au Massif du Sud dans Bellechasse.

### Chapitre 3

Le dernier chapitre, *Not enough habitat, or not enough birds? Low habitat occupancy by Bicknell's Thrush (Catharus bicknelli) in Québec's Laurentian*

*Highlands* (Aubry et al. en révision), vérifie si la superficie d’habitat en nidification représente un facteur limitant pour l’espèce dans un environnement fortement modifié par d’intenses activités d’exploitation forestière et les épidémies de tordeuse du bourgeon de l’épinette. J’y présente deux approches statistiques contrastées, chacune basée sur des milliers de points d’écoute, visant à estimer le taux d’occupation des habitats optimaux pour l’espèce dans la sapinière boréale humide du Plateau Laurentien, au nord de Québec.

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## Chapitre 1

# Response of Bicknell's Thrush (*Catharus bicknelli*) to boreal silviculture and forest stand edges: a radio-tracking study*

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* Aubry, Y., A. Desrochers, and G. Seutin. 2011. Response of Bicknell's Thrush (*Catharus bicknelli*) to boreal silviculture and forest edges: a radio-tracking study. Canadian Journal of Zoology 89(6):474-482. doi:10.1139/z11-011.

## Résumé

Les objectifs sociétaux et la loi exigent que la conservation de la biodiversité, particulièrement la protection des espèces menacées, soit intégrée dans la planification et la gestion du territoire. La grive de Bicknell (*Catharus bicknelli* (Ridgway, 1882)) est une espèce menacée nichant dans les forêts montagnardes dominées par le sapin baumier (*Abies balsamea* (L.) P. Mill.) du nord-est de l'Amérique du Nord. Nous avons suivi 34 grives de Bicknell munies de radio-émetteurs dans le sud du Québec, dans le but d'examiner la taille, l'emplacement et la composition en habitat des domaines vitaux dans des secteurs ayant subi différents traitements sylvicoles. Les domaines vitaux des grives de Bicknell contenaient une proportion significativement plus importante de forêts denses que de secteurs soumis à des éclaircies précommerciales. À l'intérieur de leurs domaines vitaux, les grives se retrouvaient aussi davantage dans les peuplements denses que dans les peuplements éclaircies, et n'évitaient pas les lisières de peuplements. En fait, elles se retrouvaient de manière disproportionnée en bordure des peuplements récemment éclaircies. Nous concluons que la grive de Bicknell peut coexister avec des pratiques sylvicoles suivant lesquelles une mosaïque de paysages est dominée par des peuplements denses de sapins baumiers entremêlés de peuplements éclaircis.

## Abstract

Society and regulatory regimes require that biodiversity conservation, and especially the protection of threatened species, be integrated into land-use planning and management. Bicknell's Thrush (*Catharus bicknelli* (Ridgway, 1882)) is an at-risk species breeding in montane balsam fir (*Abies balsamea* (L.) P. Mill.) dominated areas of northeastern North America. We monitored 34 individual Bicknell's Thrushes by radio telemetry in southern Quebec to examine the size, location, and habitat composition of their home ranges in areas where clear-cutting and precommercial thinning occurred. Home ranges of Bicknell's Thrush comprised more dense balsam fir stands and fewer thinned stands than available. Within home ranges, thrushes were found more frequently in unthinned balsam fir stands than in thinned stands, and they did not avoid edges. In fact, they were found disproportionately near edges of recently thinned stands. We conclude that Bicknell's Thrushes may coexist with forest management practices that maintain a landscape mosaic dominated by dense balsam fir patches interspersed with thinned stands.

## Introduction

Natural stand dynamics shape balsam fir (*Abies balsamea* (L.) P. Mill.) forests (Desponts et al. 2002) through fire, windthrow, “fir waves” (*sensu* Sprugel 1976), damage by winter weather conditions, and insect and disease outbreaks. At high elevations in this ecosystem, the size of natural disturbances is generally <5 ha (Reiners and Lang 1979; Leblanc 1998), resulting in a complex mosaic of small stands that is dynamic at small scales but stable over larger areas (Sprugel 1976; Reiners and Lang 1979). In contrast, largescale forestry, as well as the development of areas for recreational uses, tourism, communications, energy, or transportation purposes, cause medium-term or permanent loss of original habitat and in many cases creates larger and more homogenous stands. High-altitude fir forests affected by silviculture, industry, recreation, and windmills typically occur as a mosaic with “hard” edges adjoining open and forested areas. Biotic and abiotic conditions at those edges are often very different from those found deep in the forest (Murcia 1995; Ries et al. 2004). Sharp edges created by forestry may negatively affect forest-interior birds (e.g., Brand and George 2001; Ries et al. 2004), but the negative impact of edges is less apparent in boreal-forest birds than in most temperate species (Ibarzabal and Desrochers 2001).

North American thrushes of the genus *Catharus* Bonaparte, 1850 do not exhibit a consistent response to forest edges. Swainson’s Thrush (*Catharus ustulatus* (Nuttall, 1840)) and Bicknell’s Thrush (*Catharus bicknelli* (Ridgway, 1882)) have been shown to be associated with edges (Brand and George 2001; Rimmer et al. 2004), whereas Hermit Thrush (*Catharus guttatus* (Pallas, 1811); Freemark and Collins 1989; King et al. 1997) and Veery (*Catharus fuscescens* (Stephens, 1817); Freemark and Collins 1989; Parker et al. 2005) are not. The Bicknell’s Thrush is one of only three boreal-forest birds considered to be at-risk in Canada (COSEWIC 2005). It is a specialist of high elevation, cool, fir-dominated forests, and has one of the smallest breeding ranges of all forest-bird species that breed north of Mexico (Rimmer et al. 2001). On its breeding grounds, Bicknell’s

Thrushes do not defend exclusive territories but instead occupy overlapping home ranges that are generally larger for males than for females (Rimmer et al. 2001; McFarland et al. 2008). Home-range size, location, and habitat composition of Bicknell's Thrushes appear to be influenced by the distribution and abundance of food (Strong et al. 2004), the social system (Goetz et al. 2003), and likely by local population density (this study). All of these factors may be influenced by the natural (Nixon et al. 2001; Rimmer et al. 2004) or anthropogenic (Nixon et al. 2001; Rimmer et al. 2004; Chisholm and Leonard 2008) composition and arrangement of forest stands, and thus may greatly vary among different parts of the restricted breeding range of this species.

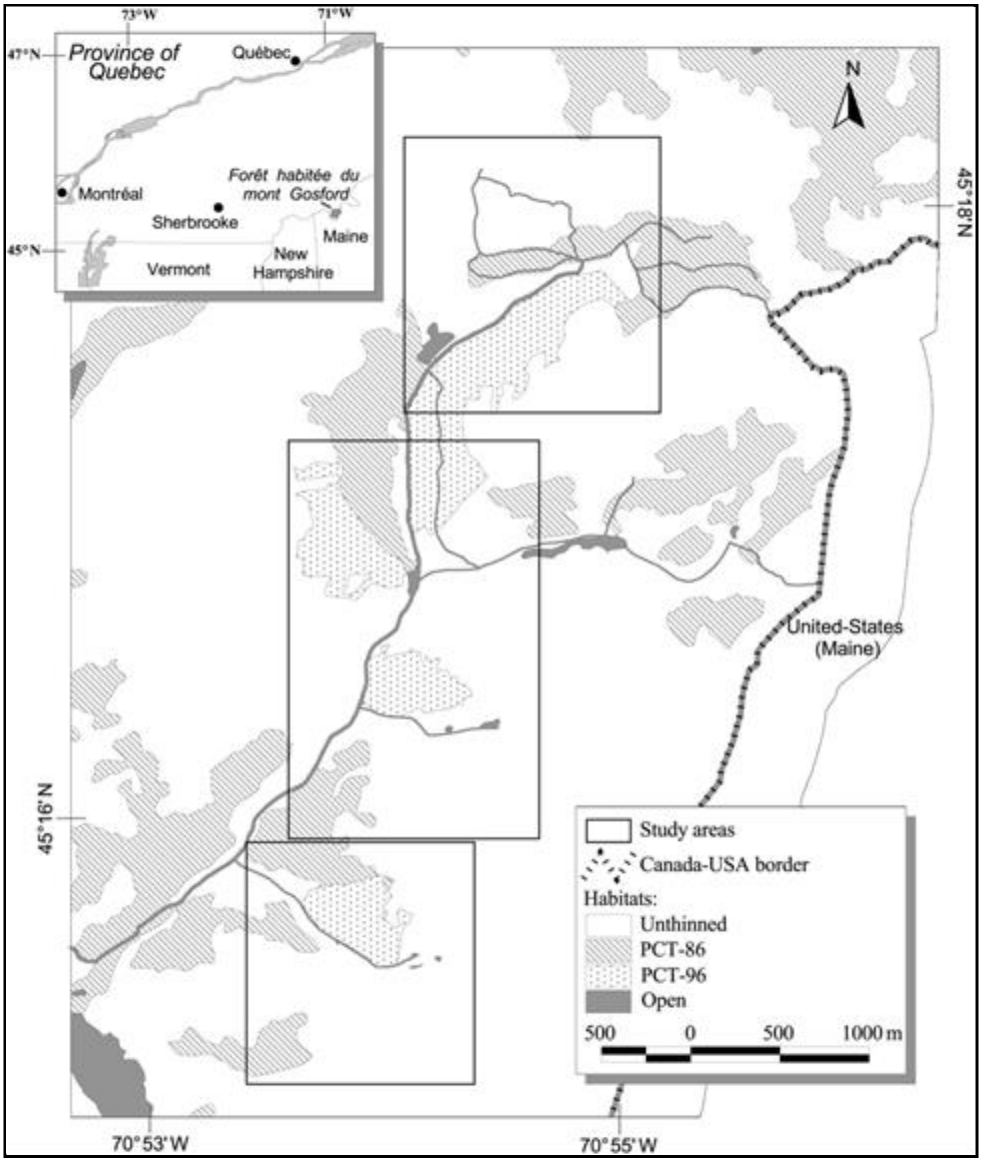
We studied home-range sizes and locations of Bicknell's Thrushes within home ranges, in an area that had been subjected to clear-cutting and precommercial thinning in southern Quebec. We tested whether the presence of Bicknell's Thrush was independent of silvicultural treatment and proximity to forest stand edges. Our results allow us to derive recommendations regarding forest patch heterogeneity, composition, and edge management to help maintain regional populations of this at-risk species.

## Materials and methods

### Study area

Mount Gosford, Quebec (1189 m above sea level (a.s.l.); 45°18′N, 70°52′W; Fig. 1.1), part of a managed area known locally as the "forêt habitée du mont Gosford", is characterized by slopes >15°, and occasionally >30° (Comité de gestion provisoire de la forêt habitée du mont Gosford 1997). Within this area, our study was conducted in the Clearwater Brook valley (1436 ha; 800–1193 m a.s.l.), dominated by balsam fir with white spruce (*Picea glauca* (Moench) Voss), red spruce (*Picea rubens* Sarg.), and paper birch (*Betula papyrifera* Marsh.) occurring in small and dispersed patches. The area was almost entirely clear-cut in the early 1970s, with only a few residual forest pockets left intact.

**Figure 1.1**. Study area located at Mount Gosford, Clearwater Brook valley, Quebec, Canada.



We grouped forest stand types of the study area into four main types (Fig. 1.1; Table 1.1). The first type (unthinned) consisted of fir-dominated and a few mixed forest stands that had not undergone silvicultural treatments over the past 35 years, resulting in high stem densities. The second type (PCT-86) consisted of fir-dominated stands that were subject to precommercial thinning in 1986 and characterized by intermediate stem densities and high abundance of fruit-bearing trees and shrubs. The third type (PCT-96) consisted of forest stands thinned in 1996 and 2002 with low stem densities at the time of study. Finally, a fourth stand type comprised open areas (46 ha; roads, wetlands, and other unforested areas) contributing to the amount of edges in the landscape. Stem density (≥1.3 m in height) of the various stands was estimated based on 30 randomly located circular plots in each habitat, each composed of three 40 $m^2$ circular subplots all located >50 m from stand edges. The method was based on the forest inventory standards for permanent sample plots established by Quebec's Ministère des Ressources naturelles et de la Faune (Ministère des Ressources naturelles et de la Faune 2006). Habitat types were mapped on an orthophotograph (fall 2000, updated in 2001), on which trails, roads, and forest stand polygons (size >4 ha) were superimposed. Forest stand attributes were obtained from Quebec's digital ecoforestry maps. During this study, no management activity was carried out in the areas where telemetry was conducted.

**Table 1.1**. Stem density (mean ± SE) for forest habitats in the sector of the Clearwater Brook valley, Mount Gosford, Quebec, during 2002 (n = 30 plots/habitat).

| | | Density (no. of stems/ha) | | | | |
|---|---|---|---|---|---|---|
| Treatment | Area (ha) | Balsam fir | Spruce[a] | Birch[b] | Fruit trees[c] | Total |
| Unthinned | 1180 | 8250 ± 1292 | 86 ± 26 | 4808 ± 657 | 444 ± 132 | 13 592 ± 1 313 |
| PCT-86 | 120 | 2614 ± 149 | 97 ± 31 | 4092 ± 595 | 1272 ± 487 | 8 075 ± 907 |
| PCT-96 | 90 | 1656 ± 127 | 28 ± 9 | 1575 ± 190 | 33 ± 28 | 3 292 ± 139 |

**Note:** For an explanation of the treatments refer to the Materials and methods section.
[a] White spruce (*Picea glauca*) and red spruce (*Picea rubens*).
[b] Paper birch (*Betula papyrifera*) and yellow birch (*Betula alleghaniensis* Britt.).
[c] American mountain ash (*Sorbus americana* Marsh.) and pin cherry (*Prunus pensylvanica* L.f.).

### Capture and radio-tracking

Sixty Bicknell's Thrushes were captured during 30 May–14 July of 2002, 2003, and 2004 (under the following permits: Animal Care Protocols, Laval

University 2001048 and 2003012; Canadian Wildlife Service SCFQc 200003). A radio transmitter (model BD2G; Holohil Systems Ltd., Carp, Ontario, Canada) was fitted over the rump of each captured bird using the harness method described by Rappole and Tipton (1991). Malfunctioning of transmitters, individuals moving out of the study area, and predation affected 13 birds; thus, 47 birds were available for the different analyses.

Bicknell's Thrushes were tracked by telemetry between 4 June and 26 July of each year, corresponding to the species' nesting and fledgling care periods. To avoid any impact on bird behaviour, locations were obtained by triangulation from fixed receiving stations located in open vantage points at the periphery of the zone occupied by Bicknell's Thrushes; three observers in constant radio contact, each equipped with a portable receiver (R1000; Communications Specialists Inc., Orange, California, USA) and a portable three-element Yagi antenna, located the strongest signal of an individual and simultaneously took compass bearings to the target. The bearings were used to estimate the location of the bird using the LOAS software, version 2.13 (Ecological Software Solutions, USA). This software keeps only the points for which the triangulation process results in probable final position therefore eliminating outlier locations. Initially 21–139 bearings were taken for the 47 birds monitored for this study with 21–125 final locations representing up to 43% of bearings discarded. The locations were taken evenly between 0430 and 2030 Eastern Standard Time (EST). Estimates of the locations of a given individual were spaced in time by a minimum of 30 min to ensure the biological independence of the data (Barg et al. 2005); this resulted in a mean daily time interval between consecutive localizations of 3.18 h in 2002, 3.27 h in 2003, and 2.24 h in 2004.

### Size, composition, and use of home ranges

We analyzed home-range parameters of 34 individual Bicknell's Thrushes for which we collected 21 or more locations in a given year. Because 10 individuals were studied in more than 1 year, we estimated 47 annual home ranges (2002: *n* = 14; 2003: *n* = 19; 2004: *n* = 14) based on 757 locations in 2002, 1277 in 2003, and 1066 in 2004. Of those, six were based on <30 locations (n = 21, 23, 24, 25, 27 and 28). For the 47 annual home ranges, we calculated 95% home range and 50% core-range contours using the nonparametric fixed kernel density estimator method (Animal Movement version 2.04b in ArcView version 3.2; Worton 1989; Millspaugh and Marzluff 2001). We used least-squares cross validation (LSCV) to estimate smoothing parameters and reduce bias and overestimation (Seaman and Powell 1996). Hereafter, we use the terms "home range" and "core area" for 95% and 50% fixed kernel, respectively.

Because analyses revealed no effect of year or a sex × year interaction for either home-range parameters (2002, 2003, and 2004; 95% fixed kernel; $F_{[2,41]}$ = 2.2, $p$ = 0.1; $F_{[2,41]}$ = 1.60, $p$ = 0.2, respectively) or core-area parameters (2002, 2003, and 2004; 50% fixed kernel; $F_{[2,41]}$ = 2.5, $p$ = 0.1; $F_{[2,41]}$ = 1.1, $p$ = 0.3, respectively), we pooled observations for an individual across years. We used a mixed-model approach (GLIMMIX; SAS Institute Inc. 2009) to compare home-range parameters, with year as random effect, and sex, year, sex*year, area, and area$^2$ as fixed effects.

We used compositional analysis (Aebischer et al. 1993) to assess the use of the four recognized forest stand types by individuals at two spatial scales. Open areas were included in the analyses because they adjoined forest stand edges, even though they represent <4% of home-range area (range 0.5%–8.0%). We evaluated second-order selection (home-range location within the entire area; sensu Johnson 1980) by comparing the proportion of home ranges represented by each habitat (unthinned, PCT-86, PCT-96, and open) with overall proportions in the study area in the corresponding year. The delineation of the study area followed the outside contour of all individuals' home ranges found in them in the corresponding year (ArcView version 3.2; Environmental Systems Research Institute, Inc. (ESRI), Redlands, California, USA). The proportion of each habitat type within each plot of the study area was considered available habitat. At a smaller scale (“third-order selection” sensu Johnson 1980), we compared for each individual the proportion of telemetric locations in each habitat type relative to the proportion of each habitat type in its home range. Thirty-nine home ranges were used in this analysis; for the remaining eight, either PCT-86 or PCT-96 habitat was missing from the available habitat. For habitats present in the study area and not used, we substituted the zero value by $1 \times 10^{-8}$, three orders of magnitude smaller than the smallest observed nonzero value, following Aebischer et al. (1993).

We performed compositional analysis using the BYCOMP. SAS version 2002 program (Ott and Hovey 1997), with type I error risk $\alpha = 0.05$. Because model residuals were not normally distributed, we used the randomized Wilks’ $\lambda$ ($\Lambda$) coefficient (based on 999 reiterations). A $X^2$ test was used to assess whether habitat use deviated significantly from random ($X^2 = -N \cdot \ln \Lambda$, where $N$ is the number of home ranges and df = 3). Preference indices were created from pairwise comparisons of mean of the log-ratios of habitat use (unthinned stands vs. PCT-86, PCT-96, and open).

### Response to stand edges

We used the approach of Desrochers and Fortin (2000) to assess Bicknell’s Thrush association to edges. We compared, for each individual, the mean observed distance to edges to the expected distances throughout their home range. To estimate mean observed distance to edges, we drew a circle with a 175 m radius around each location estimated by radiotracking, corresponding to the mean radio-tracking error estimated using the method of White and Garrott (1990). We estimated radio-tracking error with 20 transmitters disseminated within the study area, each of which was located five times, following a random selection, for each of the two field study triangulation setup that we used. Each circle contained a grid of equidistant points 10 m apart. For each grid point in these circles, the mean distance to edges within the different habitats was calculated. The mean of all point means for an individual provides an index of its use of edges in each habitat type. To estimate the expected distance to edges in a home range, a grid of points 10 m apart was generated for the entire home range of an individual. The distance to edges with different habitats was calculated for each grid point; the mean distance across all points found in a given stand type was the expected value for each individual. We used a one-sample Student's t test to compare observed and expected distances to edges from within each habitat. Data were pooled for individuals that we radio-tracked for more than one breeding season, as preliminary analyses failed to reveal significant year-to-year differences. For any given individual, we limited the analysis to habitats represented by at least 10 observations within this habitat. We assumed that each radio-tracking location of a given individual was independent because (i) only 15% of the sequences of distances to a given habitat edge were temporally autocorrelated (SAS PROC AUTOREG; SAS Institute Inc. 2009) and (ii) observations were separated by >30 min.

To draw inferences about edge use at the population level, we performed a meta-analysis across individuals of association with each edge type. To this end, we conducted a paired-sample t test, with each pair consisting of observed and expected distances to edges for a given individual ($n$ = 49), weighted by the number of locations per individual. Because preliminary analyses failed to reveal significant differences between sexes for any habitat combination (Student's $t$ test with unequal variances; all $p > 0.05$), results for all individuals were combined for this meta-analysis.

## Results

### Size, composition, and use of home ranges

Unthinned stands were largely dominated by balsam fir, whereas a large number of fruit- bearing trees and shrubs were inventoried in the PCT-86 and unthinned stands (Table 1.1). Home ranges of females were significantly smaller than those of males (Table 1.2; $F_{[1,43]} = 4.13$, $p = 0.05$). However, core areas used by females and males did not differ significantly in size (Table 1.2; $F_{[1,43]} = 0.06$, $p = 0.80$). All male home ranges overlapped with at least 2–6 other male home ranges. Contiguous home ranges overlapped by 0.07%–91.77%, with a mean ± SE of 36.7% ± 2.0%.

**Table 1.2.** Number of radio-tracking locations of Bicknell's Thrush (*Catharus bicknelli*), mean area of home ranges (ha; 95% and 50% kernels), and mean area of the unthinned stands within the home ranges (ha) in Clearwater Brook valley, Mount Gosford, Quebec, during 2002–2004.

| | | No. of locations | | Home range size (ha) | | Unthinned stands in home range (ha) | |
|---|---|---|---|---|---|---|---|
| | *n* | Mean | Range | Mean ± SE | Range | Mean ± SE | Range |
| **Home-range (fixed kernel 95%)** | | | | | | | |
| Females | 16 | 60.7 | 23 - 125 | 13.90 ± 2.36 | 1.89 - 35.61 | 10.53 ± 2.16 | 1.51 – 34.93 |
| Males | 31 | 56.9 | 21 - 108 | 19.81 ± 1.70 | 2.40 - 42.70 | 13.72 ± 1.25 | 2.37 – 31.39 |
| **Core area (fixed kernel 50%)** | | | | | | | |
| Females | 16 | 30.9 | 9 - 49 | 2.00 ± 0.47 | 0.25 – 7.9 | 1.58 ± 0.46 | 0.24 – 7.86 |
| Males | 31 | 25.1 | 8 - 52 | 2.12 ± 0.22 | 0.20 - 6.19 | 1.70 ± 0.21 | 0.09 – 5.67 |

Unthinned stands accounted for 71% of home-range areas and 79% of core areas. These proportions did not differ significantly between all years (71% home-range areas: $t = 0.38$, $p = 0.7$; 79% core areas: $t = –0.78$, $p = 0.4$, respectively). The compositional analysis revealed a significantly nonrandom representation of habitat types in Bicknell's Thrush home ranges relative to their availability in the study area, with an over-representation of unthinned stands (Wilks' $\lambda$ ($\Lambda$) = 0.88 and $-N \cdot \ln \Lambda = 7.8$, df = 3, $p < 0.001$; Table 1.3 and Fig. 1.2) and an under-representation of PCT-86 ($p = 0.0015$) and PCT-96 ($p = 0.0005$) thinned stands. Compositional analysis of estimated radio-telemetry locations within home ranges revealed that habitat used differed significantly from habitat availability within their home ranges (Wilks' λ (Λ) = 0.82 and $-N \cdot \ln \Lambda = 7.6$, df = 3, $p < 0.001$; Fig. 1.2), with unthinned stands favoured over all other habitat types, PCT-86 under-used (p = 0.0068), as well as open habitat ($p = 0.0041$). A preference ordination matrix ranked home ranges with high amounts of unthinned stands highest ($p < 0.05$), followed by home ranges with high proportions of open, PCT-86, and PCT-96, respectively. An additional preference matrix ranked the occurrence of telemetry locations highest in unthinned stands, followed by PCT-96, PCT-86, and open stands, respectively.

**Table 1.3:** Compositional analysis: proportion (mean ± SE; *n* = 47) of available habitats (study area), used habitats (home range; 95% fixed kernel), and radio-tracking estimated locations within home ranges of Bicknell's Thrush (C*atharus bicknelli*) in Clearwater Brook valley, Mount Gosford, Quebec, during 2002-2004.

| Habitat | Study area | Home ranges | Radio-tracking estimated locations |
|---|---|---|---|
| Unthinned | 0.652 ± 0.007 | 0.714 ± 0.020 | 0.745 ± 0.022 |
| PCT-86 | 0.097 ± 0.012 | 0.097 ± 0.016 | 0.090 ± 0.017 |
| PCT-96 | 0.207 ± 0.010 | 0.138 ± 0.021 | 0.119± 0.022 |
| Open | 0.043 ± 0.003 | 0.050 ± 0.006 | 0.045 ± 0.006 |

### Response to stand edges

In terms of mean distance to edge, Bicknell's Thrushes did not predominantly use interiors of unthinned stands (Table 1.4). In fact, despite the low spatial accuracy of radio-tracking locations, 36% of the 400 differences between observed and expected distances to edges were significant, and there were 50% more edge associations than stand–interior associations (87 vs. 58; $X^2$ for equal proportions = 5.8, $p = 0.02$). Individuals using thinned stands, especially recent ones (PCT-96), showed the greatest tendency to occur near edges of adjacent stands (Table 1.4). However, Bicknell’s Thrushes seemed to avoid edges between PCT-86 and PCT- 96 stands.

**Figure 1.2.** Compositional analysis of Bicknell’s Thrush (*Catharus bicknelli*) for preference of habitat categories in Clearwater Brook valley, Mount Gosford, Quebec, during 2002–2004. Unthinned habitat is used as a reference habitat (horizontal axis). Bars show log-ratio of selected habitat versus unthinned stand (mean ± SE), with negative values representing lower than expected use. Open bars represent proportional habitat use within study area (95% fixed kernel); shaded bars represent proportions of radio locations for each individual relative to the proportion of each habitat within the home range. Stars denote significant deviation from random use ($p < 0.05$).

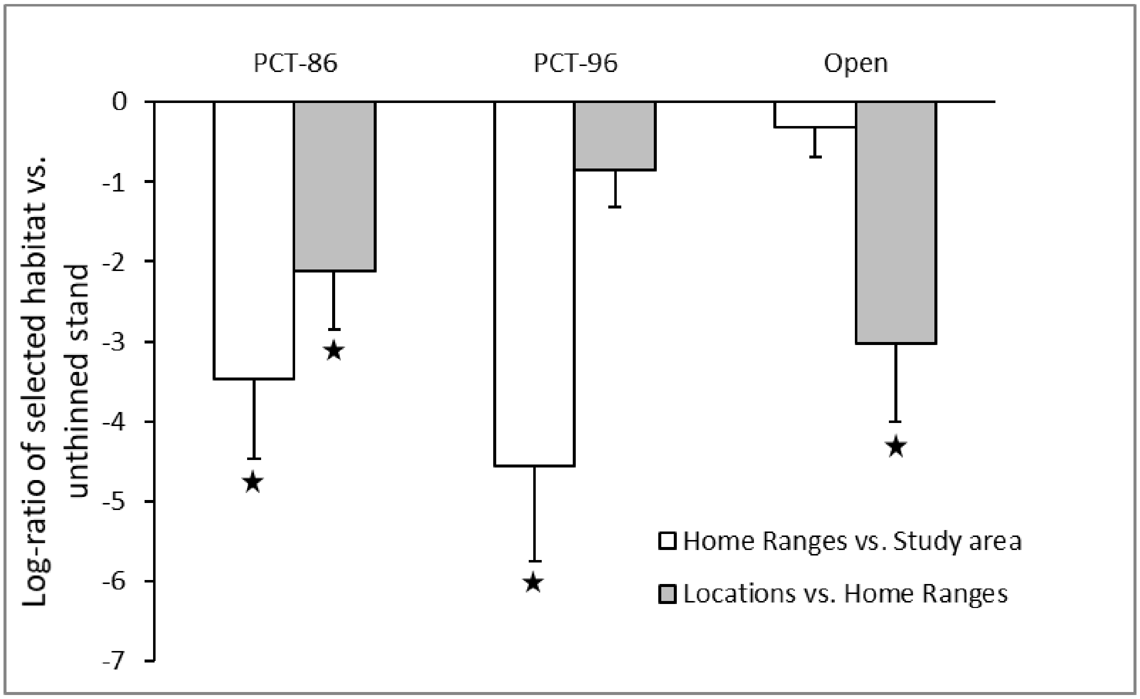


**Table 1.4.** Response of Bicknell's Thrush (*Catharus bicknelli*) to stand edges in Clearwater Brook valley, Mount Gosford, Quebec, during 2002–2004.

| | Used stand | | | |
|---|---|---|---|---|
| Edge type | Unthinned | PCT-86 | PCT-96 | Open |
| Unthinned (*n* = 47) | -4.22 ± 2.88 | 4.17 ± 6.96 | -3.15 ± 6.31 | -3.61 ± 4.26 |
| PCT-86 (*n* = 24) | -0.47 ± 2.02 | -0.92 ± 1.87 | 25.16 ± 5.83** | 2.40 ± 4.73 |
| PCT-96 (*n* = 30) | -13.97 ± 3.53** | 24.39 ± 8.84* | -14.02 ± 3.31** | -17.6 ± 4.77* |

**Note:** Values represent observed distances minus expected distances (in metres; mean ± SE). Negative numbers indicate associations with edges, whereas positive numbers indicate edge avoidance. ***p* ≤0.01 * *p* ≤0.05

## Discussion

### Size, composition, and use of home ranges

Bicknell's Thrush home ranges at Mount Gosford were larger than those of 77 of the 84 songbird species of the eastern Canadian boreal forest (reviewed by Gauthier and Aubry 1995), and those reported for the species in Vermont (3.2–5.4 ha for females and 5.6–12.0 ha for males; McFarland et al. 2008). These size differences could be related in part to methodological differences. In contrast to our triangulation approach, Vermont researchers, in a ski slopes vs. undisturbed habitat study, established visual contacts with radiotagged individuals (homing method) and georeferenced those points after initially locating them by radio-tracking. The homing method can have an influence on the movement of the target thrush by forcing the observer to be in view of the bird, thus introducing a disturbance effect, whereas the triangulation method generates an estimated position of a distant bird with an associated error without disturbing the bird. However, it is unlikely those methodological differences led to threefold increases in estimated home-range sizes. In both instances, the difference in home-range size between the sexes likely reflects the ecology of the species during the breeding period. In Quebec and Vermont, males often visited and contributed to the feeding of more than one brood (Goetz et al. 2003; Rimmer et al. 2004; Y.

Aubry unpublished data), whereas females spent most of their time incubating the eggs and caring for the young of their own brood. Lower population densities of the Bicknell's Thrush in Quebec (0.16–0.21 birds/ha) compared with in the USA (0.5–1.2 birds/ha; Y. Aubry, unpublished data; K.P. McFarland, personal communication) may have influenced the movements of the males with nests spaced farther apart, therefore affecting the size of their home ranges. Differences in home-range size between the Vermont and Quebec study areas could be related to food availability, a factor correlated with habitat structure and age. The Vermont study areas, located in montane environments, consisted of standing forests that have not been logged in the last century. In our study area, an exploited-forest environment, logging was conducted approximately 40 years ago; this difference in stand maturity may have resulted in significant differences in the composition of the invertebrate communities and biomass. In a redwood forest, Willett (2001) observed a decline in diversity and abundance of spiders and other arthropods in second growth stands compared with old growth ones. The diversity and abundance of those organisms were negatively correlated with the number of times a site had been logged. Niemelä (1997) reported higher carabid abundance and diversity in early regenerating boreal forest stands (<10 years) than in 20–60 year old stands. In a comparison of arthropods found in the forest edge and interior forest, Van Wilgenburg et al. (2001) noted a reduction in abundance and biomass of leaf-litter arthropods at the forest edge abutting recent clearcut, whereas in the same context, the abundance of shrub arthropods did not differ.

The preference of Bicknell's Thrush for dense fir stands during the breeding period, as well as its high proportion of locations in unthinned fir stands in their home range, is consistent with the findings of other studies (Wallace 1939; Rimmer et al. 2001; Nixon et al. 2001; Connolly et al. 2002). Our results are also consistent with those of Chisholm and Leonard (2008), in industrial forests of New Brunswick, who reported greater abundance of Bicknell's Thrush in structurally complex forest stands and large remaining unthinned stands surrounding thinned stands. Furthermore, in our study area, 13 of the 14 nests located from 2002 to 2004 were in densely vegetated areas (unthinned stands), the remaining one being in an unthinned small patch within a PCT stand. This preference is in agreement with the “total foliage hypothesis” (Martin 1993), whereby individuals select nest sites in habitats with high stem density to inhibit the transmission of cues (visual, auditory, or olfactory) used by predators to find nests.

Apart from a significant reduction in the relative abundance of fir, an important difference between unthinned and PCT stands is the more open canopy associated with the decline in stem density. The relatively closed fir canopy in the unthinned stands and PCT-86 resulted in less light in the understory, a lower temperature, and higher humidity than in PCT-96 (Thibodeau et al. 2000). Shaded areas harbour different (Strong et al. 2002a; Maleque et al. 2006), sometimes richer (Burke and Goulet 1998), invertebrate communities and could therefore be attractive to thrushes. Strong et al. (2004) demonstrated that the reproductive success of Bicknell’s Thrush is positively correlated with invertebrate biomass.

Another potentially important component of the habitat is the presence of fruit-bearing trees and shrubs that may have contributed to the use of the PCT stands. Nixon et al. (2001) and Connolly (2000) also mention the abundance of fruit trees in occupied sites. Fruit may be an important food source during the rearing of young and during molting before the start of fall migration (Major 2010; Vitz and Rodewald 2007). We observed the use of fruit trees and shrubs by thrushes as soon as the fruit matured (mid-July), at which point breeding is generally far advanced; we captured adult and juvenile Swainson’s and Bicknell’s thrushes by placing clusters of elderberries (genus Sambucus L.) to lure them near the nets. Several authors have reported similar behaviour, with both adult and juvenile Wood Thrushes (*Hylocichla mustelina* (J.F. Gmelin, 1789)) feeding, from the time of dispersal from the nest site until fall migration, on a variety of fruits that successively reach maturity during that period (Anders et al. 1998; Vega Rivera et al. 1998a, 1998b, 1999). Major (2010) observed an increased in fruit trees and shrub abundance <10 years after PCT, similar to what we observed (PCT-96 vs. PCT-86).

### Response to stand edges

In our study area, Bicknell's Thrushes were not forest-interior birds. Although many birds did not show a significant preference for edges, most of them were associated with that habitat. Most published analyses of responses to edge are based on song counts and document the general location of home ranges, without providing detailed information on the use of edges by individuals within their home range. Triangulation errors from radio-tracking likely limited our ability to detect edge responses, but cases where edge responses were significant favoured the hypothesis that Bicknell's Thrushes were not edge averse. The edges in our study area were much more subtle than those in the majority of studies on edge effects (see Ries et al. 2004), because they generally originated from the uniform balsam fir stands that dominate the region. In keeping with our results, a study of a dense network of alpine ski trails in Vermont (Rimmer et al. 2004), where edges are more pronounced, found that Bicknell's Thrush did not avoid edges. Furthermore, >60% of the nests they were located within 50 m of ski trails or work road edges (K.P. McFarland, personal communication (2009)).

In high-elevation forests of the northeastern United States, the landscape consists of a heterogeneous mosaic of small stands. Disturbance processes are continuous and maintain the dynamic stability of these areas. These forests are subject to many sources of natural disturbance, such as windthrow, mortality owing to severe winters, fir waves (Sprugel 1976), and on a smaller scale, insect and disease outbreaks, fire, and avalanches. The result of these disturbances is a high level of landscape heterogeneity and an abundance of edges. Balsam fir stands in the Clearwater Brook valley (Mount Gosford) have not been affected by outbreaks of spruce budworm (Choristoneura fumiferana (Clemens, 1865)) (F. Villemaire, personal communication), and the fire cycle in the stands is very long owing to the elevation and high humidity (>530 years in the balsam fir and spruce forests of nearby Maine and New Hampshire; Fahey and Reiners 1981). This disturbance regime is similar to that of the Laurentian Plateau and Gaspé Peninsula (Leblanc 1998; Dallaire 2004), where Bicknell’s Thrushes also occur. To those disturbances, climate and human disturbances have contributed to the heterogeneity and mosaic structure of the local landscape.

The development of high-elevation sites to establish facilities for communication, energy, and recreational–tourism uses, often coincides with the presence of Bicknell’s Thrushes. The development and expansion of ski centers significantly reduce and alter the species’ habitat. Although the Bicknell’s Thrush uses edges of open areas, it is still sensitive to the size of the habitat islands between the trails. Small islands and those separated by large open areas (>50 m) are avoided by the species (Strong et al. 2002b; Rimmer et al. 2004). In addition, the development of ski trails in the understory (glade) would have to be limited if not avoided, because it is associated with a significant reduction in stem density and the elimination of branches up to 3-4 m above the ground, which compromises the integrity of the species’ habitat (Y.A., personal observation). Also, the creation of forest fragments and their isolation would have negative consequences regarding food resources (Burke and Goulet 1998).

Despite their lack of association with forest interior, Bicknell’s Thrushes seem to maintain a minimum area of several hectares of dense fir forests (unthinned stand) within their home range. At the local scale, large fragments of mature and old-growth forests would make it possible to maintain the diversity of invertebrates that would colonize regenerating sites. At the landscape level, silvicultural practices and other treatments should promote the retention of a mosaic dominated by dense fir stands. Based on a concomitant study with the same population (Y. Aubry, unpublished data), groups of up to 10 tracked individuals with up to 4 females occupy an area of 57.6 ± 6.6 ha (range 21.9–77.8 ha). Therefore, to maintain the social structure of the species (Goetz et al. 2003), retention of large areas of dense balsam fir would be important. Furthermore, in the postbreeding period, habitats used by juveniles and adults need to be characterized, and the importance of fruit trees during the fledgling care and pre-migratory molt period of adults and young needs to be assessed.

Bicknell’s Thrush is a globally rare and vulnerable habitat specialist, such that in exploited forest environments, adaptive resource management of its habitat at both ends of its restricted migratory range is essential to ensure its long-term conservation. This study reveals that Bicknell’s Thrushes have large home ranges encompassing a high proportion of untreated dense balsam fir stands. They will also use thinned stands, although in much lower proportion, but not for nesting. In our study, Bicknell’s Thrushes did not avoid edges created by forestry practices; in fact, they showed an apparent preference for them. Our results likely reflect the current situation, for Quebec at least, in a highland industrial-use forest environment and represent basic guidelines for the conservation of this species. On its breeding range, the type of structural heterogeneity that the Bicknell’s Thrush appears to prefer should be emulated in forest managements, recreational developments, and other projects that affect its habitat. Although there is no other study within large expanses of control undisturbed forest at similar latitude and altitude, our results prompt us to make three recommendations regarding the management of the fir forests used by Bicknell’s Thrushes during breeding: (1) maintain large extents of dense fir stands; (2) maintain the supply of fruit trees and shrubs; and (3) promote the creation or maintenance of stand edges with high stem density.

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Chapitre 2

# Regional patterns of habitat use by a threatened forest bird, the Bicknell’s Thrush (*Catharus bicknelli*), in Quebec*

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## Résumé

Les modèles de fréquentation de l’habitat sont souvent utilisés pour orienter la gestion de l’habitat et des populations dans un contexte de conservation d’une espèce menacée. Nous avons examiné la fréquentation de forêts de haute altitude par la Grive de Bicknell (*Catharus bicknelli* (Ridgway, 1882)) dans deux régions des Appalaches du Québec méridional. Nous avons examiné la contribution de paramètres de la végétation et de la topographie *à* deux échelles spatiales ainsi que la relation spatiale avec un compétiteur potentiel, la Grive à dos olive (*Catharus ustulatus* (Nuttall, 1840)). Dans les deux régions, la Grive de Bicknell fréquentait davantage les sites localisés à hautes altitudes, particulièrement les peuplements qui n’ont pas fait l’objet d’éclaircies, sinon très peu. La Grive à dos olive était présente *à* toutes les stations où la Grive de Bicknell était présente. Ces résultats sont similaires *à* ceux obtenus par d’autres travaux de recherche dans le nord-est de son aire de nidification. Nous concluons que les coupes d’éclaircie devraient être pratiquées le moins possible dans les habitats de nidification à haute altitude de la Grive de Bicknell.

## Abstract

Conservation of threatened species often uses habitat models to inform management of habitat and populations. We examined habitat use by Bicknell's Thrush (*Catharus bicknelli* (Ridgway, 1882)), a federally "Threatened" species, in two Appalachian regions, shaped by forestry activities, of southern Quebec. Within its breeding range, the species inhabits mountain tops and forests subjected to various logging activities. We assessed the role of vegetation and topography at two spatial scales, as well as spatial relationships with Swainson's Thrush (*Catharus ustulatus* (Nuttall, 1840)), identified as a potential competitor by some authors. In both regions, Bicknell's Thrushes were most likely to be reported at high elevations, in forest stands with high tree stem densities that underwent little or no stem reduction from forestry activities. Swainson's Thrushes were present at all sites where Bicknell's Thrushes were reported. These results are consistent with findings from studies in northeastern parts of its breeding range. We conclude that forest stand thinning should be kept to a minimum throughout the high-elevation nesting habitat of Bicknell's Thrush.

## Introduction

Land-based efforts to conserve threatened species and their critical habitat rely heavily on habitat-use models to inform management of habitat and populations (Camaclang et al. 2015). The predictive performance of habitat-use models depends primarily on the goals and on the data selected to develop the model (Guisan and Zimmermann 2000). In many cases, models are derived from data collected in a limited portion of the target species' range and then broadly applied without first assessing potential spatial variation in the species' habitat use (Fielding and Haworth 1995; Laughlin et al. 2013). Furthermore, many published habitat-use models have only considered covariates pertaining to vegetation structure and composition, although several abiotic factors (e.g., topography, climate, site biochemistry, historical use) are increasingly documented as being important to the definition of avian habitat (Fielding and Haworth 1995; Tilgar et al. 1999, 2002; Norris et al. 2003; Seoane et al. 2004; Nocera and Forbes 2010; McFarland et al. 2013). Conspecific and heterospecific densities sometimes are important habitat attributes (Greene and Stamps 2001; Forsman et al. 2008; Nocera and Forbes 2010) through either conspecific and interspecific competitions (Petit and Petit 1996; Confer et al. 2003) or attraction (Slagsvold 1980; Reed and Dobson 1993; Mönkkönen and Forsman 2002; Bourque and Desrochers 2006). Failure to consider key factors in habitat-use models can lead to inadequate identification of critical habitat and erroneous conclusions about a species' ecological needs and, thus, misguided conservation investments and land-use planning decisions (Camaclang et al. 2015).

In northeastern North America, five species of thrushes (genus *Catharus* Bonaparte, 1850) tend to segregate their distributions according to habitats along an elevational gradient (Able and Noon 1976; Sabo and Whittaker 1979; Noon 1981). Among those is the threatened

Bicknell's Thrush (*Catharus bicknelli* (Ridgway, 1882), typically referred to as *Catharus minimus bicknelli* (Ridgway, 1882) before 1995; AOU 1995; COSEWIC 2009), the most habitat-specific thrush in United States, being confined to conifer tangles of mountain tops (sensu Dilger 1956) and with the most restricted range of the thrushes occurring north of Mexico. Published studies portray Bicknell's Thrush mostly as a specialist of patchy, high-elevation coniferous-dominated forests, occurring at lower elevation only in Canada (Ouellet 1993; Gauthier and Aubry 1995; Rimmer et al. 2001; Lambert et al. 2005; Frey 2008) and locally in Maine (Townsend et al. 2015). This northeastern endemic has been designated as “Threatened” under Canadian law (Government of Canada 2012) and as a conservation priority by *Partners in Flight* in the State of the Birds of United States of America's Watch List (Rosenberg et al. 2014).

Bicknell's Thrush potential habitat has been modeled for the northeastern United States based on elevation, latitude, and forest type (Lambert et al. 2005). That model performed well in that part of the species' range, where the species is mostly restricted to subalpine and high-elevation environments. Lambert et al.'s (2005) model performs well where a natural perturbation regime dominates the landscape, but it may not perform as well north of 45°, in Maine and southeastern Canada, e.g., due to a lower elevation ecotone between spruce–fir and deciduous forests and more frequent forestry practices. When applied to Quebec, Lambert et al.'s (2005) model could not reliably discriminate suitable Bicknell's Thrush habitat. For example, Lambert et al.'s (2005) model includes vast areas of unsuitable habitat either at too low elevation or deeply transformed by anthropogenic perturbations like forestry (K. McFarland and Y. Aubry, unpublished data).

North of 45° latitude, anthropogenic activities such as forestry are shaping vast areas of potential breeding habitat for the species. Forestry practices, like clear-cuttings, which are followed by the establishment of a vigorous succession, are ultimately treated with precommercial thinning. The results are a significant reduction in stem density, impairing the habitat suitability for this thrush species (Connolly 2000; MRNFP 2003; Aubry et al. 2011; McKinnon et al. 2014; K. McFarland and Y. Aubry, unpublished data). Forestry practices are important to consider because most of Bicknell's Thrush range in Canada is allocated for forest harvesting [illegible]SEWIC 2009). Inappropriate logging prescriptions derived from poorly performing habitat-use models could unnecessarily negatively impact local or regional economies.

Besides changes in vegetation structure, possible interactions with the closely related Swainson's Thrush (*Catharus ustulatus* (Nuttall, 1840)) could influence Bicknell's Thrush habitat selection. While some authors have reported the co-occurrence of Bicknell's and Swainson's thrushes (Wallace 1939; Nixon et al. 2001), others have hypothesized that heterospecific competition results in spatial segregation (Able and Noon 1976; Sabo 1980; Noon 1981; Mack and Yong 2000; Rimmer et al. 2001).

In a previous telemetry study (Aubry et al. 2011), we illustrated the importance of unthinned habitat for Bicknell's Thrush during the breeding season. We also showed that the species use habitat edges and could incorporate thinned habitat in their home ranges. Bicknell's Thrush is not a species of the forest interior; it appears to tolerate human impacts as long as high stem-density stands are readily available in the landscape.

Here, we analyze geographic variation in habitat use by Bicknell's Thrush, based on multiyear surveys in two regions of its Canadian range. We assessed the relative roles of habitat, topography, tree composition, silvicultural practices affecting the structure of the habitat, ground cover, and elevation and its variation at local and two spatial scales, as well as Swainson's Thrush abundance, on abundance of Bicknell's Thrush. We tested whether Bicknell's Thrush abundance is higher (*i*) where precommercial thinning has not occurred, (*ii*) at higher elevations or in steeper terrain, and (*iii*) when Swainson's Thrush abundance is relatively low. We discuss how the results of this study may inform future efforts to designate and manage this threatened species' critical habitat over its entire breeding range.

## Materials and methods

### Study areas

Our study was conducted in two areas approximately 150 km apart, both in the Appalachian Mountains range. First, Mont Gosford, Quebec (elevation: 790–1193 m above sea level; 45.3°N, 70.87°W), adjacent to the Quebec–Maine border at the edge of the White Mountains, Maine, is characterized by slopes, sometimes greater than 30°. The study area (±70 $km^2$) was dominated by balsam fir (*Abies balsamea* (L.) Mill.) with small and patchy occurrences of white spruce (*Picea glauca* (Moench) Voss), red spruce (*Picea rubens* Sarg.), and white birch (*Betula papyrifera* Marshall). The area was almost entirely clear-cut in the early 1970s, with only a few residual forest pockets left intact. Unthinned stand ages over both study areas were >25 years. Precommercial thinning operations were conducted in some early-successional stands in 1986 and 1996 (1980s and 1990s hereafter) (for more details see Aubry et al. 2011). Precommercial thinning reduces stem density from >40 000 down to 1875–3125 stems/ha (MRNFP 2003) to favor the growth of commercial tree species, balsam fir in our case. No other significant forestry activities occurred in the Mont Gosford study area since then.

The second site, Massif du Sud (elevation: 680–917 m above sea level; 46.6°N, 70.48°W), is a 120 $km^2$ plateau comprising 20 summits standing out in a rolling hill, agroforestry environment. The study area covered 45 $km^2$ of the plateau dominated by balsam fir. Since the early 1980s and up to 2007, forestry activities targeting old coniferous stands created a complex mosaic of forest stands differing primarily in tree density, structure, and age rather than species composition (Paulette 2010). Since 2012, this territory supports wind-energy infrastructure (75 turbines for 150 MW). In addition, the territory supports downhill, glade (alpine skiing in a forested area with no understory and reduced tree density), and cross-country skiing, as well as other, all-season, low-intensity recreational activities (e.g., horse riding, hiking, ATV, and mountain-bike trails; Paulette 2010; MRC de Bellechasse and MRC des Etchemins 2013). The proportion of unthinned stands was lower than at Mont Gosford.

## Point counts

At Mont Gosford, we monitored Bicknell's and Swainson's thrushes at 99 point-count stations in 2001 and 129 stations in 2002, 2003, 2004, and 2007. All stations were visited once each year. Point-count stations were located along forestry roads (*n* = 11), foot trails (*n* = 78), and off trails (*n* = 40). All stations were ≥250 m apart and located ≥50 m from stands with a different tree composition and (or) structure. At Massif du Sud, we conducted point counts only in 2007, along forestry roads (*n* = 80) and foot trails (*n* = 129) at 209 stations.

All point counts in both study areas were conducted between 2 and 28 June, during thrushes' dawn and dusk choruses (hours of 0310–0745 and 1800–2130; Ball 2000). At each station, thrushes within 100 m of the observer were counted, first during three consecutive 5 min passive listening periods, followed by 1 min of broadcasting of Bicknell's Thrush calls and songs, followed by another 5 min of listening during which we counted all previously reported birds, and any individuals deemed new based on their location. During surveys, the position of each thrush was indicated on a 1:1000 map to reduce the risk of double counting. Other than Bicknell's and Swainson's thrushes, other thrush species were rarely observed (<5% of all point counts conducted) and were ignored from further analyses. In this study, we use species abundance and reporting rate at point count according to the results that we are presenting.

Our survey protocol was selected based on estimates of Bicknell's Thrush detection probabilities derived from an occupancy model with constant probability of occupancy across all sites where Bicknell's Thrushes were reported at least once (Y. Aubry and M. Mazerolle, unpublished data). Detection probability for a given 5 min period depended on the survey technique (passive listening vs. post-playback). Detection probabilities reached 88%–96% at the end of the sampling period that we used (i.e., 20 min with playback), whereas a sampling period of 5 or 10 min without playback yielded detection probabilities <53% and <78%, respectively. Given uncertainty about the population closure of site occupancy (sensu Mackenzie et al. 2006) by Bicknell's Thrushes during those surveys, we interpret our estimates of detection probabilities as minima. Dettmers et al. (1999) also reported better performance of habitat models for species with low detectability, like Bicknell's Thrush, as count duration increases (from 3 to 20 min).

### Vegetation and topography

The habitat was characterized using vegetation and topography variables, within 100 and 250 m of each point-count station. Vegetation variables were tree species, ground cover, and the structure of the forest stands (Table 2.1). For tree species, we classified forest stands from eco-forestry GIS layers (Government of Quebec 2009; ESRI, Inc. 2010) and field observations as follows: balsam fir dominant; balsam fir with white birch as subdominant; other (no balsam fir dominant). We classified stand structure according to silvicultural activities since the early 1970s as follows— “unthinned”: characterized by high stem density; “thinned in 1986 (1980s)”: medium to low stem densities and high abundance of fruit trees (e.g., mountain-ash, *Sorbus americana* Marshall; shadbush, *Amelanchier bartramia* (Tausch) M. Roem.; pin cherry, *Prunus pensylvanica* L. f.); “thinned in 1996 (1996s)”: low stem densities at the time of point counts (see Aubry et al. 2011). We visually estimated ground cover in the field, from 1 m above ground within 10 m of the point-count center, and classified it as “open” if ground was dominated by moss, organic litter, or mineral or rocks and “closed” if it was dominated by ferns and herbaceous plants. Topography variables were elevation at point counts and its variation within 100 and 250 m as an index of the topographic heterogeneity of the habitat (Canadian Digital Elevation Data 2000; available from http://geogratis.gc.ca/api/en/nrcan-rncan/ess-sst/ 3A537B2D-7058-FCED-8D0B-76452EC9D01F.html). Habitat with important elevation variations could represent a habitat exempt of forestry activities that will be more under the influence of a natural perturbation regime and represents a habitat of quality for Bicknell’s Thrush.

### Statistical analysis

We used generalized linear models (GLMs) with a negative binomial error structure (PROC GENMOD; SAS Institute, Inc. 2009), with point-count stations as repeated-measure subjects for the Mont Gosford multiyear data set. Because Bicknell’s Thrush is nonterritorial when breeding (Goetz et al. 2003; Aubry et al. 2011) and both males and females vocalize (Ball 2000; Rimmer et al. 2001), we used the number of individuals counted as the response variable. We grouped regressors into three sets: vegetation (type and structure within 100 and 250 m of point-count station, as well as

**Table 2.1.** Point-count station variables and description at Mont Gosford and Massif du Sud, Quebec, Canada.

| Variable | Description |
|---|---|
| **Vegetation** | |
| Tree species per 100 m | Tree species dominating the stand within 100 m radius; three categories: balsam fir (*Abies balsamea*) dominant, balsam fir with white birch (*Betula papyrifera*) subdominant, and other (no balsam fir dominant) |
| % Unthinned per 100 m | Proportion of unthinned stand within 100 m radius |
| % Thinned in 1980s per 100 m | Proportion of stand thinned in the 1980s within 100 m radius |
| % Thinned in 1990s per 100 m | Proportion of stand thinned in the 1990s within 100 m radius |
| % Unthinned per 250 m | Proportion of unthinned stand within 250 m radius |
| % Thinned in 1980s per 250 m | Proportion of stand thinned in the 1980s within 250 m radius |
| % Thinned in 1990s per 250 m | Proportion of stand thinned in the 1990s within 250 m radius |
| Ground cover | Dominant ground cover: open (moss, litter, mineral) or closed (ferns, herbaceous plants) |
| **Topography** | |
| ΔElevation per 100 m | Elevation variation within 100 m radius |
| ΔElevation per 250 m | Elevation variation within 250 m radius |
| Elevation | Elevation above sea level at the center of the station |
| **Swainson's Thrush** | Abundance of Swainson's Thrush (*Catharus ustulatus*) at point count in the survey period |

ground cover), topography (elevation at point-count station and the difference between highest and lowest points within 100 and 250 m), and interspecific interactions (Swainson's Thrush abundance). We designed eight models and selected among them using the quasi-likelihood information criterion corrected for small sample size ($QAIC_C$) (Pan 2001) for the Mont Gosford multiyear data set and Akaike's information criterion corrected for small sample size ($AIC_C$) for the Massif du Sud single-year data set. In all models, year was included as a covariable to account for annual variation in the Bicknell's Thrush abundance.

As detection is not perfect, our modeling approach offers limited inference regarding occupancy. However, because detection probability approached one (discussed above), we consider that raw counts were sufficient for the aims of this study. Furthermore, population closure of occupancy status, as required by occupancy models, is difficult to define in the case of Bicknell's Thrush given the large home range of males (e.g., Aubry et al. 2011) and the complex mating system of the species (Goetz et al. 2003).

We also ran GLMs with Bicknell's Thrush reporting rates (presence or absence at a point-count station) data as the response variable and a binomial distribution. The best models were similar between abundance and reporting rates as response variables, with the only change being the loss of elevation at station as a significant parameter at Mont Gosford (vegetation, topography, and Swainson's Thrush—$QAIC_C$ = 811.3 and $QAIC_C$ weight = 0.989 for Mont Gosford; $AIC_C$ = 212.0 and $AIC_C$ weight = 0.765 for Massif du Sud). For simplicity, we therefore present only GLMs based on abundances.

Finally, we used a principal components analysis (PCA; PROC FACTOR procedure) (SAS Institute, Inc. 2009) to visually explore the relationships between the 11 environmental variables recorded and the co-occurrence of both thrush species and not for statistical inference purposes.

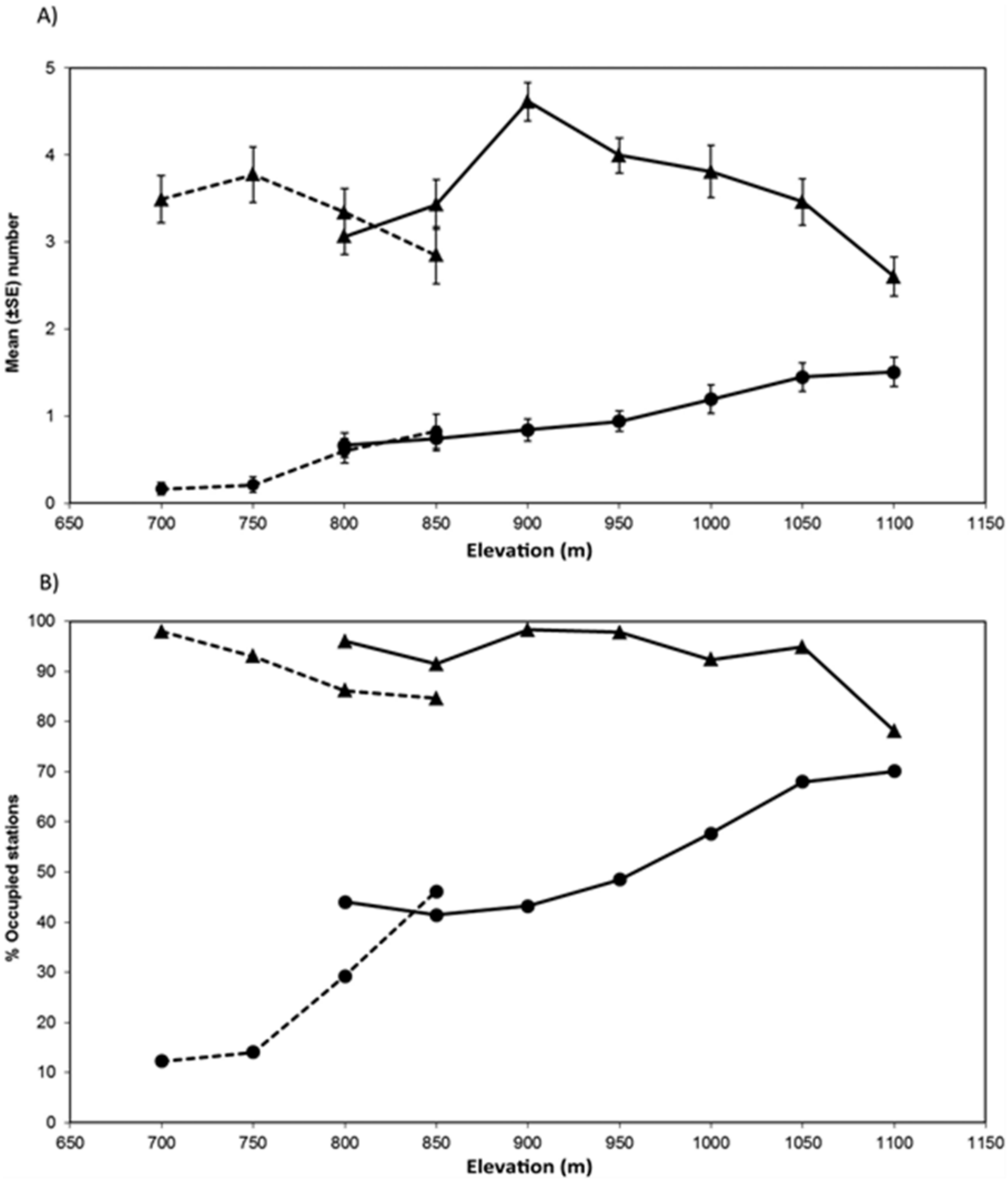
## Results

Bicknell's Thrush reporting rates and abundances were substantially lower than those of Swainson's Thrush at both sites (Table 2.2; Figs. 2.1A, 2.1B). At Mont Gosford, we observed important annual variation in Bicknell's Thrush reporting rates (35%–67% of stations; Table 2.2) and abundances (0.69 ± 0.11 to 1.58 ± 0.15 individuals per station (mean ± SE); Table 2.2). When reported, Bicknell's Thrush numbers varied from 1.64 ± 0.13 to 2.34 ± 0.17 individuals per occupied station (mean ± SE; Table *2.2*). At Massif du Sud, Bicknell's Thrush was reported at 24% of stations, where 1.78 ± 0.16 individuals were present, on average, when reported (Table 2.2).

At both study areas, GLMs accounting for vegetation, topography, and Swainson's Thrush abundance performed best (Table 2.3). None of the tree species variables turned out significant. At Mont Gosford, the proportion of stand thinned in the 1980s within 100 m was negatively associated ($p < 0.001$) with Bicknell's Thrush abundance, whereas elevation of point count, elevation variation within 250 m, and Swainson's Thrush abundance were positively associated ($p < 0.001$) (Table 2.4). At Massif du Sud, only two of these variables, elevation of point count and Swainson's Thrush counts, were significant and positively associated with Bicknell's Thrush abundance (Table 2.4). Model estimates for given variables at 100 and 250 m spatial scales should be interpreted with caution, as these regressors were sometimes highly correlated with one another. However, there were no pairwise correlations greater than 0.29 between regressors belonging to different groups (vegetation, topography, or Swainson's Thrush). Because collinear variables were always combined or removed as groups between models, we assume that comparisons among models are reliable.

With a principal components analysis (Table 2.5), we reduced the variation from all habitat covariates to two factors accounting for 58% of the total

**Figure 2.1**. (A) Mean number (±SE) and (B) proportion of stations where Bicknell’s Thruhes (*Catharus bicknelli*; circles) and Swainson’s Thrushes (*Catharus ustulatus*; triangles) were reported according to elevation (50 m interval) at Mont Gosford (2001-2007; solid line), and Massif du Sud (2007; broken line), Quebec, Canada.



variance (33% and 25% for factors 1 and 2, respectively). The first two components were strongly associated to stand structure. The unthinned area was negatively correlated with factors 1 and 2, whereas the area thinned in the 1980s was positively correlated with both factors. Factor 2 was negatively correlated with the area thinned in the 1990s and was positively correlated with elevation and its variation. For both factors, correlations with ground cover and Swainson's Thrush were weak. Bicknell's Thrush stations broadly overlapped with those of Swainson's Thrushes (Fig. 2.2), but with what seems to be an apparent Bicknell's Thrush preference for unthinned stand. However, stations with Bicknell's Thrushes only were mostly clustered in unthinned stands represented in the left quadrant of the ordination (Fig. 2.2).

## Discussion

### Habitat-use models

Three results from our study suggest geographical consistency in Bicknell's Thrush breeding habitat relationships. First, the species tended to preferentially use sites at high elevations that underwent little or no thinning and where Swainson's Thrushes were abundant. These results are consistent in part, at least, regarding high-elevation affinities of the species, with the findings of studies conducted in nonindustrial habitat, in the southern part of the species' range (Atwood et al. 1996; Lambert et al. 2005). Second, Bicknell's Thrush at our study sites in managed forests used dense regenerating stands and was notably less abundant in recently thinned stands. The same pattern was noted in other studies conducted in managed forests (Nixon et al. 2001; Connolly et al. 2002; Chisholm and Leonard 2008; Aubry et al. 2011). Third, the minimum elevations at which we found Bicknell's Thrush at Mont Gosford (790 m) and Massif du Sud (680 m) closely matched predictions under Lambert et al.'s (2005) model (i.e., 781 and 679 m, respectively).

**Table 2.2.** Reporting rates (%) and abundance (mean ± SE) of Bicknell's Thrush (*Catharus bicknelli*) and Swainson's Thrush (*Catharus ustulatus*) at Mont Gosford and Massif du Sud, Quebec, Canada.

| | **Mont Gosford** | | | | | **Massif du Sud** |
|---|---|---|---|---|---|---|
| **Year** | **2001** | **2002** | **2003** | **2004** | **2007** | **2007** |
| *N* | 99 | 129 | 129 | 129 | 129 | 210 |
| **Bicknell's Thrush** | | | | | | |
| Reporting rate | 56% | 64% | 67% | 43% | 35% | 24% |
| Global abundance | 0.91 (0.11) | 1.26 (0.13) | 1.58 (0.15) | 0.79 (0.10) | 0.69 (0.11) | 0.43 (0.07) |
| Abundance when Bicknell's reported | 1.64 (0.13) | 1.95 (0.15) | 2.34 (0.17) | 1.82 (0.13) | 1.98 (0.20) | 1.78 (0.16) |
| **Swainson's Thrush** | | | | | | |
| Reporting rate | 98% | 87% | 96% | 95% | 91% | 91% |
| Global abundance | 3.48 (0.17) | 3.39 (0.26) | 4.33 (0.26) | 3.88 (0.20) | 3.29 (0.18) | 3.40 (0.16) |
| Abundance when Bicknell's reported | 3.38 (0.24) | 3.49 (0.25) | 4.52 (0.31) | 4.23 (0.33) | 3.31 (0.32) | 3.98 (0.31) |
| Abundance when Swainson's reported | 3.56 (0.17) | 3.90 (0.21) | 4.5 (0.26) | 4.07 (0.20) | 3.62 (0.17) | 3.76 (0.14) |

**Table 2.3.** Model selection at the point count level using abundance of Bicknell's Thrush (*Catharus bicknelli*) as the response variable and eight a priori models as explanatory variables for Mont Gosford (2001-2007) and Massif du Sud (2007), Quebec, Canada.

| **ID** | **Model** | **Mont Gosford** | | | | **Massif du Sud** | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *K* | $\text{QAIC}_c$ | $\Delta\text{QAIC}_c$ | $\text{QAIC}_c$ weight | *K* | $\text{AIC}_c$ | $\Delta\text{AIC}_c$ | $\text{AIC}_c$ Weight |
| **8** | **Vegetation, *Topography, †Swainson's Thrush abundance** | **16** | **975.8** | **0.0** | **0.999** | **16** | **332.7** | **0.0** | **0.978** |
| 5 | Vegetation - Topography | 15 | 989.9 | 14.1 | <0.01 | 15 | 342.0 | 9.3 | <0.01 |
| 7 | Topography - Swainson's Thrush abundance | 5 | 1022.8 | 47.0 | <0.01 | 5 | 341.4 | 8.8 | <0.01 |
| 6 | Vegetation - Swainson's Tthrush abundance | 13 | 1029.4 | 53.6 | <0.01 | 13 | 350.6 | 17.9 | <0.01 |
| 3 | Topography | 4 | 1030.8 | 55.0 | <0.01 | 4 | 348.1 | 15.5 | <0.01 |
| 2 | Vegetation | 12 | 1039.6 | 63.7 | <0.01 | 12 | 356.0 | 23.3 | <0.01 |
| 4 | Swainson's Thrush abundance | 2 | 1131.4 | 155.6 | <0.01 | 2 | 360.0 | 27.4 | <0.01 |
| 1 | Null | 1 | 1136.9 | 161.1 | <0.01 | 1 | 362.6 | 29.9 | <0.01 |

**Note**: The variable "year" is present in all models. *K*, number of parameters; QAICc, quasi-likelihood information criterion corrected for small sample size; AICc, Akaike's information criterion corrected for small sample size. The best model (i.e., with the values of QAICc weight and AICc weight closest to 1 is set in boldface type.

*Vegetation variables: tree species, ground cover, % thinned in 1980s and 1990s, and unthinned within 100 and 250 m.

†Topography variables: elevation at point count and variation within 100 and 250 m.

**Table 2.4.** Model-averaged parameter estimates for response of Bicknell Thrush (*Catharus bicknelli*) abundance to vegetation, topography and Swainson's Thrush (*Catharus ustulatus*) counts at Mont Gosford and Massif du Sud, Québec, Canada.

| **Variable** | **Mont Gosford** | | | | **Massif du Sud** | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | SE | *Z* | *P* | Estimate | SE | $X^2$ | *P* |
| Balsam Fir dominant | -0.164 | 0.292 | -0.56 | 0.6 | -0.444 | 0.502 | 0.78 | 0.4 |
| Balsam Fir and White Birch | -0.023 | 0.245 | -0.10 | 0.9 | -0.470 | 0.454 | 1.07 | 0.3 |
| Other - no Balsam Fir | 0.000 | 0.000 | | | 0.000 | 0.000 | | |
| % Unthinned / 100 m* | -2.546 | 1.354 | -1.88 | 0.06 | 69.118 | 579.961 | 0.01 | 0.9 |
| % Thinned in 1980s / 100 m* | **-2.918** | **1.317** | **-2.22** | **0.03** | 68.128 | 579.955 | 0.01 | 0.9 |
| % Thinned in 1990s / 100 m* | -2.501 | 1.603 | -1.56 | 0.1 | 69.668 | 579.959 | 0.01 | 0.9 |
| % Unthinned / 250 m* | -0.416 | 2.614 | -0.16 | 0.9 | -0.332 | 11.365 | 0.00 | 0.9 |
| % Thinned in 1980s / 250 m* | 0.411 | 2.639 | 0.16 | 0.9 | 3.933 | 11.416 | 0.12 | 0.7 |
| % Thinned in 1990s / 250 m* | -1.497 | 3.024 | -0.50 | 0.6 | 0.489 | 11.271 | 0.00 | 0.9 |
| Closed (*vs* open) ground cover | -0.169 | 0.154 | -1.10 | 0.3 | -0.296 | 0.384 | 0.59 | 0.4 |
| Δ Elevation / 100 m* | -0.006 | 0.006 | -0.98 | 0.3 | 0.008 | 0.023 | 0.13 | 0.7 |
| Δ Elevation / 250 m* | **0.013** | **0.047** | **3.40** | **<0.001** | -0.011 | 0.011 | 1.04 | 0.3 |
| Elevation at point count | **0.002** | **0.001** | **2.26** | **0.02** | **0.013** | **0.003** | **18.83** | **<0.001** |
| Swainson's thrush abundance | **0.091** | **0.021** | **4.27** | **<0.001** | **0.234** | **0.068** | **11.82** | **<0.001** |

**Note:** Significant variables are in boldface type.
*Collinear (sometimes |r| > 0.70 between 100 m and 250 m variants of the same variable).

**Table 2.5.** Correlations between individual variables and the first two principal components for the ordination of point-count stations at Mont Gosford and Massif du Sud, Quebec, Canada, from 2001 to 2007.

| | Component | |
|---|---|---|
| Variable | 1 | 2 |
| % Unthinned per 100 m | -0.929 | -0.243 |
| % Thinned in 1980s per / 100 m | 0.454 | 0.790 |
| % Thinned in 1990s per 100 m | 0.721 | -0.507 |
| % Unthinned per 250 m | -0.970 | -0.103 |
| % Thinned in 1980s per 250 m | 0.468 | 0.775 |
| % Thinned in 1990s per 250 m | 0.730 | -0.567 |
| Closed (*vs* open) ground cover | 0.350 | 0.291 |
| Δ Elevation per 100 m | -0.131 | 0.524 |
| Δ Elevation per 250 m | -0.245 | 0.513 |
| Elevation at point count | -0.405 | 0.450 |
| Swainson’s Thrush abundance | 0.102 | 0.059 |
| % of total variance explained | 33 | 25 |

In contrast, our analyses indicated no geographical consistency in Bicknell’s Thrush relationship with tree species and habitat topographic heterogeneity. In New Brunswick, Nixon et al. (2001) found that white birch was an important component of its habitat that did not materialize in our study likely because of the balsam fir prevalence at both sites. The variation of elevation within a 250 m radius from the point count was significantly positively associated with the presence of Bicknell’s Thrush at Mont Gosford, but not at Massif du Sud. An association with steep terrain has been noted in most of the species’ US range (Frey 2008). Those differences may simply reflect heterogeneous habitat availability at the various sites. For instance, our two study areas exhibit different overall topographies, with 70% of all point counts having an elevation variation >80 m within 250 m at Mont Gosford, compared with 30% at Massif du Sud.

**Figure 2.2.** Habitat ordination for Bicknell's Thrush (*Catharus bicknelli*) and Swainson's Thrush (*Catharus ustulatus*) at Mont Gosford and Massif du Sud, Quebec, Canada, from 2001 to 2007.

Bicknell's Thrush shows strong site fidelity (Rimmer et al. 2001; Y. Aubry, personal observation) and may remain in disturbed forest stands, either following clear-cutting or thinning activities or after a fire because of the presence of a female or conspecifics and remaining of suitable habitat. By focusing on habitat structure, elevation, and terrain, we may have overlooked behavioural characteristics that may influence habitat use. To refine Bicknell's Thrush habitat-use models, other parameters could be explored, including habitat fragmentation, patch size and isolation, and the presence and number of conspecifics (Mönkkönen et al. 1999; Mönkkönen and Forsman 2002; Frey 2008; Cunningham and Johnson 2012; Laughlin et al. 2013).

### Overall abundance among regions

Overall numbers of Bicknell’s Thrushes were lower at Massif du Sud than at Mont Gosford, though their abundance at occupied sites was similar. This may reflect reduced availability of suitable habitat in the more recently logged and thinned forests at Massif du Sud.

Connolly (2000) similarly hypothesized that a difference in abundance of Bicknell’s Thrushes at two study sites in southern Quebec was linked to contrasting forest management histories. She recorded higher densities at Mont Mégantic, where the last forestry activities had occurred in the late 1950s, than at Mont Gosford, where large clearcuts occurred in the 1970s and thinning as recently as 1996.

Interestingly, Nixon et al. (2001) reported Bicknell’s Thrush densities in harvested forest landscapes dominated by young regenerating clearcuts in New Brunswick (16 individuals per 100 ha) that were similar to those we noted at Massif du Sud (13.7 individuals per 100 ha). In contrast, we obtained estimates of 22–50.3 individuals per 100 ha at Mont Gosford where the forest was less recently impacted by forestry operations. It should be noted though that drawing similarities and differences between Nixon et al. (2001) and our results is compounded by the fact that we used different survey protocols (6 min of passive listening vs. 20 min with playback, respectively) associated with different detection probabilities ($p$ = 0.40 vs. 88% to 96%).

Overall, these results suggest that Bicknell’s Thrush numbers at the landscape level are negatively impacted by the recency of forestry operations, particularly at Mont Gosford where the unthinned stands dominate the study area compared with Massif du Sud where they are more limited and dispersed through a complex mosaic of thinned and clear-cut stands. In New Brunswick, the presence of Bicknell’s Thrush in thinned or heavily managed area is linked to the amount of residual unthinned patches (Chisholm and Leonard 2008), which is vital for its nesting activities (McKinnon et al. 2014). Even if Bicknell’s Thrushes are incorporating thinned stands in their home range, unthinned stands are a dominant component when available (Aubry et al. 2011).

In Quebec, where most of Bicknell’s Thrush habitat is on crown land, precommercial thinning has been intense and wide spread since the mid-1970s. Precommercial thinning, as well as other forest management activities, have contributed to transform the structure and composition of the forest and have increased the difficulty of modeling Bicknell’s Thrush habitat. Efforts should be made to locate database with more objective data or data not formatted principally for forest and timber management.

### Relationships between Bicknell’s and Swainson’s thrushes

We observed Bicknell’s and Swainson’s thrushes at all sampled elevations at both our study areas, actually co-occurring at a majority of point-count stations. Conversely, several studies reported an elevational segregation between Bicknell’s and Swainson’s thrushes (Able and Noon 1976; Morse 1979; Noon 1981; Dellinger et al. 2007) that Holmes and Sawyer (1975) related to differential adaptation to a temperature gradient. Wallace (1939) reported that the two species were “not found together” on the northeast side of Mt. Mansfield, Vermont, in the mid-1930s, whereas they “distinctly overlapped, and nests of both in close proximity were found at less than 2900 feet [884 m] and at more than 3000 feet [914 m]” on the southwest side. However, K. McFarland (personal communication, 2015) reports that Swainson’s Thrush is now present up to the tree line (±1250 m) at the same sites, indicating a possible upward elevational shift since the 1930s. On a broader scale, in 2007, Swainson’s Thrushes were observed at a majority of stations surveyed at all elevations in the northeastern United

States (Mountain Birdwatch Monitoring Program; elevational range 630–1472 m, $n$ = 705 point counts; J. Scarl, personal communication) and in the Canadian Maritime region (High Elevation Landbird Monitoring Program; elevational range 87–781 m, $n$ = 232 point counts; H. Lightfoot, personal communication). All these results suggest that if the two species were formerly segregated, this may not be the case anymore.

Where Bicknell's and Swainson's thrushes co-occur, agonistic interactions between the two species have been reported (Able and Noon 1976; Sabo and Whittaker 1979; Rimmer et al. 2001) and interpreted as evidence of competition (Sabo 1980; Noon 1981). The positive correlation in the abundance of the two species at both our study areas should not be interpreted as evidence for or against interspecific competition, because our study was not specifically designed to assess interspecific competition (Connell 1983). Nixon et al. (2001) did not find a correlation between the densities of the two species in New Brunswick, but this may be because of the generally low-elevation range and that the ubiquitous Swainson's Thrush had saturated available habitat at their study areas. Specifically designed studies would be required to assess the occurrence of interspecific competition and, if present, whether it is mitigated through microhabitat or niche partitioning, or behavioral strategies (Dilger 1956; Noon 1981; Dellinger et al. 2007; Laughlin et al. 2013).

We did not investigate niche relationships here, but niche overlap with Swainson's Thrush could affect Bicknell's Thrush foraging activities, nest-site selection, productivity, and possibly home-range size, although in this case, the presence of female would be more important considering the male-biased ratio and the limited number of females in the population. Also, if dense stands are a limiting factor, some impact on productivity and competition between females for nesting sites could become an issue.

Our habitat models were built on a single year of data for Massif du Sud. The value of those models should lead us to caution, as we may not exclude influences of regional temporal variation in abundance and possible density-dependence in habitat use. Furthermore, high quasi-bi-annual predation rate by squirrel at nest has an influence on Bicknell’s Thrush yearly abundance (Townsend et al. 2015).

Our study contributes to a better understanding of the breeding habitat of Bicknell’s Thrushes. In particular, we have confirmed consistency in Bicknell’s Thrush breeding-habitat relationships over two areas submitted to very distinct forest management regime and could extrapolate the results to other areas with forestry activities. Our results are also consistent with the hypothesis that Bicknell’s Thrush numbers are related to the amount of forest habitat not impacted by recent forestry activities like recently shown for managed forests in New Brunswick (Chisholm and Leonard 2008; McKinnon et al. 2014). However, factors not related to habitat may contribute to the low abundance of this threatened species, compared with the co-occurring Swainson’s Thrush. For instance, conspecific attraction may cluster individuals sufficiently to leave areas of suitable habitat unoccupied (Muller et al. 1997). Thus, even if our study provides support for the use of habitat models to understand Bicknell’s Thrush populations over large geographical areas, we need to better understand individual and group behaviours and the species’ population dynamics, as well as more specific habitat factors such as tree height, subcanopy entanglement complexity, abundance of seed trees for the American red squirrel (*Tamiasciurus hudsonicus* (Erxleben, 1777)) (which is the most important nest predator), or squirrel abundance, to develop better, locally relevant habitat-use models. Better models will be especially valuable for areas of managed forests, where erroneous prescriptions based on weak models would be costly.

Finally, this study reveals also the importance of Mont Gosford and Massif du Sud as two regional strongholds for Bicknell's Thrush protection and conservation. Those sites would benefit from a strong conservation framework based on the species habitat requirements encompassing all species activities such as nesting, foraging, molting, and migration. Repeated research activities that have been conducted since the late 1990s are a solid base for long-term studies and monitoring for the benefit of the communities and the protection of this threatened species.

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Chapitre 3

# Not enough habitat or not enough birds? Low habitat occupancy by Bicknell’s Thrush (*Catharus bicknelli*) in Québec’s Laurentian Highlands*

# Pas assez d’habitat ou pas assez d’oiseaux ? Faible taux d’occupation de l’habitat par la Grive de Bicknell (*Catharus bicknelli*) sur le Plateau Laurentien, Québec*

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* Aubry, Y., A. Desrochers, and G. Seutin. (en révision) Not enough habitat or not enough birds? Low habitat occupancy by Bicknell’s Thrush (*Catharus bicknelli*) in Québec’s Laurentian Highlands. *Avian Conservation and Ecology-Écologie et Conservation des Oiseaux* (ACE-ECO).

## Résumé

En Amérique du Nord, les populations d’une grande proportion d’oiseaux migrateurs occupant les forêts boréales et de l’Est sont en déclin. La perte d’habitat est le facteur limitant le plus cité. Nous avons estimé le taux d’occupation d’habitats favorables à la Grive de Bicknell (*Catharus bicknelli*), cette espèce forestière menacée, sur le Plateau Laurentien, Québec. Cette région a été façonnée autant par des activités forestières intenses que par des perturbations naturelles. L’espèce utilise des peuplements de 20 ans et plus; plusieurs individus ont également été signalés dans des peuplements plus vieux au sommet de montagnes où la foresterie et les perturbations naturelles étaient moins répandue. L’occupation par la Grive de Bicknell était associée à la haute élévation où les éclaircies précommerciales étaient moins fréquentes. Tant le taux d’occupation que l’analyse multivariée indiquent la vacance par la Grive de Bicknell d’habitat favorable sur le Plateau Laurentien. Malgré la faible occupation des sites à fort potentiel et les effectifs en apparence réduits de la Grive de Bicknell, le maintien des habitats de reproduction demeure essentiel au rétablissement de l’espèce, mais une hausse des effectifs risque de ne pas se matérialiser sans mesures additionnelles de protection en dehors des aires de reproduction.

## Abstract

In North America, a high proportion of migratory bird species inhabiting boreal and eastern forests is declining. Habitat loss is frequently cited as limiting factor. We estimated occupancy of suitable nesting habitat by Bicknell’s Thrush (*Catharus bicknelli*), a forest dwelling threatened species, in the Laurentian Highlands of Québec. Forests in this region are shaped by intensive forestry activities and natural disturbances. The species was found primarily in stands of about 20 years or more, with higher occupancy in older stands on hilltops where recent forestry activities and natural perturbations have been much less prevalent. Bicknell’s Thrush occupancy was significantly associated with high elevations in landscapes with relatively low amounts of precommercial thinning. Occupancy and multivariate niche approaches indicated that a large extent of potential habitat was unoccupied by breeding Bicknell’s Thrushes. We conclude that maintaining sufficient amounts of suitable breeding habitat in this exploited forest landscape remains important to enable the species’ recovery, but that an increase in its numbers may not materialize without further measures to reduce threats outside of its breeding habitat.

## Introduction

In North America, a high proportion of migratory bird species inhabiting boreal and eastern forests is declining (Sauer et al. 2013). Habitat loss, impairment and fragmentation on breeding or wintering grounds, or at stopover sites may play a significant role in these declines. The endangered status of several species has been directly linked to forest management issues. In North America alone, examples include Olive-sided Flycatcher (*Contopus cooperi*; Robertson and Hutto 2007), Rusty Blackbird (*Euphagus carolinus*; Powel et al. 2010), Cerulean Warbler (*Setophaga cerulea*; Buehler et al. 2008), Kirtland's Warbler (*Setophaga kirtlandii*; Long 2009), and Barrow's Goldeneye (*Bucephala islandica*; Vaillancourt et al. 2009; Gouvernement du Québec 2013). Those impacts, real or imagined, have triggered calls for action by the scientific, philanthropic and environmental advocacy communities, as exemplified by the ''Boreal Birds Need Half'' campaign (Wells et al. 2014), which assumes that habitat limitation is a pervasive issue. Accordingly, forestry operators on breeding grounds are being asked to adopt more sustainable and bird-friendly practices (Booth et al. 1993, Franklin et al. 2002, Cyr et al. 2009, Bélanger 2010, Marzluff et al. 2000; Drapeau et al. 2016).

An essential requirement for effective and efficient recovery planning for a species at risk is the identification of the key limiting factors through its annual cycle (Faaborg et al. 2010, Rushing et al. 2016). Habitat availability is one of the most frequently cited limiting factors for a wide range of taxa (Hoekstra et al. 2005, Maxwell et al. 2016). This may be especially true for migratory species that depend on different habitats, each potentially under different threats, at different times through their annual cycle. Habitat may be limiting for a species at risk because it is rare, of low quality, inaccessible, or for more subtle reasons as in the case of species with spatially-aggregated social systems (Macedo and Bianchi 1997, Bourque and Desrochers 2006) or a highly biased sex-ratio (Donald 2007).

To determine whether habitat availability limits a population, a logical first step is to determine how much suitable habitat is available yet unoccupied (Nelson and Buech 1996, Rappole et al. 2003, Gibson et al. 2007, Engler et al. 2014). High vacancy rates would generally negate the hypothesis that habitat availability is limiting, at least in the geographic area considered (Hoekstra et al. 2005, Nielsen et al. 2006). However, apparently unoccupied areas could also reflect inadequacies of the survey method (i.e., low detection probability of the focal species; Gu and Swihart 2004) or of the habitat sampling design (i.e., failure to include important habitat variable for the species under consideration).

Bicknell's Thrush (*Catharus bicknelli*) has one of the most restricted breeding ranges of all North American forest-breeding migratory birds (COSEWIC 2009, McFarland et al. 2013, Townsend et al. 2015, Hill and Lloyd 2017). At the continental scale, the species ranks as one of the highest conservation priorities (Rich et al. 2004, Rosenberg et al. 2014), while it is legally considered as threatened in Canada (Government of Canada 2012) and vulnerable in Quebec (Gouvernement du Québec 2009). Most of Bicknell's Thrush breeding habitat in Canada occurs in southern Quebec in the Appalachian Range and on the Laurentian Highlands north of the St. Lawrence River (COSEWIC 2009). In the latter region, suitable breeding habitat occurs primarily at high elevation in dense balsam fir dominated stands within industrial forestland where clear-cuts and forest management practices aiming at reducing stem density (hereafter called precommercial thinning) lessen habitat quality (Higdon et al. 2006, Chisholm and Leonard 2008, COSEWIC 2009, Aubry et al. 2011, 2016). Habitat loss and impairment have been suggested as the major threats to the species (COSEWIC 2009, Lloyd and McFarland 2017). Consequently, there have recently been pressures and efforts to limit the extent and intensity of precommercial thinning throughout the species' range (Chisholm and Leonard 2008, BSC 2009, Gouvernement du Québec 2014, Lambert et al. 2017). Such changes can be costly to the industry, directly and indirectly affecting regional economies and, if misguided, impinge the credibility of science conservation advisors.

To better guide Bicknell's Thrush conservation efforts, we studied habitat occupancy in Quebec's Laurentian Highlands. Specifically, we assessed whether habitat availability may limit the species recovery by testing the hypothesis that optimal breeding habitat is saturated in the region. We defined habitat as optimal where estimates of occupancy are highest. We also tested the hypothesis that precommercial thinning is associated with lower occupancy of Bicknell's Thrush breeding habitat, as found in other regions (Aubry et al. 2011). The species need dense stand as a concealment for its nest and avoid potential predation. Therefore, we predict that thinned stands are less occupied than unthinned stands. To test those two hypotheses, we performed site occupancy modeling as per Mackenzie et al. (2002). However, Bicknell's Thrushes have large home ranges on their breeding grounds and a spatially-aggregated social system (Aubry et al. 2011, Townsend et al. 2015), likely due to their polygynandric mating system (Goetz et al. 2003; Townsend et al. 2015), which may undermine the assumption of closure of the occupancy state required by occupancy models (MacKenzie et al. 2003). Thus, we also assessed occupancy using a graphical approach that represents Bicknell's Thrush niche space based on a two-dimensional reduced projection of topographic and vegetation variables.

## Methods

### Study area

The 17,350-km$^2$ study area is located north of the St. Lawrence River, centered approximately 75 km north of Quebec City, Quebec, at the south-east edge of the Laurentian Highlands. It is part of the balsam fir-white birch bioclimatic domain (Grondin et al. 1998; Fig. 3.1) lying between 47° and 48.35°N and 70° and 72.30°W. The elevation varies from 130 to 1,100 m and the mean annual temperature is 0° C. Abundant precipitations (1.2 - 1.6 m/year) are associated with a long fire cycle (> 500 years; Boucher et al. 2014). The vegetation is dominated by balsam fir (*Abies balsamea)* and paper birch (*Betula papyrifera*); black spruce (*Picea mariana*) occurs increasingly towards the north of the study area, and deciduous trees are often abundant in regenerating clear-cuts and recently burned areas (Grondin et al. 1998). Disturbances are mostly from anthropic origin, with forestry activities having occurred at all elevations since 1900 but more intensively at low elevation (Boucher and Grondin 2012, Boucher et al. 2014).

We determined stand age and the extent of precommercial thinning over the study area from forest inventory data (Gouvernement du Quebec 2015). We converted the original forestry and topographic map layers to rasters with a 10-m resolution, with the Spatial Analyst extension of ArcGIS (ESRI 2010) We calculated stand ages based on documented years of clearcutting and other stand-renewing events (i.e., fire and major spruce budworm outbreaks). In places where only age classes were known, we determined stand age as the midpoint of the age class for even-aged stands, or as the lowest age class for heterogeneous stands.

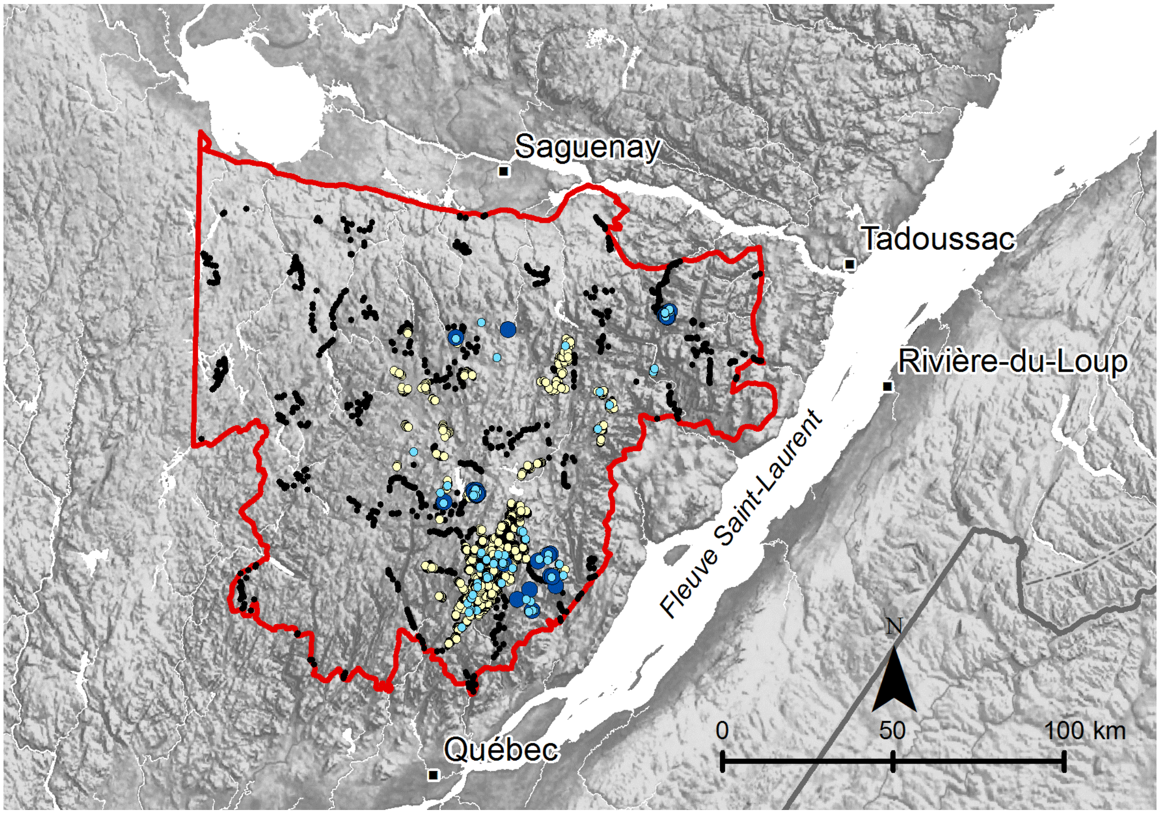

**Figure 3.1**. Study area, delimited by the red line, in the Laurentian Highlands, Québec, Canada. Beige and blue dots represent point count stations with no, or at least one Bicknell’s Thrush reported, respectively. Light and dark blue dots represent detections of one or multiple Bicknell’s Thrushes, respectively. Black dots represent point counts eliminated from the analyses. (Map sources: Digital elevation model© Government of Québec, all rights reserved, 2004, and Natural Resources Canada for waterways)

## Point counts

We compiled data from 7830 fixed radius point counts conducted for different projects in the study area between 1995 and 2016 (Fig. 3.1). Those projects focused on all bird species (>95% of sites randomly selected) covered a broader range of altitudes, while surveys targeting Bicknell's Thrush covered sites with elevation > 800 m. The projects were: second Quebec Breeding Atlas, Forêt Montmorency bird monitoring program, regional environmental impact assessments, Mountain BirdWatch monitoring scheme, Huron-Wendat Bicknell's Thrush monitoring project, and provincial and federal governments' Bicknell's Thrush surveys. We retained 4818 point counts for analysis based on three criteria: a duration of 15 to 30 min (mean = 18 min), conducted before 9:00 (*n* = 4,700) or after 19:00 (n = 118), and between 22 May and 25 July. Those periods correspond to high Bicknell's Thrush vocal activity (Ball 2000). Nine percent of the point counts used playbacks of Bicknell's Thrush calls and songs. Retained point counts were distributed among 2500 stations separated by at least 150 m, often (54%) along forestry roads. We surveyed 31 % of the point count stations more than once in a year (Appendix 3.1), and surveyed 38 and 114 stations on two and three different years respectively. Forty observers, all with experience with Bicknell's Thrush vocalizations, participated in the point counts. We recorded all Bicknell's Thrushes within 75 or 100 m-radii, depending on the data source. We assumed that the radius difference was sufficiently small across surveys, and that the distance between point counts was sufficient across the study areas, to prevent major biases (Yip et al. 2017).

## Site occupancy

We fit nine competing single-season site occupancy models (Mackenzie et al. 2006) to measure site occupancy by Bicknell's Thrush, given imperfect detection during point counts. Models were fit by maximum likelihood with the unmarked package 0.11-0 in R Version 3.3.1 (Fiske et al. 2011, R Development Core Team 2016). The models considered various combinations of 11 site-related occupancy and 4 point count-related detection variables, identified from the published literature on the species (Table 3.1). We introduced the variable Year in the models to account for high bi-annual nest predation by red squirrel (*Tamiasciurus hudsonicus*, Townsend et al. 2015) which may affect recruitment and demographic parameters, and hence occupancy. Elevation was selected because the species is known to be associated with mountain type habitat (Aubry et al. 2016, Townsend et al. 2015) and we used the standard deviation of elevation within 1 km of point count as an index of rugged topography. Bicknell's Thrushes often establish their home range in regenerating or young forest stands (Townsend et al. 2015) ≥ 1,5-2 m high (personal observation). To account for a possible nonlinear response to forest age (Ter Braak and Looman 1986), we included a quadratic stand age term in the models. We used the standard deviation of stand age as an index of habitat heterogeneity. We included distance of point count from nearest road in view of concerns of a possible edge effect expressed earlier (Hanowski and Niemi 1995; but see Hutto et al. 1995, Lituma and Buehler 2016). Moreover, Bicknell's Thrush may respond to edges, as shown in a recent study where the species was not avoiding stand edges in an industrial forest (Aubry et al. 2011), or as in a ski trail study where a higher nest density was observed in forest edges where vegetation was dense (Rimmer et al. 2004).

We computed Goodness-of-Fit for the best occupancy model using a parametric bootstrap approach (MacKenzie and Bailey 2004) with 100 replicates. The best, single-season model fit the data well with no apparent over dispersion (function 'parboot' of package 'unmarked', $p = 0.21$). To facilitate convergence and parameter estimation, all numerical variables were standardized before analysis. We used the Akaike information criterion to identify the best model (Table 3.2).

### Niche space occupancy

We conducted a Principal Component Analysis (function "prcomp" in R) using the three vegetation and topography variables that were identified as significantly related to Bicknell's Thrush occupancy in the best performing occupancy model (Table 3.3), along with mean stand age (within 100 m of point count) that also appeared to be associated with occupancy (Fig. 3.2). We used the first two principal components to represent Bicknell's Thrush niche space, and calculated two-dimensional kernel densities of Bicknell’s Thrush occurrences (R package MASS, function ‘kde2d’; Venables and Ripley 2002). The proportions of occupied point count stations falling in each kernel density category provided estimates of Bicknell’s Thrush occupancy.

**Table 3.1**. Site-related occupancy, and point count-related detection variables included in Bicknell’s Thrush occupancy models for the Laurentian Highlands, Quebec, Canada.

| Variable | Description |
|---|---|
| Occupancy | |
| Year | Year of point count |
| Longitude | Easting (meters, MTM7 projection) |
| Latitude | Northing (meters, MTM7 projection) |
| Elevation | Elevation, above sea level (m) |
| ElevationSD1000 | Standard deviation of elevation within 1 km of point count |
| % Deciduous | Proportion of raster with deciduous-dominated stands within 1 km of point count |
| Age100 | Mean stand age within 100 m of point count |
| Age100quad | Quadratic term of the stand age within 100 m of point count |
| Age1000 | Mean stand age within 1 km of point count |
| AgeSD1000 | Standard deviation of stand age within 1 km of point count |
| PCT1000 | Proportion of raster with precommercial thinning in the last 20 years within 1 km of point count |
| DistRoad | Distance to nearest road (m) |
| Detection | |
| Playback | Use of Bicknell’s Thrush playback during point count (dichotomous) |
| Date (Julian) | Days since 1 January |
| Time of Day | Evening or morning (dichotomous) |
| Duration | Duration of point count (min) |

## Results

Bicknell’s Thrush were reported at 121 (2.5%) of the 4,818 point counts, and at 115 (4.6%) of the 2,500 point count stations (Fig.3.1). Table 3.2 presents and compares the various occupancy models examined. The model incorporating all variables (model Full) did not perform best. The best model is presented in details at Table 3.3. The best performing occupancy model (as did most other models) identified three point count-related detection variables that were significantly associated with the probability of detecting Bicknell's Thrush (Table 3.3): date (increasing from May to July), duration (increasing with length) and use of playback (increased from about 0.14 to about 0.81 when used). We visually inspected the spatial distribution of point counts according to these variables and failed to identify distribution patterns that would bias further analyses and conclusions. Detection probabilities in the morning were 0.16 ± 0.04 without playback and rose significantly to 0.63 ± 0.15 with playbacks. Detection probabilities were higher, but not significantly so (Table 3.3), in the evening, both without or with playbacks (0.36 ± 0.24, 0.83 ± 0.15, respectively).

The best performing occupancy model identified four site-related occupancy variables and one interaction that were significantly associated with Bicknell's Thrush occupancy (Table 3.3): year, elevation, and the proportion of deciduous-dominated stands showed a positive relationship, while the extent of precommercial thinning related negatively to occupancy. Occupancy increased significantly between 1995 and 2016 in the study area (Table 3.3; Fig. 3.3). An analysis where all variables except Year were set to their mean value over the entire study area, thereby removing confounding factors, revealed that the temporal trend was consistent through time.

Bicknell's Thrushes were seldom reported below 800 m elevation (*n* = 6/121), and site occupancy was greater than 0.7 at only a handful of stations (*n* = 10) at the highest elevations (Fig. 3.4).

The best performing occupancy model did not identify a direct relationship for distance to the nearest road but rather an effect through an interaction with elevation and stand age. To better understand the relationship between stand age and occupancy, we contrasted the kernel density distributions of stand age at stations where Bicknell's Thrushes were observed and not observed (Fig. 3.2). The distributions were substantially different, revealing higher occupancy of the youngest (20 – 30 years old) and oldest (> 70 years old) stands, and lower occupancy of mid-age stands.

**Table 3.2**. Comparison of nine models for Bicknell's Thrush occupancy in the Laurentian Highlands, Quebec, Canada, using combinations of topographic, vegetation, landscape and temporal variables (see Table 3.1). All models included the four point count-related detection variables: playback, Julian date, time of day, duration. Data from 2500 point count stations surveyed between 1995-2016.

| Model | K | AICc | Delta AICc | AICc Weight | Cum. Wt | Log Likelihood |
|---|---|---|---|---|---|---|
| Year, Elevation x (Age100, Age100quad), %Deciduous, PCT1000 | 14 | 855.91 | 0 | 0.99 | 0.99 | -413.87 |
| Full | 18 | 865.15 | 9.24 | 0.01 | 1 | -414.44 |
| Elevation x (Age100, Age100quad), ElevationSD1000, PCT1000 | 13 | 872.54 | 16.63 | 0 | 1 | -423.2 |
| Elevation | 7 | 876.73 | 20.82 | 0 | 1 | -431.34 |
| Elevation, ElevationSD1000 | 8 | 876.93 | 21.01 | 0 | 1 | -430.43 |
| Year (trend) | 7 | 921.04 | 65.13 | 0 | 1 | -453.5 |
| Latitude, Longitude, Age100, Age100quad, PCT1000 | 11 | 922.1 | 66.19 | 0 | 1 | -450 |
| Latitude, Longitude, %Deciduous, PCT1000, AgeSD1000 | 11 | 926.39 | 70.48 | 0 | 1 | -452.14 |
| Null | 6 | 935.62 | 79.71 | 0 | 1 | -461.79 |

**Table 3.3**. Parameter estimates for the best performing occupancy model for Bicknell's Thrush in the Laurentian Highlands, Quebec, Canada. Data from 2500 point count stations surveyed between 1995-2016.

| Variable | Estimate | SE | *z* | P(>\|*z*\|) |
|---|---|---|---|---|
| Occupancy | | | | |
| (Intercept) | -2.874 | 0.27 | -10.7 | <0.001 |
| Year (trend) | 0.659 | 0.20 | 3.43 | <0.001 |
| Elevation | 1.036 | 0.16 | 6.4 | <0.001 |
| Age100 | 6.2 | 7.77 | 0.80 | 0.4 |
| Age100 (quadratic) | 9.068 | 9.29 | 0.986 | 0.3 |
| % Deciduous | 0.428 | 0.13 | 3.26 | 0.001 |
| PCT1000 | -0.304 | 0.12 | -2.45 | 0.015 |
| Elevation x Age100 | -15.117 | 6.49 | -2.33 | 0.02 |
| Elevation x Age100 (quadratic) | -4.017 | 8.47 | -0.47 | 0.6 |
| Detection | | | | |
| (Intercept) | -7.5853 | 2.29 | -3.32 | 0.0009 |
| Playback | 2.1695 | 0.60 | 3.61 | 0.0003 |
| Julian Date | 0.0261 | 0.01 | 2.22 | 0.03 |
| Time of Day | 1.065 | 0.98 | 1.09 | 0.3 |
| Duration | 0.0749 | 0.037 | 2.00 | 0.045 |

In the niche space occupancy analysis, the first two axes of the principal component analysis accounted for 71% of the total variance (PC1: 0.44; PC2 0.27; Table 3.4). High values for the first factor reflected low elevation, but high deciduous and precommercial thinning cover. High values for the second factor reflected high elevation and young stands, independent of deciduous dominance or precommercial thinning.

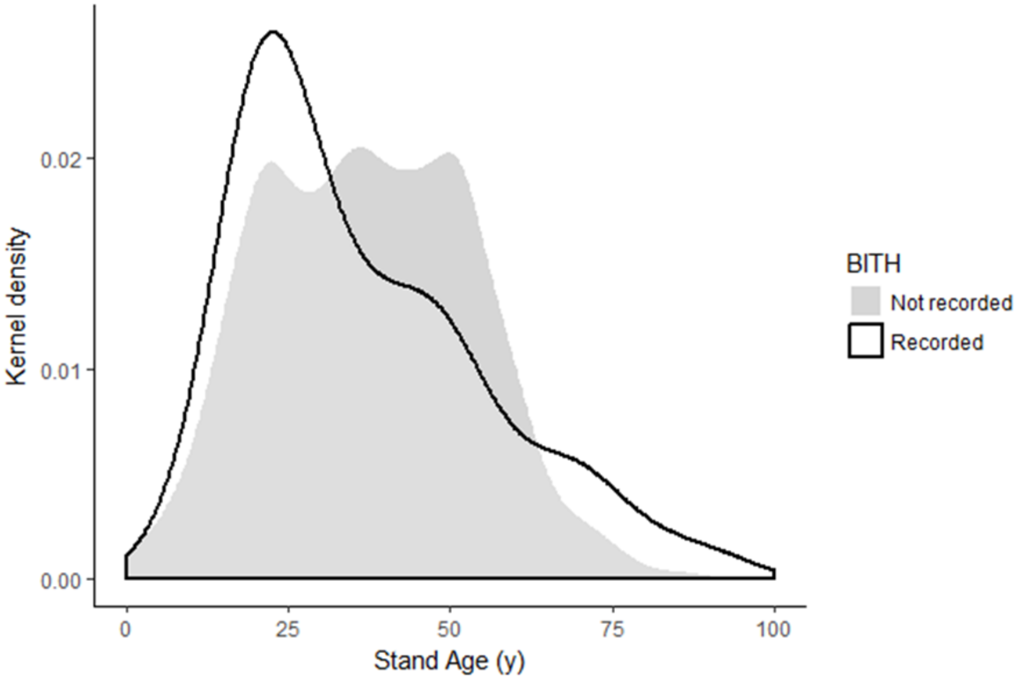

**Figure 3.2**. Kernel density distribution of stand ages (Age 100; Table 3.1) for point count stations where Bicknell's Thrush were recorded, or not recorded, in the Laurentian Highlands, Quebec, Canada. Data from 2500 point count stations surveyed between 1995-2016.

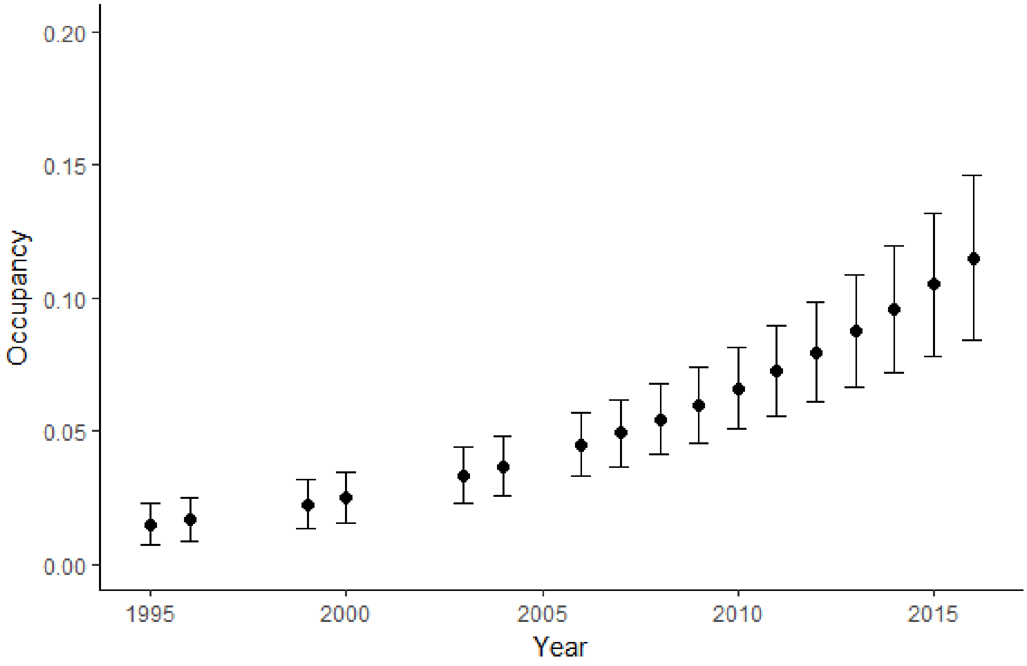

**Figure 3.3**. Bicknell's Thrush site occupancy in relation to year in the Laurentian Highlands, Quebec, Canada. To prevent confounding effects, occupancy estimates were obtained by setting all other variables fixed at their mean value over the entire study area. Data from 2500 point count stations surveyed between 1995-2016.

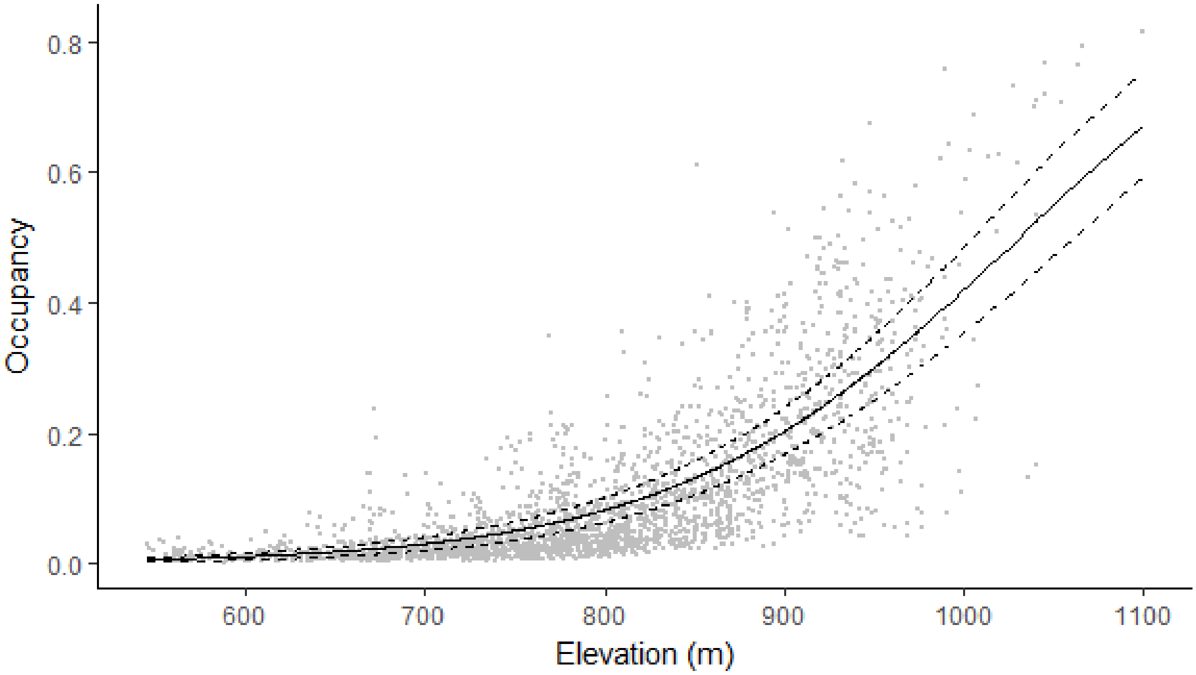

**Figure 3.4.** Bicknell's Thrush site occupancy in relation to elevation in the Laurentian Highlands, Quebec, Canada. The vertical scatter in occupancy estimates comes from the effect of other variables included in the best performing occupancy model presented in Table 3.3. The solid line represents occupancy estimated from model with elevation as the sole covariate, and other covariate values set at the mean of all point count stations. Data from 2500 point count stations surveyed between 1995-2016.

**Table 3.4**. Factor loadings for the first two factors of a principal component analysis of topographic and vegetation variables at Bicknell's Thrush point count stations in the Laurentian Highlands, Quebec, Canada. Data from 2500 point count stations surveyed between 1995-2016.

| Variable | PC1 | PC2 |
|---|---|---|
| Elevation | -0.60 | 0.31 |
| %Deciduous | 0.58 | 0.03 |
| PCT1000 | 0.53 | 0.17 |
| Age100 | -0.08 | -0.93 |

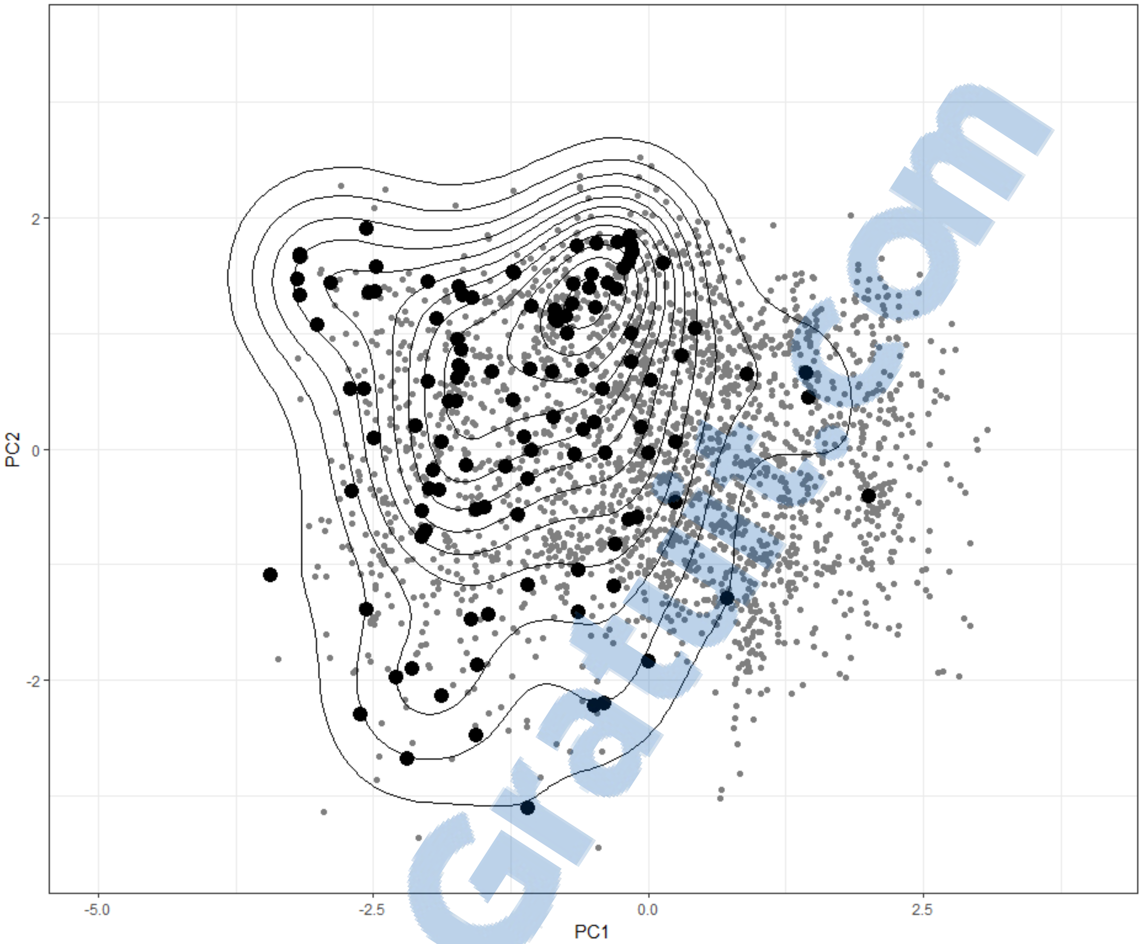

**Figure 3.5**. Kernel density estimates of Bicknell's Thrush occurrence in the Laurentian Highlands, Quebec, Canada, based on a principal component analysis of topographic and vegetation variables (Table 3.4). Contour lines represent increments in kernel density from 0.01 to 0.12 by increments of 0.01. Grey and black dots represent point counts with Bicknell's Thrush not reported, and reported, respectively. Data from 2500 point count stations surveyed between 1995-2016.

Of the 2,500 point count stations surveyed, 1969 felt within the two-dimensional niche space defined by kernel density > 0.05 (Fig. 3.5). Bicknell's Thrush was largely unreported at stations in the lower right quadrant of the biplot, corresponding to lower elevation, high thinning and more deciduous stands (Table 3.4). Bicknell's Thrush reporting rate was consistently low, reaching less than 8% at point count stations in the most suitable habitat (i.e., kernel density estimates > 0.10; Fig. 3.6).

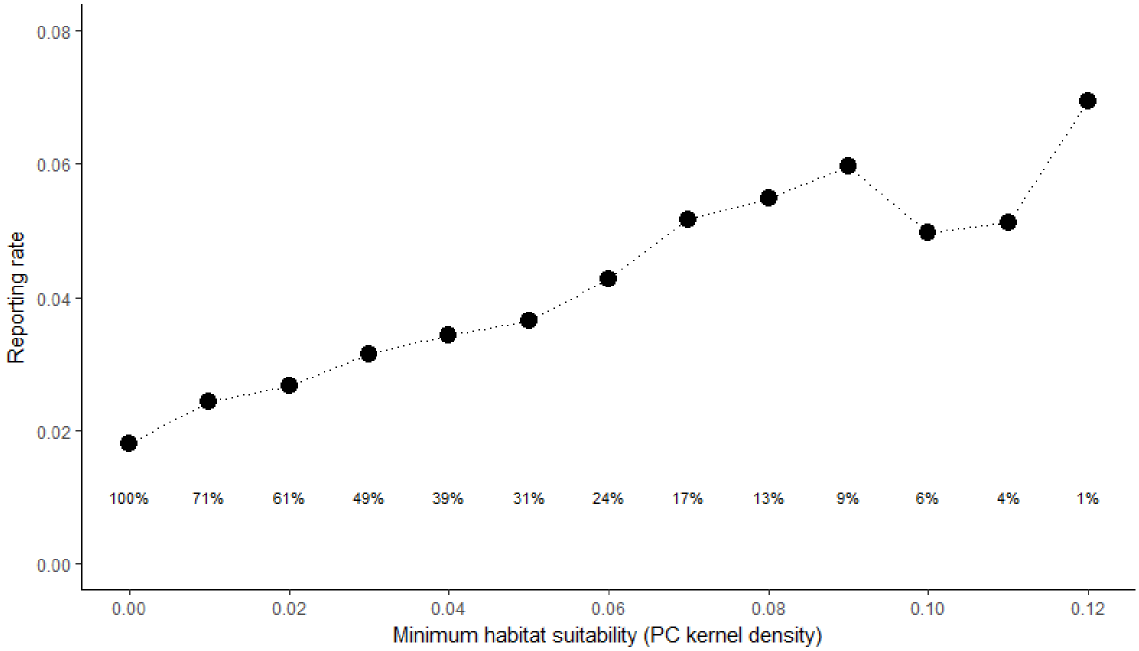

**Figure 3.6**. Reporting rates of Bicknell's Thrush at point count stations within available suitable habitat in the Laurentian Highlands, Quebec, Canada. Large kernel density estimates can be interpreted as an increase in habitat suitability. Sample sizes are shown below each density point. Data from 2500 point count stations surveyed between 1995-2016.

## Discussion

The scientific and advocacy communities have repeatedly argued for amendments to forestry practices to support the protection and recovery of species at risk. In many cases, the advocated policy rests on the assumption that current practices limit the amount of suitable habitat for a target species, thereby limiting its population numbers and distribution. Such logic holds true only if suitable habitat is largely occupied, if not saturated. Our study of Bicknell's Thrush site occupancy in the Laurentian Highlands of Quebec, using two contrasted approaches, revealed that a large extent of potential habitat was unoccupied. Similar conclusions were reached from studies of several other avian species at risk, such as the Golden-cheeked Warbler (*Setophaga chrysoparia*; Rappole et al. 2003), Kirtland's Warbler (*Setophaga kirtlandii*; Nelson and Buech 1996), Lesser Kestrel (*Falco naumanni*; Serano and Tella 2003), and White-browed Treecreeper (*Climacteris affinis*; Radford and Bennett 2004).

There is an apparent discrepancy between the positive regression estimate of % deciduous in Table 3.3, and the low reporting rates in the right quadrants of Fig 5, corresponding to high %deciduous values. This apparent discrepancy is likely due to the fact that occupancy estimates control for other covariables such as elevation, which is not the case in the principal component analysis. Furthermore, the amount of deciduous was estimated within 1000 m around point count. At that scale and in an environment where forestry activity is dynamic and prevalent such as in our study area, young deciduous dominated stands are common in the early stages of regenerating balsam fir forest. Despite that Bicknell's Thrush is known as a balsam fir specialist, this situation has also been documented in New Brunswick (Nixon 2001).

Our site occupancy models likely over-estimated occupancy rates because the large home ranges of Bicknell's Thrush (≥ 10 ha; Aubry et al. 2011) likely resulted in violations of the closure assumption (MacKenzie et al. 2006, Rota et al. 2009). On the other hand, imperfect detection may have led us to underestimate occupancy rates in the niche space occupancy analysis. This is unlikely since in a companion study (Aubry and Mazerolle, unpublished data), we estimated detection probabilities at ≥ 0.74 and ≥ 0.88 using point count techniques similar to those used here (i.e., 3 x 5 min. survey periods without and with an additional playback period, respectively). Biased occupancy rate estimates can also result from uneven accessibility of habitat patches across a study area (e.g., less access to high elevation sites). This was not at play in our research since the study area was covered by forestry roads, with almost no site beyond 300 m from a road, i.e. beyond the audible range of Bicknell's Thrush calls. It is thus unlikely that imperfect detection has introduced a bias of sufficient importance to alter our conclusion.

Bicknell's Thrush nesting habitat quality seems to be mostly driven by elevation and associated vegetation dynamics (e.g., wind throw, fir waves *sensu* Sprugel 1976) in both the Northeastern United States (Lambert et al. 2005, Hale 2006) and in Quebec (Aubry et al. 2016). In Vermont, in highly protected areas, occupancy of high-elevation habitat approaches 100% (Frey et al. 2012).

Extrapolating from Lambert et al's (2005) elevational habitat model, we should have recorded Bicknell's Thrush as low as 550 to 600 m in our study area. A similar model adapted for Quebec latitudes predicted occurrences at even slightly lower elevations (Rimmer, unpublished report). However, we recorded the species below 800 m (641-777 m) in only six occasions, corresponding to an estimated occupancy rate of < 8%. The discrepancy between model predictions and our observations may be due to habitat quality impairment at low elevation resulting from major fires and intensive logging through the 20th century (Boucher and Grondin 2012), the prevalence of precommercial thinning, and possibly nest predation by red squirrel.

Even at higher elevations, site occupancy by Bicknell's Thrush was generally well below saturation (Fig. 3.4). The most parsimonious explanation for this is an insufficient number of birds due to limiting factors acting outside of the breeding grounds. However, alternative phenomena may lead to a lack of breeders in optimal habitat. First, territory abandonment may occur over a large scale because of nest predation by red squirrels (McFarland et al. 2008). This was observed by Whitaker et al. (2015; personal communication) who noted that Gray-cheeked Thrushes (*Catharus minimus minimus*) in Newfoundland were now restricted to higher elevations than before the 60's when the red squirrel, primarily a lowland species, was introduced to the island (Payne 1976). Second, polygynandry in Bicknell's Thrush may lead to clustering through conspecific attraction (Nocera and Forbes 2010) and, in turn, reduce the suitability of small habitat patches, as is the case with several other forest songbirds (Bourque and Desrochers 2006, Desrochers et al. 2010).

During the study period, Bicknell's Thrush numbers appeared to have been stable in the United States (Hill and Lloyd 2017), while they were declining in the Canadian Maritimes and southeastern Quebec where the species became extirpated from several locations (Whittam 2015, Atlas of the breeding birds of Québec 2018). Contrastingly, we documented a significant increase in occupancy in the Laurentian Highlands of Quebec. This may be associated with a strong increase in early-successional dense forest stands following a major spruce budworm outbreak which began in the early 70's (Hardy et al. 1983) and lasted for over two decades in our study area (Gray et al. 2000).

Although large areas of apparently suitable Bicknell's Thrush habitat appear to be unoccupied in the Laurentian Highlands of Quebec, habitat conservation efforts and thrush-friendly forestry practices should not be abandoned. Habitat availability can rapidly become a concern if management of successional dynamics and forest structure pushes large areas of forest outside the suitable stand age and density for the species. This appears to be the case in northwestern New Brunswick where, if current forest management plans are maintained, Bicknell's Thrush potential habitat will have entirely disappeared by 2027 (Higdon et al. 2006). Similarly, a proposal to vastly expand old-growth areas in support of the conservation of woodland caribou (*Rangifer tarandus caribou*) in the Laurentian Highlands of Quebec (Équipe de rétablissement du caribou forestier du Québec 2013) may conflict with the maintenance of suitable habitat for Bicknell's Thrush. Considering the ephemeral habitat suitability status, it is therefore prudent to preserve more habitat than what a target population may occupy at a specific time (Rompré et al. 2010; Frey et al. 2012). This rationale underlies the recent publication by the Government of Quebec of guidelines aimed at reducing precommercial thinning in Bicknell's Thrush occupied and potential habitat, as well as avoiding incidental destruction of nests, eggs and young (Gouvernement du Québec 2014).

In the Laurentian Highlands of Quebec, there appears to be a shortage of Bicknell's Thrush, not of its breeding habitat. Without discontinuing efforts to conserve breeding habitat, greater attention should be paid to other potential limiting factors. Current challenges for the species outside the breeding range are habitat loss and degradation due to anthropogenic and natural causes on its wintering grounds in the Greater Antilles (Hill and Lloyd 2017, Lloyd et al. 2017).

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**Appendix 3.1**. Frequency of first, second, and later visits to point counts conducted in the study area, 1995-2016. Laurentian Highlands, Québec, Canada.

| **Year** | **Visit sequence number** | | | | |
|---|---|---|---|---|---|
| | **1** | **2** | **3** | **4** | **5** |
| **1995** | 164 | 138 | 0 | 0 | 0 |
| **1996** | 110 | 2 | 0 | 0 | 0 |
| **1999** | 134 | 124 | 75 | 0 | 0 |
| **2000** | 150 | 86 | 0 | 0 | 0 |
| **2003** | 143 | 98 | 0 | 0 | 0 |
| **2004** | 123 | 102 | 71 | 25 | 4 |
| **2006** | 170 | 52 | 0 | 0 | 0 |
| **2007** | 143 | 61 | 23 | 8 | 2 |
| **2008** | 16 | 0 | 0 | 0 | 0 |
| **2009** | 120 | 87 | 30 | 0 | 0 |
| **2010** | 130 | 124 | 110 | 90 | 0 |
| **2011** | 143 | 132 | 121 | 110 | 19 |
| **2012** | 258 | 0 | 0 | 0 | 0 |
| **2013** | 200 | 116 | 70 | 0 | 0 |
| **2014** | 203 | 132 | 32 | 0 | 0 |
| **2015** | 153 | 105 | 29 | 0 | 0 |
| **2016** | 140 | 113 | 27 | 0 | 0 |

# Conclusion générale

Cette thèse démontre qu'en période de nidification, la Grive de Bicknell est sensible à la structure et à la composition de l'habitat. On pourrait la qualifier de spécialiste de la Sapinière à bouleau blanc dense. Dans un contexte où ces sapinières font l'objet de récolte et d'aménagement, des traitements sylvicoles réduisant la densité des tiges compromettent l'intégrité de son habitat de nidification. Par ailleurs, dans certains secteurs de sa répartition québécoise où l'habitat potentiel est plus abondant, il semble bien que la quantité d'habitats ne soit pas un facteur limitant la présence de l'espèce.

Dans le premier chapitre, en utilisant des données de suivi télémétrique, on a observé que le domaine vital de la Grive de Bicknell est très grand et comporte une proportion importante de sapinière non-éclaircie. Bien qu'elle puisse se retrouver dans des habitats éclaircis, elle n'y niche pas. La présence de parcelles d'habitat traités par éclaircies, adjacentes à des parcelles non-traitées, amène la création de bordures qu'elle n'évite pas, au contraire elle s'y retrouve plus qu'à l'intérieur des peuplements. Aussi, la juxtaposition de parcelles forestières de structure et de composition variables ne serait pas un enjeu de conservation dans des forêts sous aménagement.

Les résultats du deuxième chapitre, à partir de stations d'écoute à deux sites soumis à des régimes d'aménagement forestier différents et qui présentent des mosaïques forestières distinctes, sont cohérents avec le premier chapitre. L'abondance de la Grive de Bicknell, au mont Gosford était négativement associée à la présence d'éclaircies précommerciales réalisées une quinzaine d'années auparavant alors que la relation était positive en ce qui a trait à l'altitude, au profil topographique plus accentué dans un rayon de 250 m des points d'écoute et à l'abondance de Grive à dos olive. Au Massif du Sud, l'altitude et l'abondance de Grives à dos olive étaient positivement associées à l'abondance de la Grive de Bicknell. Dans les deux sites, l'espèce a démontré des affinités pour des habitats à plus haute altitude où peu ou pas de traitements d'éclaircies ont été réalisés. Par ailleurs, les données d'abondance des Grives de Bicknell et à dos olive ne permettent pas de présumer qu'il y ait une relation de compétition entre les deux espèces, la Grive à dos olive étant présente sur la majorité des stations inventoriées.

Dans le troisième chapitre, on observe une présence accrue de la Grive de Bicknell dans les jeunes sapinières (>15-30 ans) et l'analyse du taux d'occupation de stations d'écoute réalisée sur le Plateau Laurentien corrobore, à l'instar des deux premiers chapitres, son association à des altitudes élevées dans des paysages avec peu de peuplements éclaircis. Par contre, elle est absente de nombreux habitats jugés potentiels. Les effectifs très limités de cette grive et son système social pourraient contribuer au faible taux d'occupation dans ce secteur important de sa répartition au Québec, voire au Canada.

Au Québec, la Grive de Bicknell se retrouve dans des sapinières de milieux montagnards et à moyenne altitude et plus marginalement dans des sapinières côtières (habitat qui n'est pas considéré dans la présente thèse). À haute altitude, en milieu montagnard, au régime de perturbations naturelles de chablis et de mortalité par vague (c-à-d.. : « fir wave » *sensu* Sprugel 1976), s'ajoutent les perturbations anthropiques telles la construction de tours de télécommunication, la mise en place d'éoliennes et la création de sentiers de villégiature et de stations de ski. Dans ces cas, on assiste à une perte d'habitat, alors que lors des processus de perturbations naturelles, il y a rajeunissement de l'habitat par succession. Dans ces milieux, l'exploitation y est souvent plus limitée pour des raisons d'accessibilité, de rendement plus faible ou de protection des vieux peuplements. La mosaïque forestière y est dynamique et dominée par des peuplements de petites tailles. À moyenne altitude, l'exploitation forestière est la principale source de perturbation bien que les épidémies y soient régulières, voire périodiques. La mosaïque des peuplements est constituée de parcelles de grande taille et la rotation des coupes y est assez rapide, limitant la persistance de vieux peuplements.

Dans ce contexte, en milieu montagnard, on peut observer une plus grande abondance et stabilité de l’habitat potentiel de la Grive de Bicknell. À moyenne altitude, l’abondance de jeunes peuplements en régénération présente une perspective de renouvellement de l’habitat potentiel, tant et aussi longtemps que la structure dense des peuplements est maintenue. Cette situation favorable à l’espèce ne peut se concrétiser que si la gestion du territoire et des activités forestières prend en compte ce besoin dans les secteurs occupés par l’espèce en proscrivant les traitements d’éclaircie. L’examen de l’évolution de l’âge des peuplements à la Forêt Montmorency, une forêt axée sur la recherche et l’enseignement en milieu boréal, démontre bien comment la gestion du territoire influence la composition du paysage forestier et affecte les communautés d’oiseaux (Desrochers et Drolet 2017). Dans ce cas-ci, la plupart des espèces d’oiseaux suivis sur une période de 20 ans ne semblaient pas en déclin. Par contre, au nord-ouest du Nouveau-Brunswick, la gestion forestière intensive d’un grand territoire risque de provoquer, en 2027, la quasi-disparition d’habitats pour plusieurs espèces de mammifères et d’oiseaux (Higdon et al. 2006). Bien que la Grive de Bicknell soit peu abondante dans ce secteur, il y a peu de chances qu’elle y persiste compte tenu de la disparition de l’habitat potentiel. Ces situations illustrent bien le besoin d’intégrer la ressource faunique dans la gestion du territoire et des activités d’exploitation forestière.

Au-delà de la mosaïque forestière, l’isolement de l’habitat peut être importante pour l’espèce. Un sommet ou un massif isolé au milieu d’un environnement agro-forestier où on ne retrouve pas d’habitat potentiel de l’espèce, à l’exemple du Massif du Sud, du mont Mégantic ou du mont Sutton, favorise la création de sous-populations. Dans ces milieux le recrutement de jeunes individus est plus limité que pour les sites occupés localisés dans des environnements forestiers où l’habitat potentiel est plus abondant, tel le Plateau Laurentien. Le recrutement des jeunes individus y est d’autant plus limité par la faible productivité générale de l’espèce. D’ailleurs, cette philopatrie pourrait également avoir comme effet de créer des individus spécialistes des habitats montagnards et d’autres spécialistes des habitats de moyennes altitudes, orientant la sélection de l’habitat lors de l'établissement, l'année suivante, des jeunes individus selon l'habitat dans lequel ils sont nés, comme ça se produit chez d'autres espèces (Bolnick et al. 2003; Haughland et Larsen 2004; Selonen et al. 2007; Rousseau et al. 2011).

Les actions de conservation de la Grive de Bicknell en période de nidification pourraient bien devoir être modulées en fonction de facteurs géographiques. Pour des sites relativement isolés régionalement, tout doit être fait pour maintenir la qualité locale de l'habitat, réduire la taille des interventions et réduire celles qui n'auraient pas d'impact positif à court terme sur la disponibilité d'habitats favorables à l'espèce. Alors que dans un contexte où l'habitat ne semble pas être limité régionalement, la taille et les types d'interventions ne représenteraient pas un enjeu aussi important bien que le maintien d'habitats favorables à proximité des secteurs occupés par l'espèce serait primordial. L'aménagement par triade pourrait être une approche à explorer : par la création de zones consacrées à la récolte intensive de matière ligneuse, d'autres consacrées à la conservation, alors qu'un troisième type de zones seraient aménagées selon les principes de l'aménagement écosystémique (Messier et al. 2009; Rioux et Poulin 2009; Tittler et al. 2012).

Au Québec, un enjeu de conservation récent, celui du caribou forestier, pourrait avoir certains impacts sur les actions de conservation de la Grive de Bicknell tant sur le Plateau Laurentien qu'au cœur de la Gaspésie. La conservation des vieux peuplements de sapinière à bouleau blanc et la réduction des perturbations devraient avoir des effets positifs sur les individus fréquentant l'habitat montagnard. Par contre, les individus fréquentant les jeunes peuplements denses à moyenne altitude, favorisés en début de succession, pourraient disparaitre de façon temporaire localement ou du moins diminuer appréciablement régionalement puisque les peuplements plus vieux seraient favorisés (Équipe de rétablissement du caribou forestier du Québec 2013). Par contre, la restauration du régime de perturbations naturelles rétablirait la dynamique régionale de succession de la sapinière et la présence de petite parcelle de jeunes sapins denses.

La gestion d’une espèce dans un cadre de conservation peut représenter de réels défis. Si cette espèce est mobile, voire migratrice, comme c’est le cas ici, les actions tant souhaitables qu’efficaces sur les aires de nidification pourraient être neutralisées par ce qui se passe ailleurs (Runge et al. 2014). Cependant, il ne faudrait pas utiliser cet argument pour ne pas agir. Déjà l’autorité gestionnaire de la ressource forestière au Québec a mis en place une mesure de protection de la Grive de Bicknell, celle-ci, entre autres, protège les peuplements de sapins en milieu montagnard (p. ex. : MS4 et RS4) et maritime, maintient et favorise la présence de peuplements de fortes densités et maintient, dans le temps, des habitats favorables à l’espèce (Gouvernement du Québec 2014). Par ailleurs, les résultats de cette thèse ont contribué à l’élaboration de ce document et au programme de rétablissement de la Grive de Bicknell (Environnement et Changement climatique Canada 2016).

## Limites de la thèse

Les résultats de cette thèse sont principalement orientés vers des environnements où les activités forestières modifient le paysage. Plusieurs des variables retenues lors des analyses proviennent des bases de données écoforestière du gouvernement provincial et ne sont que catégoriques. Certaines données provenant de nouvelles technologies, telles les données LiDAR, permettraient l’utilisation de paramètres différents et plus précis (p.ex. : la hauteur et la densité des tiges) et de raffiner les résultats des modèles, bien que les conclusions ne devraient pas diverger de ce qui est présenté ici. L’ensemble des résultats ne concerne que la période de reproduction, depuis l’arrivée des oiseaux au printemps jusqu’au départ des oisillons du nid. En période de mue et pré-migratoire, il serait possible que les besoins écologiques de la Grive de Bicknell diffèrent sensiblement de ce qui est rapporté ici. Avant d’extrapoler les résultats présentés à d’autres régions que le Québec, il faut retenir qu’au Nouveau-Brunswick la tenure des terres est en partie privée et en partie publique.La forêt de sapin est intensivement cultivée et amménagée et présente une croissance beaucoup plus rapide qu’au Québec. Aux États-Unis, en Nouvelle-Angleterre, la Grive de Bicknell occupe exclusivement des habitats montagnards. Seul le Maine pourrait avoir des conditions qui pourraient être similaires au Nouveau-Brunswick ou au Québec.

Récemment, on a remis en cause la validité du statut taxonomique de la Grive de Bicknell (Retter 2017) malgré les études génétiques corroborant son statut d’espèce à part entière (Ouellet 1993; Outlaw et al. 2003; McEachen et al. 2004; Wilson et al. 2004; FitzGerald 2017). Bien qu’il soit fort improbable que l’on regroupe ces deux espèces, les populations des Grives de Bicknell et à joues grises sont totalement allopatriques. A ce jour, on ne connait pas de région où les deux espèces pourraient être en contact sur les aires de nidification. Aussi, rien ne nous autoriserait de se soustraire à nos responsabilités vis-à-vis de la Grive de Bicknell.

## Encore des inconnus

Plusieurs facettes de l’écologie de la Grive de Bicknell sont encore obscures. Nous ne savons pas quel type d’habitat la grive et ses jeunes utilisent après avoir quitté le nid jusqu’au départ pour la migration vers les aires d’hivernage et quel rôle pourraient jouer les arbres fruitiers durant cette période. Le taux de survie des jeunes la première année semble variable si on en juge par le nombre de jeunes oiseaux capturés en début de saison de reproduction l’année suivante. On ne sait rien de la survie des jeunes avant qu’ils ne partent en migration la première année. Si le ratio des sexes est relativement équilibré à la naissance, on ne connait pas quand dans le cycle vital de l’espèce la mortalité des femelles devient importante pour qu’elles ne représentent qu’environ un tiers de la population. Relativement à la relation interspécifique entre les Grives à dos olive et de Bicknell, on pourrait vérifier si cette dernière bénéficierait d’une certaine protection à l’égard de la prédation des nids quand la Grive à dos olive est plus abondante ou que c’est pure coïncidence. Alors que l’on observe des Grives de Bicknell dans des habitats montagnards et dans des habitats à moyenne altitude, sommes-nous en présence d’une situation de philopatrie altitudinale ou de spécialisation phénotypique où des individus sont spécialistes d’un de ces deux types d’habitats? En lien avec la présence de l’écureuil roux il faudrait évaluer le rôle que jouent l’altitude, la composition et l’âge des peuplements et la production de cônes relativement à la présence de ce prédateur dans l’habitat occupé *versus* inoccupé par la Grive de Bicknell. Nous savons que cette grive utilise des peuplements de très fortes densités et de taille minimale des arbres de deux mètres, mais ne savons pas à partir de quelle densité, quelle hauteur et quel âge ces peuplements ne sont plus favorables à l’espèce.

Telle une boite de Pandore, l’étude d’une espèce ne peut se solder que par plusieurs autres éléments à explorer, aussi je souhaite que d’autres passionnés découvrent l’univers unique de la Grive de Bicknell et comblent les lacunes de nos connaissances sur cette espèce fascinante.

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