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BREEDING HOME RANGE AND HABITAT USE OF A RARE HIGH-ELEVATION SONGBIRD IN INDUSTRIAL FORESTS OF NEW BRUNSWICK

by

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ABSTRACT

This thesis estimates home ranges, habitat selection, habitat use, and nest success of the Bicknell's Thrush (*Catharus bicknelli*), a threatened songbird species inhabiting industrial forests in north-central New Brunswick. Home ranges were estimated as 18.14 ± 5.33 ha (90% AKDE) for females, and 13.2 ± 2.2 ha (90% AKDE) for males. A population estimate, derived from the number of female home ranges within a potential habitat model, was calculated at 5 275 (4 077 – 7 469) individuals in New Brunswick. Compositional analysis showed significant habitat preference in both sexes at the home range vs. landscape level, but no significant preference at the relocations vs. home range level. Compositional analysis indicates that they prefer unthinned habitat but interactions between precommercial thinning treatments and year since the treatment increased likelihood of use as years increased. Different females showed different preferences to habitat, and 4/5 females nested in forest that had been thinned previously, with three of those nests succeeding. I discuss management and conservation implications of these results for this species in New Brunswick.

DEDICATION

To all those who have believed in and supported me in my adventures.

In loving memory of Edmund Ward (1930 -2020).

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CHAPTER 1 – GENERAL INTRODUCTION

The Bicknell's Thrush (*Catharus bicknelli*) is a rare, neotropical migratory songbird that breeds in clumped distributions in isolated patches of high elevation forests restricted to the north-eastern United States and eastern Canada (Townsend et al. 2015) and winters in the Greater Antilles. Previously recognized as a sub-species of the Gray-cheeked Thrush (*C. minimus*), the Bicknell's Thrush is considered to have the most restricted breeding range of all North American bird species (Townsend et al. 2015). The species also shows a skewed sex ratio (COSEWIC 2009) and has been shown to exhibit a polygynandrous breeding behaviour in some parts of their range (Goetz et al. 2003). Bicknell's Thrush are considered habitat specialists due to their occurrence across the north-eastern United States at high elevations, where their habitat consists of dense, stunted conifer trees, typically balsam fir (*Abies balsamea*) or red spruce (*Picea rubens*) (McFarland et al. 2008). However, in the late 1980s, many observations summarized by Ouellet (1993) showed high instances of Bicknell's Thrush in regenerating forests in Quebec, leading researchers to speculate that these habitats are replicating high elevation forests found in Vermont, New York, and New Hampshire. It has been hypothesized that Bicknell's Thrush's preference for young coniferous forest habitat reflected an adaptation to regrowth forests due to natural disturbance phenomena (such as fire, insect damage, and wind blow-down) (Lambert et al. 2005), and much of their occupied habitat within Canada is modified by timber harvest (COSEWIC 2009). Bicknell's Thrush occupy broadleaf montane forests in the Dominican Republic, Haiti, and, to a lesser extent, Cuba, Jamaica, and Puerto Rico (Rimmer and McFarland 2001, Townsend and Rimmer 2006,

McFarland et al. 2013) during the winter non-breeding season, a completely different habitat in their overwintering grounds. In both their breeding and wintering grounds, climate change (Rodenhouse et al. 2008) and anthropogenic development, such as the construction of wind turbines (COSEWIC 2009), recreational ski slopes (McFarland et al. 2008), and the management of forests for commercial use (Chisholm and Leonard 2008) are contributing to their declining population.

Population Estimates

The population estimate of Bicknell's Thrush in Canada is reported by COSEWIC (2009) as a range between 40 570 and 49 258 individuals, estimated using the potential habitat model by Lambert et al. (2005), areas of coniferous forest at preferred elevations, and point count data from Quebec, Nova Scotia, and New Brunswick. The population estimate of Bicknell's Thrush in New Brunswick was estimated at 2 851 individuals, with lower and upper confidence limits of 1 137 and 10 652 respectively, by Campbell and Stewart in 2012, who also reported a decrease in Bicknell's Thrush occurrence by 11.5% annually from 2002-2011. These estimates are based on data from the High Elevation Landbird Program (HELP) of Birds Canada (BC, formerly Bird Studies Canada), which has monitored Bicknell's Thrush throughout the province of New Brunswick since 2002 (Campbell and Stewart 2012). The High Elevation Landbird Program, and the revised protocol (Mountain Bird Watch 2.0) now in use since 2016, monitors Bicknell's Thrush by conducting one early morning or evening survey per location at sites selected across the potential habitat area (Campbell and Stewart 2012, Campbell 2017). However, population estimates based on point count data may be troublesome for Bicknell's Thrush

for several reasons. First, Bicknell's Thrush have a skewed sex ratio (COSEWIC 2009) that may vary in parts of their range (Askanas 2008), so point counts based on male calls or songs are inherently biased. Second, Bicknell's Thrush are not inhabiting their potential habitat fully (Postma and Diamond unpublished, Aubry et al. 2018), so the assumption that habitats have equal abundance is invalid. Third, the detectability of Bicknell's Thrush is very low, and as much as six or more point counts may be required to determine species presence (Nixon et al. 2001). The difficulties in estimating Bicknell's Thrush population with point counts described above, and a severe decrease in Bicknell's Thrush along HELP routes, indicate why the population of Bicknell's Thrush within New Brunswick is reflected in the wide confidence intervals for the New Brunswick population. A more accurate assessment of population in New Brunswick is required, especially considering it either represents a small (2%) to large (20%) portion of the Canadian population.

Habitat Associations and Potential Habitat in NB

The population of Bicknell's Thrush in New Brunswick is almost entirely within the highlands ecoregion of the province (Birds Canada 2016). The highland ecoregion consists of two areas in northern New Brunswick: the Kejwik ecodistrict, which borders the Gaspe region of Quebec; and the Ganong ecodistrict, which encompasses the highlands in central New Brunswick (Zelazny 2003). Separated by lowlands, these areas resemble boreal forests, in that they are dominated by balsam fir, black spruce (*Picea mariana*), white spruce (*P. glauca*), and white birch (*Betula papyrifera*)– and some areas, such as the peaks of some mountains, are purely balsam fir or black spruce (Zelazny

2003). In the highland ecoregions, Bicknell's Thrush tend to inhabit young, 10-20-year-old, high elevation (typically >600 m, but as low as 450m [Nixon et al. 2002]) coniferous forests created after harvesting timber via clear-cutting (Ouellet 1993, Nixon et al. 2001, Campbell et al. 2012). The Ganong region, specifically, held old-growth balsam fir stands until 1994, when a strong windstorm blew down approximately 17 000 ha of forest – in much of the area that Bicknell's Thrush now inhabit – creating an expanse of young forest (Zelazny 2003). Despite being associated with young regrowth forests, the occupancy of these old-growth forests pre-blowdown was reported in Birds Canada's first Maritime Breeding Bird Atlas (Erskine 1993), suggesting that at some point Bicknell's Thrush inhabited older forest stands in New Brunswick. Indeed, most of the forests available to Bicknell's Thrush in New Brunswick are young forests simply due to recent historical harvests.

Potential habitat models by Lambert et al. (2005) for the Bicknell's Thrush populations in the United States and an updated model by Aubry et al. (2016) for populations in Canada have clarified what constitutes potential breeding habitat as dense, coniferous high-elevation forests; however, large areas of potential habitat remain unoccupied throughout their potential habitat range in Quebec (Aubry et al. 2018). In New Brunswick, a stratified random sampling design detecting Bicknell's Thrush presence within the potential habitat area based on that modelled by Lambert et al. (2005) yielded < 1% occurrence on 129 sites with deployed song meters (Postma and Diamond unpublished). Prior to 2012, HELP detected Bicknell's Thrush on only 33% of sites selected for Bicknell's Thrush assumed habitat. Further, detectability of Bicknell's Thrush is made difficult by their cryptic vocal nature; they call and sing only during the

pre-dawn chorus and at dusk, forcing searches to be limited ~2 – 3 hours per day (Ball 2000) and require repeated surveys to confirm presence or absence (Nixon et al. 2001). Due to low detectability and apparent unsaturation of potential habitat, the understanding of habitat preference of Bicknell's Thrush in New Brunswick has been limited to exploring the effects of anthropogenic use on Bicknell's Thrush presence in high elevation forests (Chisholm and Leonard 2008, McFarland et al. 2008, Aubry et al. 2011).

Relationship with Silviculture

In Canada, potential habitat for the Bicknell's Thrush is almost entirely managed by the forestry sector (COSEWIC 2009). Bicknell's Thrush's apparent use of young forest created by harvest conflicts with another common silviculture practice – pre-commercial thinning (PCT). In forests stands of similar age that Bicknell's Thrush prefer, tree stem density is reduced from >40 000 stems/ha to <3 125 stems/ha to promote growth in commercial tree species and improve wood harvest efficiency. Several studies have shown that Bicknell's Thrush presence is negatively affected in areas that have been treated with PCT (Chisholm and Leonard 2008, Aubry et al. 2016, Aubry et al. 2018), including reduced nesting in thinned forest (McKinnon et al. 2014). However, Bicknell's Thrush appear not to be edge-averse (McKinnon et al. 2014), and Aubry et al. (2011) showed that home ranges in Quebec have contained as much as 30% of forest area treated with PCT. Bicknell's Thrush have also been shown to use small dense patches of unthinned forest surrounded by areas treated with PCT (Chisholm & Leonard 2008, McKinnon et al. 2014). Taken together, the evidence suggests that PCT decreases Bicknell's Thrush presence on managed forests; however the extent that Bicknell's

Thrush use these forests as they age is unclear. Chisholm and Leonard's (2008) findings resulted in the development of best management practices (BMPs) that suggest conducting pre-commercial thinning before or after the Bicknell's Thrush breeding season (June 1 – July 31) and to leave patches of intact forest in thinned areas for nesting (IBTCG 2010).

Describing habitat preferences of individual birds present in known areas of occurrence would further our understanding of habitat preference in this species, considering (1) that monitoring of Bicknell's Thrush has low occurrences at many sites suggested to be occupied by the potential habitat model (Lambert et al. 2005, Aubry et al. 2016) in New Brunswick (Campbell 2017), (2) Bicknell's Thrush occurred in old-growth forests within the Ganong district pre-1994-blowdown, and (3) these habitats remain occupied despite frequent silviculture disturbances.

Nest Site Selection

The mechanism which decreases Bicknell's Thrush occurrence in thinned stands has not yet been studied. An obvious cause is direct disturbance when forests are thinned during the breeding season, as thinning drastically changes forest structure, and likely leads to the destruction of cryptic nests and abandonment of habitat. However, Bicknell's Thrush presence decreases in thinned forests even when thinning occurs after the breeding season has ended, suggesting habitat suitability is decreased directly and indirectly. The use of varying habitats by individuals (Aubry et al. 2011, McKinnon et al. 2014) and apparent preference for forest edges for nests (McFarland et al. 2008) suggests that Bicknell's Thrush still use thinned forests for foraging when unthinned forests are

near (<500 m from nest, McKinnon et al. 2014). This same evidence also suggests that individuals prefer nesting in denser forests when near edges, probably for increased protection through nest concealment. Following this, a mechanism which may explain the decrease in thinned habitat use, especially in large thinned stands with limited or distant unthinned forest edges, is a decrease in adequate forest cover for nesting.

Conservation Rationale

The combination of Bicknell's Thrush being rare (even in appropriate habitat) and the species' low detectability makes conservation of this species difficult. Because most forest operations do not occur at hours when Bicknell's Thrush call, and individuals are hard to see, the likelihood of a forestry operator detecting Bicknell's Thrush while thinning or harvesting is low. Previously, Birds Canada, through HELP and Mountain Bird Watch 2.0, advised forestry companies holding leases on potential habitat of Bicknell's Thrush presence early in the season. When a Bicknell's Thrush was present, companies would avoid conducting forestry operations until the fall when the danger of destroying nests was lowest. However, the role of verifying presence of Bicknell's Thrush does not lie with Birds Canada; although the Species at Risk Act is a federal law, the enforcement lies upon provincial resources, which in New Brunswick, through the Crown Lands and Forests Act, is the responsibility of private licensees.

The Species At Risk Act Recovery Strategy for the Bicknell's Thrush has partially identified critical habitat in New Brunswick using occupancy of habitat and biophysical attributes of suitable habitat (Environment and Climate Change Canada 2016). Suitable habitat is defined as high elevation montane forest (>750m) or high-

elevation managed forests (> 380m) of dense conifer stands (10 000 to 50 000 stems/ha), where critical habitat area from occupancy is defined as a 5 km radius around known records (Environment and Climate Change Canada 2016). However, the minimum area of critical habitat has yet to be determined (Environment and Climate Change Canada 2016). The role of the provincial government in the current provincial forestry management system is to set forest management goals, objectives and standards; to monitor activities of licensees; and to assess licensee performance (Government of New Brunswick, 2014). The management objectives fall under three themes encompassing the "pillars of sustainable forest management." The management of forest wildlife within industrial forests falls under one of these pillars ("Stewardship of the Environment") and thus is managed within an industrial context. Broad goals (such as "the full range of native forest-dwelling vertebrates are present and sustainable across their ecological ranges") are addressed in licensee 10-year Forest Management Plans. Approved plans are carried out by licensees (i.e., private companies), and management results are assessed at five-year intervals – meaning the licensees are directly responsible for the management of wildlife on Crown Lands in New Brunswick. Thus, within this framework, the importance of clear, straightforward, and achievable wildlife management is important for organizations, whose primary mandate is not wildlife conservation. An accurate estimation of population density and habitat associations in New Brunswick is necessary to support and improve current BMPs for forestry companies operating in Bicknell's Thrush habitat.

Thesis Approach

Identifying how individual birds are occupying space can greatly improve the accuracy of population estimates and habitat selection. Normally, due to practical constraints such as time and resources needed to physically identify occurrence, habitat associations with a sub-population of a species are used in lieu of presence information. For estimating population size, this is problematic for a species that does not occupy available associated habitat fully and assumed areas of occurrence may not have any individuals present. The occurrence of Bicknell's Thrush throughout their potential habitat in New Brunswick was explored recently, when automatic recording devices (ARUs) were placed throughout potential habitat predicted by Lambert et al.'s (2005) potential habitat model in a stratified-random sample design (Postma and Diamond unpublished). Postma and Diamond found only two detections out of 129 deployments throughout the NB potential habitat area in 2012 (Postma and Diamond unpublished). The following year, Postma and Diamond applied an adaptive sampling method (Thompson 2004) using known Bicknell's Thrush locations as starting points in the Ganong ecodistrict, delimiting a large contiguous area where Bicknell's Thrush occurred on the landscape over two breeding seasons. Identification of this large area of apparently continuous distribution offered the opportunity to take a different approach to estimating population size: within that area, determine how many Bicknell's Thrush home ranges there are by measuring those of females (which do not overlap, in contrast with those of males (McFarland et al. 2008, Aubry et al. 2011)) and whether they are contiguous.

This thesis builds on that approach to answer the question: How many Bicknell's Thrush occupy the area known to be occupied within the industrial landscape of the

Ganong ecodistrict? I aim to answer this question by using radio telemetry to identify (1) how much space Bicknell's Thrush use within the occurrence patch during breeding, specifically females, as they represent the breeding unit in species with male-biased sex ratios, (2) how much home ranges overlap and (3) whether home ranges are contiguous with each other. Using this information, I derive a population estimate based on how many female home ranges occur within an occupied area.

In addition, radio-tracking birds throughout the nesting season offers opportunities to answer other important questions arising from previous work, and particularly relevant to refining management for this species. The area of occurrence delineated by Postma and Diamond (unpublished) represents a heterogeneous landscape with regards to stand age, forestry treatments and frequency of disturbance. It is a "Bicknell's Thrush stronghold" (Greg Campbell, pers. comm.), and is within the 1994 blowdown regrowth forest. Using habitat within home ranges of individuals compared with that available within the patch, I ask the main question of "what drives orientation of Bicknell's Thrush home ranges within an industrial landscape?" I address this question through two competing hypotheses: (1) Bicknell's Thrush prefer home ranges that contain specific habitat associated with the species (unthinned, young forest). I aim to identify whether Bicknell's Thrush prefer plantations, natural regrowth from clear cuts, or pre-commercially thinned habitats at both the landscape and home range scale because the area of occurrence contains mostly young forest with regrowth with and without PCT. Alternatively, I hypothesize that (2) home ranges are selected by Bicknell's Thrush based on nesting location, with nests placed in dense, coniferous forests despite home ranges containing thinned habitat.

Chapters are presented as independent research articles but build on one another sequentially. Chapter 2 explores home ranges using radio-tracking, and uses that information to derive population estimates in an area that historically and currently has been most consistently occupied by Bicknell's Thrush in New Brunswick. In Chapter 3, I use radio-locations to explore habitat use by Bicknell's Thrush in the same area, using compositional analysis. Chapter 4 re-examines use of those habitats in relation to forestry treatments using a model selection framework, to relate use of habitat directly to forestry practices. Chapter 5 explores nest selection using a model selection framework, and reports nest success of five female Bicknell's Thrush using temperature loggers and changepoint analysis to determine nest vacancy. Chapter 6 summarizes each data chapter, and synthesizes discussion to fill knowledge gaps, provide suggestions for future research and improve best management practices.

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CHAPTER 2 – POPULATION ESTIMATE OF BICKNELL'S THRUSH (*CATHARUS BICKNELLI*) IN NEW BRUNSWICK USING HOME RANGE ANALYSIS

Introduction

The Bicknell's Thrush (*Catharus bicknelli*) is a high-elevation coniferous-forest specialist that has one of the most restricted breeding ranges of any North American songbird (Townsend et al. 2015). The species breeds at high elevations across southern New York, New England, Maine, Quebec, Nova Scotia, and New Brunswick (Townsend et al. 2015). In their natural habitat, Bicknell's Thrush occupy naturally occurring stunted coniferous forest or vigorous regrowth forests dominated by balsam fir (*Abies balsamea*) (COSEWIC 2009). The New Brunswick population of Bicknell's Thrush inhabits industrial forests over 450 m in elevation that are undergoing vigorous regrowth of balsam fir and red spruce (*Picea rubens*) (Ouellet 1993, Nixon et al. 2001), occupying habitats across a mosaic of stand ages and silviculture treatments.

Birds Canada's (BC) High Elevation Landbird Program (HELP) has been monitoring Bicknell's Thrush since 2002 through auditory surveys throughout the potential habitat range in the Maritimes (Whittam and Ball 2003, Campbell 2017). In 2012, BC estimated the New Brunswick population as 2 851 individuals with lower and upper confidence limits at 1 137 and 10 652, respectively (Campbell and Stewart 2012). The BC estimate used 10 years of monitoring data from HELP and a potential habitat model built on Mountain Bird Watch (a similar monitoring program) from Vermont, USA (Lambert et al. 2005, Campbell 2012). However, HELP data were collected from

non-randomly selected routes, with sites initially selected in habitat most likely to have Bicknell's Thrush as well as being accessible to volunteers (Whittam and Ball 2003), biasing the estimate with only "ideal habitat." Further, the potential habitat model included in the estimation did not hold true when ground-truthed through intensive, randomly sampled monitoring with song-meters (Postma and Diamond, unpublished). Finally, the report does not indicate if and how females were included in the population estimate (Campbell 2012), as it is unclear to what degree females call and sing versus males (COSEWIC 2009). When taken together, these factors suggest that an alternative, complementary approach to determining population size might improve estimates for New Brunswick.

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) defines the "biological" area of occupancy as "the total area of habitat occupied by all existing populations" (COSEWIC 2016). COSEWIC (2016) suggests that, for bird species, the number of breeding pairs (or breeding units) can be multiplied by the average home range to determine biological area of occupancy. Using the same logic, a rough number of breeding units can be estimated by dividing the biological area of occupancy by the average home range. To improve the breeding unit estimate, the degree to which individuals may overlap their home ranges and how distant their home ranges are from one another (within sub-populations or breeding groups) can be estimated and incorporated into effective home range size. In monogamous breeding bird species, singing male birds are usually representative of the breeding unit, since only one male would attend each nest and female. However, in male-biased breeding bird species, several males may attend one nest, and one male may attend several nests. Since

Bicknell's Thrush are polygynandrous breeders (Goetz et al. 2003), only females (being the "limiting factor" in reproduction) should be considered representative of breeding units (COSEWIC 2009). In this chapter, I will describe the estimation of Bicknell's Thrush breeding population in New Brunswick using female home range size and overlap, and an improved potential habitat model for Bicknell's Thrush assuming that the population saturates the habitat.

There have been two previous studies on home range size of Bicknell's Thrush in two locations: Quebec (Aubry et al. 2011) and Vermont (Collins 2006). In Vermont, female home range sizes ranged 3.2 – 5.4 ha (95% Fixed (Least-Squares Cross-Validated, LSCV) kernel density estimate, KDE) in high elevation habitat not managed for timber (Collins 2006, McFarland et al. 2008). In a high elevation forest in Quebec that was harvested in the 1970s and treated with pre-commercial thinning (PCT) in 1980s and 1990s, female home ranges ranged from 1.89 – 35.69 ha (95% Fixed (LSCV) KDE, Aubry et al 2011). The habitat in New Brunswick is lower in elevation than both Quebec and Vermont, and is more recently (and currently) disturbed by silviculture. I predicted that home ranges in New Brunswick would be larger than in Vermont, considering increased anthropogenic heterogeneity in habitat, and also larger than in Quebec, considering how New Brunswick disturbances have been more recent.

Home range was defined by Burt (1943) as:

…that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range.

A utilization distribution (UD), derived from adequately sampled location data, describes a home range of an individual (Worton 1989). Kernel density estimators (KDE) can effectively estimate the UD, but only when sampling locations of the individual are independent and identically distributed (IID, Worton 1995, Fleming et al. 2015). However, in tracking data, locations are inherently spatially and temporally autocorrelated (Fleming et al. 2015). Many studies examining KDE have found that sampling frequency (Otis and White 1999), number of relocations per individual (Seaman et al. 1999, Girard et al. 2002), and type of kernel estimator (e.g., LSCV, Seaman and Powell 1996, Hemson et al. 2005) can greatly affect the home range area estimate. Further, temporal autocorrelation occurs at many scales – daily, seasonally, yearly – which cannot be incorporated into an IID model (Fleming et al. 2015). Several other animal movement models have been suggested to improve estimates (e.g., correlated random walk [Johnson et al. 2008], Brownian motion [Horne et al. 2007]) but none can account effectively for changes in sampling frequencies or autocorrelation. Alternatively, continuous-time stochastic processes (CTSPs) can separate the sampling schedule from the animal movements (Calabrese et al. 2016). By identifying an appropriate movement model that incorporates autocorrelations inherent in the location data, the continuous-movement process of the individual being tracked can be more readily represented (Calabrese et al. 2016). I will use CTSP models to estimate home range area of female Bicknell's Thrush, and use these spatial data to estimate overlap.

I predict that the population estimate of Bicknell's Thrush will be larger than that calculated by Campbell and Stewart (2012). The minimum assumed home range size of BC's population estimate is 22.22 ha when calculated from Bicknell's Thrush per hectare

in the highest density development stage and assuming saturation throughout the habitat (Campbell and Stewart 2012). This assumed home range size is larger than any estimate of female home range size in Quebec or Vermont (Collins 2006, Aubry et al. 2011), and so any population calculation using a home range size smaller than ~ 22 ha will be a higher estimate than Campbell and Stewart's (2012). Any degree of overlap will increase this estimate, as it effectively shrinks how much space each individual uses exclusively. Finally, the BC population estimate incorporates densities specific to stand development stage throughout the potential model; my estimate will assume female saturation throughout the model at the same density regardless of stand development stage.

Methods

Study site

I captured and tracked Bicknell's Thrush at a field site identified as a large occurrence patch of Bicknell's Thrush in previous field studies (Postma and Diamond, unpubl. data) located at 47.20, -66.55, just north of the Christmas Mountains in central New Brunswick, Canada.

Capture and tagging

I mist-netted for Bicknell's Thrush during the summer breeding seasons (May-July) of 2016 and 2017. Technicians unravelled birds from mist-nets and placed them in soft cloth bags before processing. Birds were then weighed and measured (wing chord, sex, age [Pyle 1997]) and equipped with very high frequency (VHF) radio-transmitters (Lotek Pip Ag376 and NTQB-3-2) using leg-loop harnesses (Rappole and Tipton 1991).

The transmitters weighed 0.95 ± 0.005 g (mean of 3.2% [2.8% – 3.7%] of body weight) and are assumed to have little effect on individuals as a previous study suggested that backpack tags under 5% body mass did not affect annual survival of Bicknell's Thrush (Townsend et al. 2012). We inspected each bird in a fine nylon mesh cage for normal flight and hopping behaviour before releasing.

Tracking

Three technicians tracked individuals using Lotek SRX800 receivers connected to a rotatable 5-element yagi antenna mounted 4 meters above the ground on a stationary tower, above most trees within the immediate area. Telemetry towers were placed so that the individuals being tracked were between and roughly equidistant from each tower. We used short-range radios among the field crew to communicate sampling intervals and to verify adequate signal strengths. Each technician simultaneously recorded azimuths at pre-determined time intervals (every 5-10 minutes). Using a compass, we recorded the declination-corrected azimuth of the strongest signal direction within the 30 seconds allocated to each sampling interval. Each azimuth was adjusted dependent on the degree of declination relative to the GPS position of the observer (between 17.3 – 17.4 °W, resulting in a subtraction of field-recorded azimuths) to account for the difference between true and magnetic north. If within those 30 seconds a target moved drastically (detected by a significant drop in signal strength), the highest signal strength before and after the movement was recorded by all technicians as separate relocations and noted.

Triangulation

The R Statistical Environment (R Core Team 2019) package 'razimuth' was used to estimate relocations from azimuths and observer locations. The package 'razimuth' estimates locations using a hierarchical azimuthal telemetry model, fitted using a specialized Markov Chain Monte Carlo sampling procedure (Gerber et al. 2018). This method was chosen instead of using Lenth's maximum likelihood estimate (Berg 2015) as it: i) can provide a more robust error estimate;, ii) location estimates on azimuths that fail to reach a maximum likelihood estimate (MLE) with Lenth's method;, and iii) is a more accurate location (Gerber et al. 2018). The posterior mode and 95% isopleth of the posterior draws from the Markov Chain Monte Carlo were used as location and location error for each location estimate, based on 10 000 iterations.

Home range calculation

I used the R statistical package *ctmm* (Calabrese et al. 2016) to calculate the relative speed between each relocation and removed speeds that were > 13.1 m/s, the maximum flight speed of Grey-cheeked Thrushes (*Catharus minimus*) during migration (Gomez et al. 2017), and likely applicable to the closely-related Bicknells Thrush. I further used *ctmm* to estimate CTSP models appropriate for each individual's dataset, based on Akaike's information criterion (AIC, Akaike 1974). I again used *ctmm* to calculate 90% and 50% contour auto-correlated kernel density home range estimates (AKDE) based on the CTSP models identified earlier.

Population calculation

I used the R statistical package *ctmm* to calculate the Bhattacharyya coefficient (a measure of similarity between probability distributions (Bhattacharyya 1943). I used the Bhattacharyya coefficient instead of comparing the percentage of overlap as it more appropriately represents the overlap of AKDE home ranges (Calabrese et al. 2016). The Bhattacharyya coefficient ranges from 0 (no overlap) to 1 (complete overlap, Fieberg and Kochanny 2005). I calculated overlaps between each individual within each year.

In *ArcMap*, I modelled potential Bicknell's Thrush habitat using the methods outlined by Campbell (2017). Using New Brunswick public forest land cover data, I defined Bicknell Thrush habitat as land cover above 585m in elevation, which corresponds to the highest 75% of detections of Birds Canada's HELP program (Campbell 2017), with > 60% balsam fir and red spruce in their dominant or secondary forest layers.

Using i) the mean home range size of female Bicknell's Thrush in New Brunswick; ii) overlap calculated in New Brunswick; and iii) the New Brunswick potential Bicknell's Thrush habitat model, I calculated the maximum number of female Bicknell's Thrush (breeding unit) occurring within the potential Bicknell's Thrush habitat model according to equation 1:

Eq. 1

$$Spatial\ Population\ Estimate = \frac{Potential\ Bicknell's\ Thrush\ Habitat\ Area}{Mean\ Home\ Range\ (1 - overlap)}$$

I then multiplied my value by three according to the 2:1 male-female sex ratio of Bicknell's Thrush (COSEWIC 2009) to obtain the actual population estimate of number of individuals.

Results

I captured and tracked five female and four male Bicknell's Thrush in 2016, and five females and six males in 2017, with one female bird tracked in both years (for a total of nine females). The number of relocations varied from 19 – 339 per individual (table 2.1).

Table 2.1: Locations, continuous-time stochastic process models (OU – Ornstein-Uhlenbeck, OUF – Ornstein-Uhlenbeck Foraging, IID – Independent and identically distributed, Calabrese et al. 2016) and home range areas (ha) (50% core area and 90% home range, lower confidence interval (LCI), maximum likelihood estimate (MLE) and upper confidence interval (UCI)) of Bicknell's Thrush (*Catharus bicknelli*) captured during the summer breeding seasons of 2016 and 2017 in north-central New Brunswick, Canada.

Individual	Year	Sex	# of Re-locations	Effective Sample Size	CTSP Model	50% AKDE			90% AKDE		
						LCI	MLE	UCI	LCI	MLE	UCI
36712	2016	M	21	21	IID	4.01	6.48	9.54	24.73	39.95	58.77
85006	2016	M	19	11.63	OUf	0.35	0.68	1.13	1.56	3.06	5.06
85033	2016	M	46	37.66	OU	2.46	3.48	4.67	10.89	15.42	20.73
85032	2016	M	47	26.74	OU	2.35	3.57	5.05	13.84	21.06	29.76
85009	2016	F	176	99.27	OUf	3.06	3.77	4.54	17.95	22.08	26.63
85024	2016	F	133	133	IID	7.07	8.44	9.94	44.35	52.97	62.34
85028	2016	F	125	125	IID	6.81	8.18	9.68	38.27	45.97	54.37
85031	2016	F	75	75	IID	1.23	1.57	1.94	6.37	8.10	10.04
85023*	2016	F	234	147.29	OU	2.41	2.85	3.33	11.65	13.79	16.11
85049	2017	M	74	74	IID	0.31	0.40	0.49	1.27	1.62	2.01
85050	2017	M	21	21	IID	3.21	5.19	7.63	15.30	24.73	36.37
85052	2017	M	24	24	IID	3.29	5.13	7.38	15.84	24.73	35.56
85057	2017	M	20	20	IID	2.62	4.29	6.37	11.18	18.31	27.16
85059	2017	M	28	28	IID	2.46	3.71	5.21	14.87	22.37	31.39
85060	2017	M	79	79	IID	2.07	2.62	3.23	11.65	14.72	18.14
85046	2017	F	339	338.99	OUf	0.34	0.38	0.43	1.83	2.05	2.274
85047	2017	F	285	211.31	OU	4.17	4.79	5.46	16.15	18.57	21.16
85048	2017	F	252	104.49	OU	0.62	0.76	0.91	3.49	4.27	5.13
85055	2017	F	230	133.48	OU	1.01	1.21	1.42	4.07	4.87	5.73
85023*	2017	F	235	33.71	OU	1.70	2.46	3.36	6.05	8.76	11.95

* same individual tracked in both 2016 and 2017

I found mean ± SE home range areas of 18.1 ± 5.3 ha (90% AKDE) with core areas of 4.1 ± 1.0 ha (50% AKDE) for females, and 18.6 ± 3.3 ha with core areas of 5.1 ± 0.9 ha for males (table 2.1, figure 2.1). Mean home range for males with over 30 relocations were estimated at 13.2 ± 2.2 ha. Mean home range overlap between females was 0.11 ± 0.05 (range of 0 – 0.71), and 0.56 ± 0.10 (range of 0 – 0.95) for males (figure 2.2, 2.3).

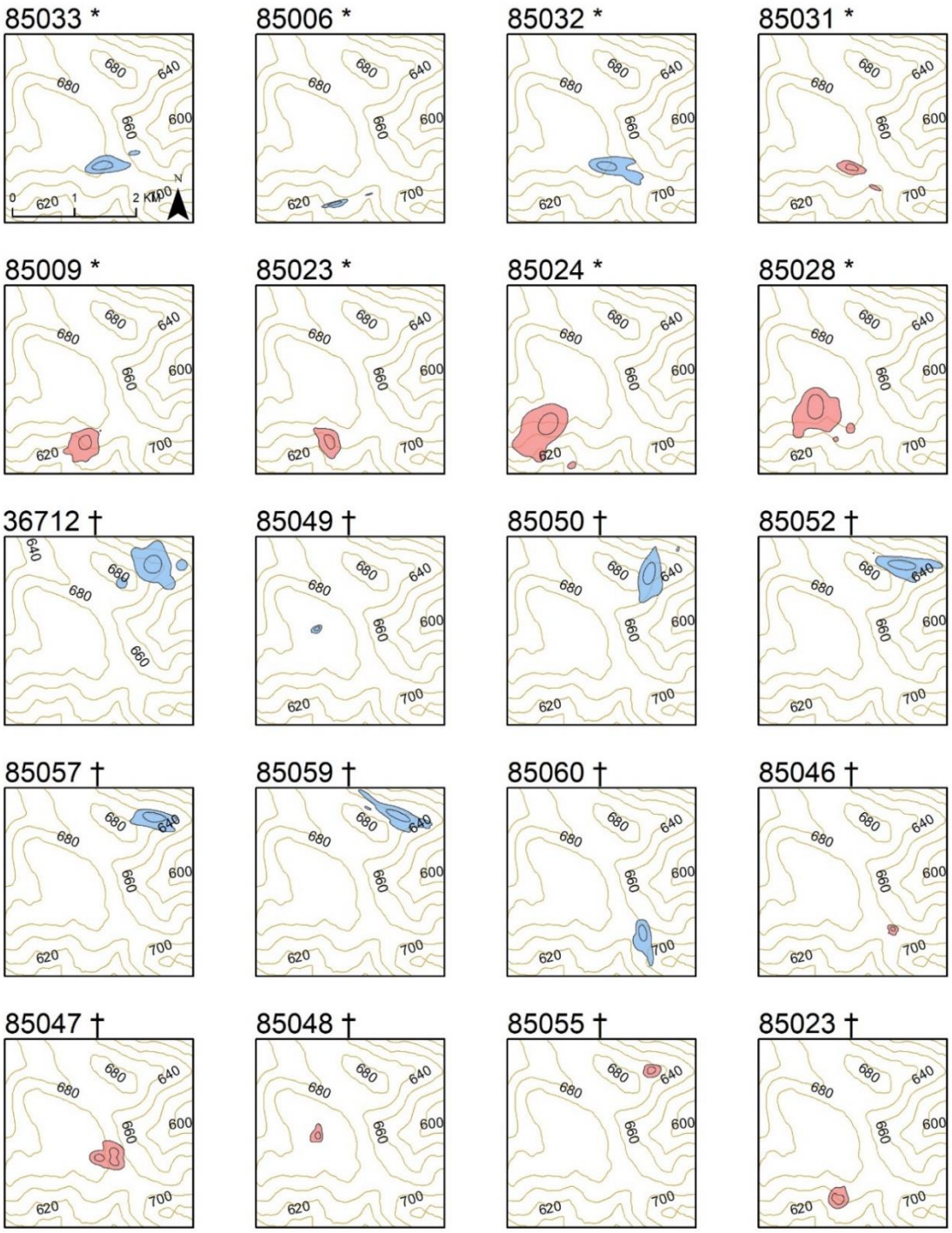

Figure 2.1: Individual home ranges calculated as autocorrelated kernel density estimates of female (pink) and male (blue) Bicknell's Thrush (*Catharus bicknelli*) captured and tracked throughout the 2016 (*) and 2017 (†) summer breeding seasons (June - July). Outer and inner contour lines represent the 90% and 50% AKDE respectively. Individual 85023 was tracked during both 2016 and 2017 breeding seasons.

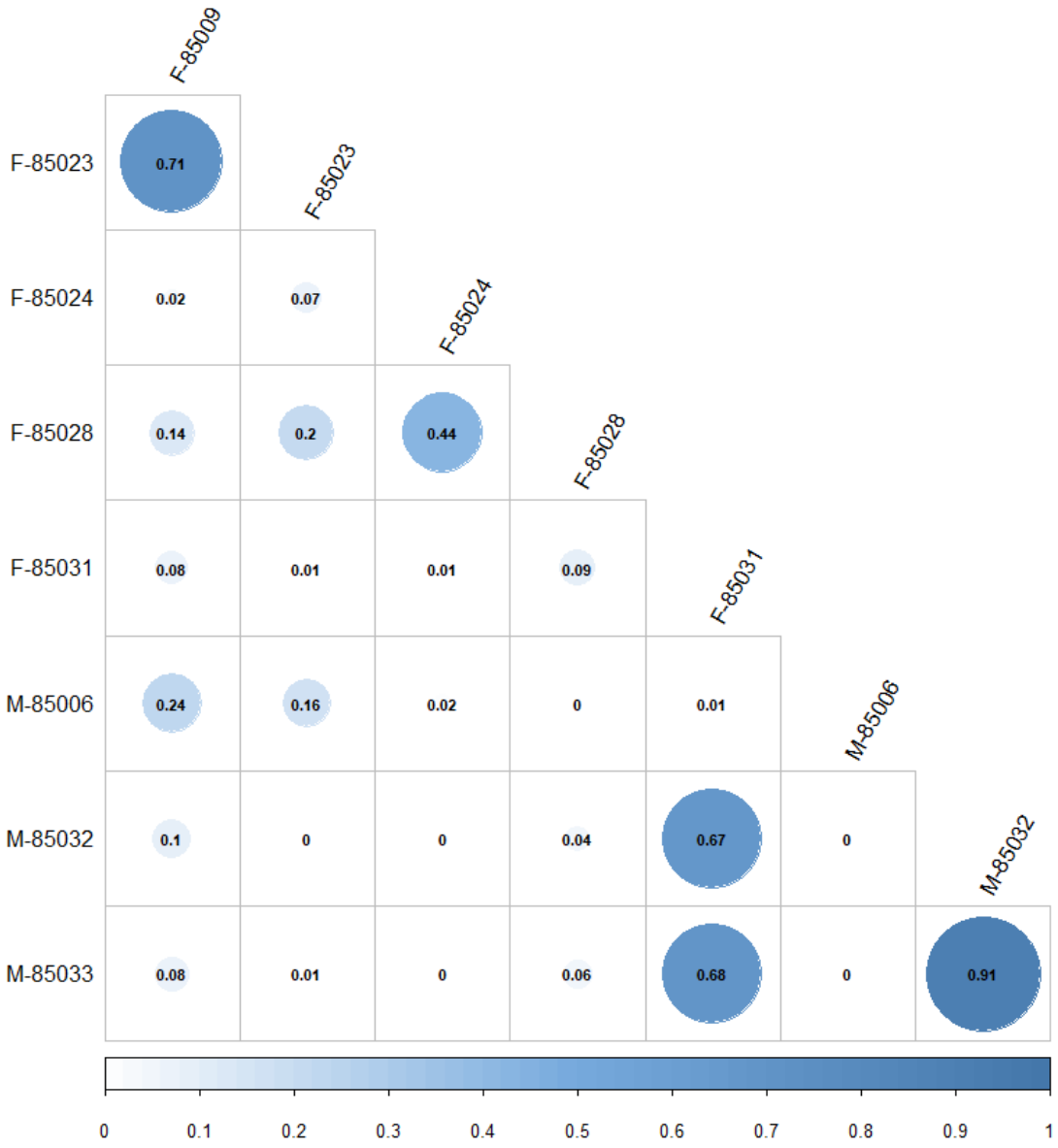

Figure 2.2: Home range overlap values (Bhattacharyya coefficients) of female Bicknell's Thrush (*Catharus bicknelli)* tracked during the breeding season (June 1 - July 31) in 2016.

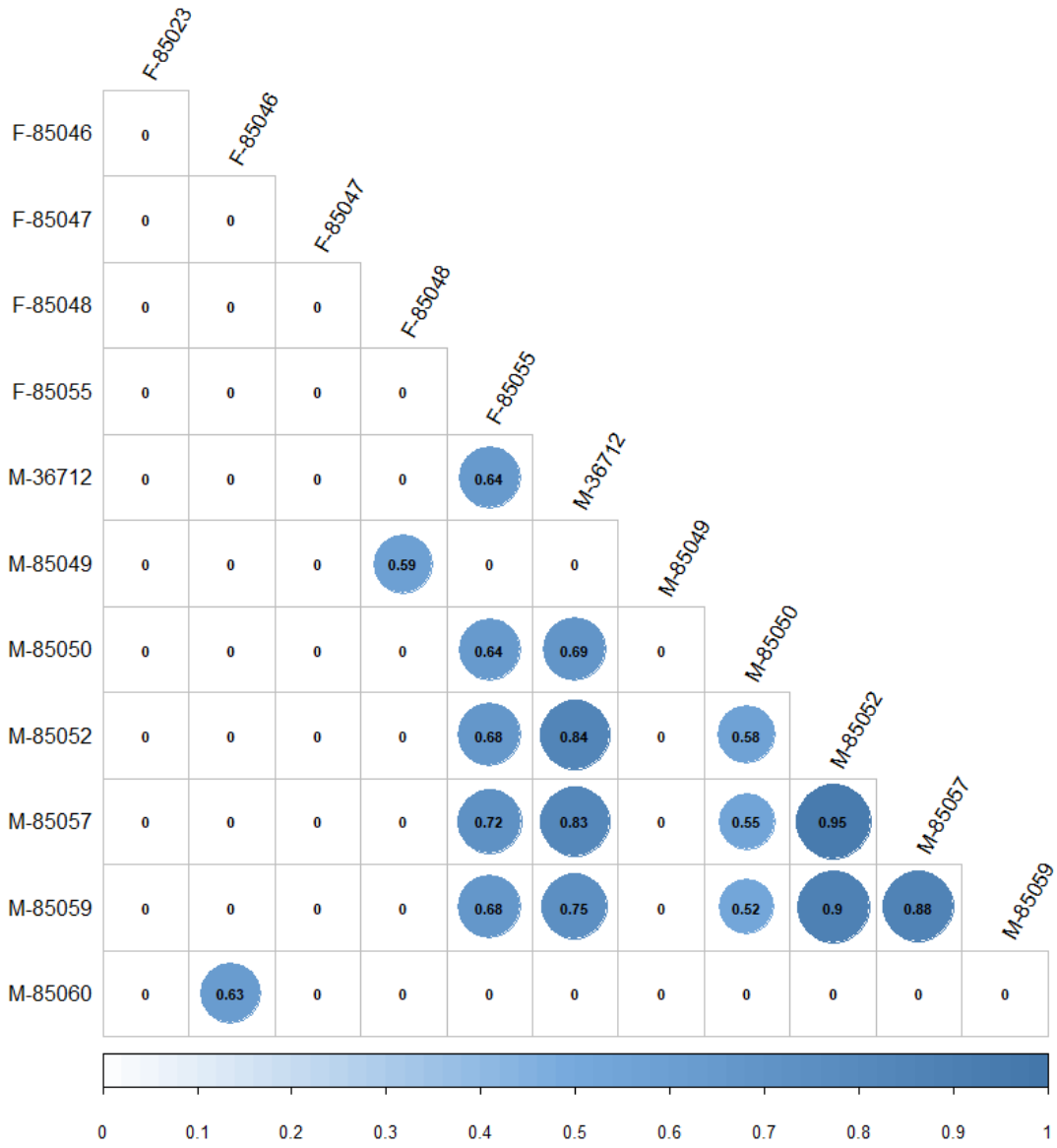

Figure 2.3: Home range overlap values (Bhattacharyya coefficients) of female Bicknell's Thrush (*Catharus bicknelli)* tracked during the breeding season (June 1 - July 31) in 2017.

The Bicknell's Thrush potential habitat area was estimated at 28 386.05 ha. The estimated maximum number of females within the predicted potential habitat area with a potential overlap of 0.11 was calculated at 1758 (1359 – 2490). The population estimate of both male and female Bicknell's Thrush (assuming two males per female) is 5 275 (4 077 – 7 469).

Discussion

Home range estimate methods

At my field site, female home range sizes (18.1 ± 5.3 ha (90% AKDE)) were larger than those in Quebec (13.90 ± 2.36 95% KDE, Aubry et al. 2011) and Vermont (5.43 ± 1.11 ha 95% KDE, Collins 2007). Quebec, Vermont, and the present study, each used different telemetry and analysis methods when estimating home ranges. In Vermont, Collins (2007) recorded at least one location per day by homing in on individuals and recording GPS positions when technicians observed the target individual. These methods introduce observer bias in the form of potentially influencing a target individual's behaviour (e.g., chasing individuals) or the observer being unable to locate individuals in difficult or cryptic terrain (White and Garrott 1990). In Quebec and New Brunswick, locations were estimated using triangulation of radio-tracked birds, which reduced direct observer bias but increased location error of relocations (Lee et al. 1985). In Quebec, individuals were sampled at least once per day with a minimum 30-minute interval (Aubry et al. 2011), whereas the present study tracked individuals at smaller sampling intervals (5-10 mins) over a four to five-hour period at multiple points throughout the field season. Each data collection method influences relocation number and sampling

interval, which can greatly affect KDE calculations (Seaman et al. 1999, Fieberg 2007, Fleming et al. 2015). Although AKDE (used in this study) can account for differences in temporal auto-correlation and sampling schedule (Calabrese et al. 2016), the differences in data collection schemes and analytical methods may contribute in part to the differences between study results and should be further explored.

Modelling Occurrence

Ideally, I would use an occurrence model of Bicknell's Thrush to estimate the number of individuals within the area, however no such model currently exists for New Brunswick. Instead, I substituted the occurrence model with a potential habitat model based on New Brunswick Bicknell's Thrush monitoring and NB forestry inventory data. A previous Bicknell's Thrush potential habitat model was based on the lowest occurrences in elevation estimated from Bicknell's Thrush monitoring in Vermont (Lambert et al. 2005), with longitude to improve the fit to Canada (Campbell and Stewart 2012). The previous potential habitat model included over 176 000 ha, with large areas of habitat unsuitable to Bicknell's Thrush. To improve this, Campbell (2017) used HELP and NB Mountain Bird Watch monitoring data to determine a minimum elevation threshold for Bicknell's Thrush in New Brunswick and combined it with appropriate habitat (minimum 60% red spruce or balsam fir) from NB forest inventory data to estimate potential habitat. At my field site the result very closely resembles an occurrence map of Bicknell's Thrush in the area studied by Chelsae Postma (pers. comm.). Although not strictly an occurrence model, the potential habitat model of Bicknell's Thrush is

likely the most accurate available representation of Bicknell's Thrush occurrence in New Brunswick.

Home range sizes

Although I calculated home range sizes for all males, only four individuals (85033, 85032, 85049, and 85060) had adequate sampling for home range analysis unbiased by relocation number. Since females were the focus of this study, male Bicknell's Thrush were tracked opportunistically (i.e. when all females were incubating, or for males that remained within tracking range while females were tracked). Male home range sizes found in this study should therefore be considered as very rough estimates of male spatial use during the breeding season.

The differences between home range sizes in New Brunswick, Quebec, and Vermont could be related to differences in each site's habitat history. Both New Brunswick and Quebec, with average home range sizes larger than Vermont, have greater amounts of relatively young forests that have been disturbed by the timber industry. As Aubry et al. (2011) suggest, the available prey biomass (mainly beetles (*Coleoptera*) and ants (*Formicidae*) for Bicknell's Thrush (Townsend 2015) could be lower in Quebec and New Brunswick than Vermont due to increased harvest. The relationship between home range and prey availability has been identified before in Vermont (Strong et al. 2004); in years with low nest-predation rates, number of chicks fledged per nest was significantly positively correlated with prey biomass on female's home range. Females may therefore increase their home range size to improve nest productivity when their initial assessment of habitat does not accurately reflect actual available prey biomass.

However, if prey availability is a driver of the differences in home range sizes, then home ranges in New Brunswick would have been smaller than those in Quebec. In Quebec, the study site contained a smaller amount of precommercially thinned forest (~30% thinned), whereas the field site where the present study was conducted had substantial (> 60%) precommercially thinned forest. Contrary to arthropod responses to harvest, thinning can increase biodiversity and biomass in invertebrates (Verschuyl et al. 2011). For example, thinned forest stands of balsam fir in Newfoundland and Nova Scotia contained significantly more egg densities and defoliation by balsam fir sawflies (*Neodiprion abietis*, Ostaff et al. 2006), suggesting an increase in sawfly biomass. Spruce budworm (*Choristoneura fumiferana*) reared in commercially thinned balsam fir stands developed five days faster than on trees from control stands, and consumed 43% more foliage, one year after thinning (Bauce 1996), suggesting thinned stands may increase insect biomass after thinning, at least in the short-term. Witcosky et al. (1986) found that three root-colonizing insect species (*Hylastes nigrinus, Pissodes fasciatus, Steremnius carinatus*) increased in abundance post-thinning. These studies suggest that thinned stands would contain more prey biomass, decreasing the amount of area an individual would need to cover to forage in their home range.

Despite the possibility of increased prey biomass, individuals may avoid remaining in prey-rich areas if there is not sufficient cover or protection from predators (Cresswell 2008). Indeed, several studies have documented the use of dense vegetation habitat by bird species that breed in non-dense vegetation (Streby et al. 2011), especially in the post-fledging stage when nests are not anchoring adults to their breeding home ranges or territories (Marshall et al. 2003, Chandler et al. 2012, Anders et al. 1998, White

et al. 2005). When food availability is equal or non-limiting, vegetation characteristics may become a larger factor in foraging decisions. As a species that nests and specializes in very dense, recovering forest stands, an individual Bicknell's Thrush that is more exposed in a thinner forest may exhibit higher vigilance or more frequent movements to avoid potential predators. This, in turn, would increase the distance moved by the individual or, alternatively, encourage the individual to move further to seek out denser forests for protection. In New Brunswick specifically, it would be highly unlikely for an avian predator to enter a tangle of balsam fir chasing prey, especially when those predators are large species like Northern Goshawks (*Accipiter gentilis*) or Northern Harriers (*Circus hudsonius*), the two species most frequently spotted in the NB study area during the field season. For mammalian predators, Bicknell's Thrush have been found in underground caches of weasel (*Mustelidae*) species in previous studies (COSEWIC 2009), and a weasel was responsible for one female death in the present study. Ermine (*Mustela erminea*) have been suggested to use open spaces within forests to hunt (Edwards and Forbes 2003), and it is possible are more abundant or successful at capturing ground-foraging birds in thinned habitat. While the prey abundance for Bicknell's Thrush might not be lower in thinned when compared to unthinned stands, the access to cover via dense vegetation in areas with more thinned forest than unthinned forest may drive home ranges to be larger for some individuals.

Overlap

Both Collins (2007) and Aubry et al. (2011) note that female home ranges overlapped very little but did not provide details; and in Quebec, a percentage of overlap

between 0.0007 to 0.9177 was reported for males only. In the present study, all females in 2016 had some degree of overlap, with two sets of females having an overlap of 0.44 and of 0.71. The pair of females with high home range overlap (85023 and 85009) nested simultaneously within 75 meters of one another. Considering the difficulty in capturing female Bicknell's Thrush, the dense habitat they typically build nests in, and the cryptic nature of their nests it is possible that my study, like previous ones, was unable to capture all females from each mating group. Although there are nest-monitoring and radio-tracking studies on Bicknell's Thrush, none report distance between nests of females with contiguous or neighbouring home ranges (Goetz et al 2003, Strong et al 2004, Collins 2006, Aubry et al. 2011). Gray-cheeked Thrush (*Catharus minimus*, a close relative of the Bicknell's Thrush) nests in Siberia were reported to be an average of 32 m between one another (Kretchmar 1997), which likely leads to some degree of home range overlap. Regardless, the degree to which 85023 and 85009 overlapped their home ranges is contradictory to previous research and overlap in females may warrant further study.

Population Estimate

The calculated population estimate based on female home ranges (5275, LCI 4 077 and UCI 7 469) is similar to that of Campbell and Stewart's (2012) estimate (4277, LCI 1705.5 and UCI 15 978) but represents a much smaller habitat area. Campbell and Stewart's 2012 estimate was for a habitat area of 220 564 hectares, compared with 28 386.05 hectares in the present study. The population estimates between these two methods are likely similar because HELP, prior to 2012, had low detections on monitoring routes in habitat that Bicknell's Thrush was not likely to use, bringing their

estimate down. Indeed, since 2012 BC has reduced their survey routes to those within the potential habitat model described here.

The High Elevation Landbird Program's 10-year report estimates Bicknell's Thrush population numbers using densities from surveys and forest development stage (regenerating, sapling, young, immature) in the surrounding 100m radius (~3 ha). Considering the size of male Bicknell's Thrush home ranges (>10 ha, the present study, Collins 2006 and Aubry et al 2011), it is possible that individuals were not actually associated with the development stage of the survey plot. Further, forest stands in New Brunswick are highly variable in their silviculture history. As previous studies have suggested (Chisholm & Leonard 2008, Aubry et al. 2011, McKinnon et al. 2014), the degree and timing of silviculture practices have an impact on habitat suitability and preference for Bicknell's Thrush. A forest stand at an appropriate development stage for Bicknell's Thrush may be compromised by the silviculture treatment most recently conducted on the area.

A recent study by Hill and Lloyd (2017) predicted Bicknell's Thrush population size for the United States' population using similar methods to Campbell and Stewart (2012) but with different predictors. Hill and Lloyd (2017) modeled Bicknell's Thrush abundances with elevation, percent canopy cover, and latitude. In Maine, the closest state with the most similar Bicknell's Thrush habitat to New Brunswick, Hill and Lloyd (2017) predicted a population size of 18 685.25 (LCRI: 12 519.15; UCRI: 27 441.02) individuals in 114 369 ha of habitat. Interestingly, using home range size and overlap from females in New Brunswick, a 2:1 male:female ratio, and the amount of potential habitat in Maine

calculates a similar, slightly inflated estimate to that of Hill and Lloyd's (2017): 21 252, with LCI of 16 425 and UCI of 30 094 individuals.

Despite how close the present study's estimate is to conventional population estimates, an understanding of how individual Bicknell's Thrush in New Brunswick use their home ranges would allow the potential habitat model to be refined, improving the estimate. Additionally, although I found a range of distances between home range edges, it is possible that I failed to capture females that are nesting immediately next to each other, making estimations of contiguity too ambiguous to use to estimate population size. Further, in the present study, females that had home ranges near each other overlapped, sometimes over half of their home range. Although no previous studies on Bicknell's Thrush home ranges have reported an overlap to that extent in females, the same caveat of contiguity applies – it is possible that, given the cryptic nature and difficulty in capturing female Bicknell's Thrush, previous studies have been unable to capture females with overlapping home ranges. Considering how overlap and contiguity affect estimating number of individual females within an area, my population estimate is only a rough approximation of the true number of Bicknell's Thrush in New Brunswick.

Finally, this population estimate assumes that individuals are saturated throughout the potential habitat. Bicknell's Thrush are polygynadrous in most of their range and have been described as aggregate breeders (Environment and Climate Change Canada 2016). Although the habitat area used for the occurrence area is already constrained to areas that have the highest densities of Bicknell's Thrush, the mating behaviour and conspecific attraction in Bicknell's Thrush may skew population estimates when they are based on individuals being equally saturated throughout the habitat. This assumption may limit the

population estimate to a “maximum potential population” for this species in New Brunswick. Further study on how mating groups of Bicknell’s Thrush orient their home ranges within and between groups and how individuals use their home ranges would improve spatial estimates.

The population estimate of Bicknell’s Thrush using female home range sizes is similar to that of previous estimates for New Brunswick but has an upper confidence interval less than half the size (~7 500 lower). Since the population estimate for all of Canada is 40 570 – 49 258 (COSEWIC 2009), this suggests that the Canada wide population estimate could be lower than reported in COSEWIC (2009) by ~15%. Further, with the recent near-disappearance of the population in Cape Breton (G. Campbell, pers. comm.), the updated potential habitat model decreasing from 220 564 ha to 28 386.05 ha, and the predicted decline of habitat quality at high elevation due to climate change (Wang et al. 2017), Bicknell’s Thrush in New Brunswick may be even more constrained in their spatial distribution than previously estimated. The use of thinned habitat and the overlapping of home ranges may suggest groups of Bicknell’s Thrush in New Brunswick are using habitat in different ways than was understood. Considering these aforementioned factors, the identification and management of habitat being used by Bicknell’s Thrush is of primary importance to conserve this species in New Brunswick.

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CHAPTER 3 – HABITAT PREFERENCE OF BICKNELL'S THRUSH (*CATHARUS BICKNELLI*) IN INDUSTRIAL FORESTS

Introduction

The International Bicknell's Thrush (*Catharus bicknelli*) Conservation Group (IBTCG) lists incompatible forestry practices on the breeding grounds as one of Bicknell's Thrush's top three population threats (Lloyd and McFarland 2017). Although tree harvest can create habitat for Bicknell's Thrush through the vigorous regrowth of balsam fir (*Abies balsamea*) (Ouellet 1993), many forests stands are treated with pre-commercial thinning (PCT), which significantly decreases stem density in the "ideal" stand age for Bicknell's Thrush occupancy (Chisholm and Leonard 2008). Since Bicknell's Thrush is a threatened species, forest managers are required by Canadian federal law to mitigate negative impacts on the species (COSEWIC 2009). In New Brunswick, most of the province's forest is managed for timber harvest, with public lands leased and operated by corporations. As such, very little "natural habitat" now exists for Bicknell's Thrush, and the species presently occurs in young, vigorously growing balsam fir (*Abies balsamea*) stands in the highlands of the north-central and north-west parts of the province (Campbell and Stewart 2012). Since most of their occupied habitat is presently young forest, it is unclear how Bicknell's Thrush will change their occurrence throughout the forest mosaic as young forest habitats are destined to outgrow young forest specialists. An understanding of how, and if, Bicknell's Thrush use forest other than mid-successional regrowth is important in planning for future conservation of this species in New Brunswick.

What drives habitat use in Bicknell's Thrush is key to identifying how land managers can alter their forestry practices to conserve the species. Forest managers are primarily choosing treatments based on potential economic yield and stand health. Still, sustainable forestry programs, such as the Sustainable Forestry Initiative (SFI), encourage forest industries to follow guidelines which include "Conservation of Biological Diversity" (Sustainable Forestry Initiative 2015). For Bicknell's Thrush, forest managers in New Brunswick are looking at alternatives to halting thinning to maintain Bicknell's Thrush habitat. For example, some companies have opted to leave patches of unthinned habitat when treating forest stands containing Bicknell's Thrush with PCT, while other thinning methods may leave strips of unthinned habitat 5-10 meters wide instead of thinning the entire stand (McKinnon et al. 2014). Both practical strategies assume (1) a known minimum space requirement for the species, or (2) that individuals of the species will use the surrounding, treated area if they have preferred habitat available for nesting. The minimum space requirement for Bicknell's Thrush can be assessed through home range size, which I estimated in Chapter 2, as well as being estimated in Vermont (McFarland et al. 2008) and in Quebec (Aubry et al. 2011). Identifying use and preference of thinned habitat in proximity to unthinned habitat would contribute to our understanding of whether Bicknell's Thrush are using thinned patches alongside unthinned forest (2).

Previous studies on the effects of forest management on Bicknell's Thrush have focused on the direct effects of PCT. Studies have suggested that PCT has a negative impact on species' occurrence (Chisholm and Leonard 2008), a lower preference for treated habitats (Aubry et al. 2011) and negative effects on abundance (Aubry et al.

2016). However, the use of older, thinned forests by Bicknell's Thrush remains unclear (Lloyd and McFarland 2017). The effect that forestry practices – such as clear-cutting, planting, and selective cutting – has on habitat preference in Bicknell's Thrush has yet to be explored. Despite occurring in an area that has been substantially managed by the forest industry, Bicknell's Thrush seem to be surviving in the high elevations throughout the Christmas Mountains despite a seemingly provincial decline (Campbell and Stewart 2012). Considering these habitats have not been "natural" for over 25 years, understanding what preferences individuals have towards differing habitat types may indicate appropriate habitat targets – especially since much of the forest is thinned.

In Chapter two, I estimated breeding home ranges of nine female and ten male Bicknell's Thrush. In this chapter, I aim to identify home range habitat selection within the known occurrence area and habitat selection within home ranges, with particular focus on forest treatment. Home range selection ("second order selection," Johnson 1980) is examined to determine what habitats Bicknell's Thrush are preferring when selecting home ranges within the landscape by comparing habitat within home ranges (used) to habitat within the landscape (available). Habitat preference within home ranges ("third order selection," Johnson 1980) illustrates the preferred use of habitat within home ranges by comparing relocations (use) to habitat within home ranges (available). If Bicknell's Thrush require thinned habitats only for nests, then when selecting home ranges, they will prefer unthinned habitats. Further, Bicknell's Thrush would show no preference within home ranges. Based on previous literature (Chisholm & Leonard 2008, Aubry et al. 2011, Aubry et al. 2016) I predicted that Bicknell's Thrush would avoid

thinned areas, with PCT-treated forest stands less preferred than non-thinned stands when selecting home ranges.

Methods

Field Methods

The field site was situated at 47.204, -66.553, in an area with consistent Bicknell's Thrush presence over recent years (McKinnon 2009, Askanas 2012, Campbell and Stewart 2012, Campbell 2017, Postma and Diamond unpublished data). The field site area consisted of an 1806.5 ha landscape between 522 and 709 meters in elevation. This forested area is fragmented into forest "blocks" under various stages of regrowth and treatments. Blocks had a mean area of 5.07 ± S.D. 10.57 ha (range: 0.5 – 127.84 ha).

We captured Bicknell's Thrush via mist-nets throughout the field season from one hour before dawn until 11:00 in the morning, and 20:00 until a half hour after dusk in the evening. Very high frequency (VHF) transmitters (Lotek Pip Ag376 and NTQB-3-2), weighing between 2.8% and 3.7% of an individual's body mass, were attached to Bicknell's Thrush using leg-loop harnesses (Rappole and Tipton 1991). It was assumed that the transmitters had a negligible effect on behaviour, as previous studies of radiotransmitters on migrating Bicknell's Thrush have suggested (Townsend et al. 2012).

Relocations were determined using triangulation, with three technicians in radio contact recording azimuths simultaneously, and tracking a maximum of two birds in the same area. Azimuths corrected for declination (-17.3 – 17.4 °W), and observer locations, were recorded at set intervals throughout each tracking period, which lasted 2 – 4 hours. For more detailed field methods, see methods in Chapter 2.

Location estimate and home range

I used the same methods as in Chapter 2 to estimate locations from azimuths and calculate home range sizes.

Habitat Variables

Variables for assessing habitat use came from three main sources: a provincial silviculture history dataset from the New Brunswick Department of Energy and Resource Development (NB DERD); the New Brunswick forest inventory database interpreted from aerial imagery on a 10-year cycle; and a private silviculture dataset from Fornebu Lumber – the timber management company currently leasing the area. The most recent silviculture treatment was extracted from all three sources of data, with the private silviculture dataset as the primary one, filled in by the New Brunswick forest inventory database as the secondary dataset, and the NBDERD silviculture history dataset as the tertiary, so that data gaps in the primary were filled by the secondary, followed by the tertiary. For second order habitat selection, habitat was one of five categories: planted, natural regeneration, PCT, fill planting, and non-forested. For third order habitat selection, habitat was one of three categories: planted, natural regeneration, and PCT. Fill-planting was available to only one individual and was included in "planted" habitat; non-forested was not included as no home ranges included any non-forested habitat. All geographic information was computed using ESRI's ArcMap GIS software.

Habitat Use

A compositional analysis (Aebischer et. al 1993) was performed to determined second and third order habitat selection in Bicknell's Thrush home ranges. I analyzed

males and females separately to identify differences in selection between sexes. For second order selection (home range selection, home range vs. landscape), I identified used habitat as area within the 90% AKDE home range of the individual, and available habitat as area within a 1 km buffer around all home ranges in the study site, representing an occurrence patch delineated in a previous study (Postma and Diamond, unpublished). For third order selection (selection within home ranges, relocations vs. home range), I compared percentage of an individual's locations in each habitat (used) to the percentage of habitat within that individual's home range (available). I replaced zero values with 0.7% (Bingham et al. 2007). A Mardia's test (Mardia 2006) was used to determine multivariate normality in used and available parameter data. If data were non-normal, a randomisation test using 999 repetitions was performed for the habitat ranking and habitat selection tests. Otherwise, a parametric chi-square and t-tests were performed to determine habitat selection and ranking, respectively. Both randomization and parametric tests used a type I error risk at $\alpha = 0.05$. Further, I investigated each individual's habitat selection using selection ratios (ω, Manly et al. 2002), which considers the number of relocations within the home range. Selection ratio values above 1 indicate preference, and values below 1 indicate avoidance. All analyses were conducted in the R statistical environment (R Core Team 2018) with the package "adehabitatHS" (Calenge 2006).

Results

Nine female individuals were tracked: five in 2016 and five in 2017, with one female tracked both years, for a total of ten home ranges. The number of relocations per female per year ranged from 75 – 339. Ten males were also tracked: four in 2016 and six

in 2017. Relocations of males ranged from 21 – 79 per individual. Mean auto-correlated kernel density home range areas were 18.1 ± 5.3 ha (90% AKDE) for females and 13.2 ± 2.2 ha (90% AKDE) for males, and together encompassed 278 ha of habitat.

Second-order Selection

Thinned habitat dominated both the habitat available in the landscape (65.8%), and the habitat used by both females (50.1% ± 12.7%, Figure 3.1) and males (71.2% ± 12.0%, Figure 3.2). Compositional analyses using parametric tests found non-random home range habitat selection by females ($\Lambda = 0.0745$, 4, $p < 0.01$, Figure 1) versus landscape availability, and ranked planted sites first and non-forested sites last (Table 3.1). Pairwise t-tests found significant differences between all habitat types in females except between PCT and fill-planting (Table 3.1).

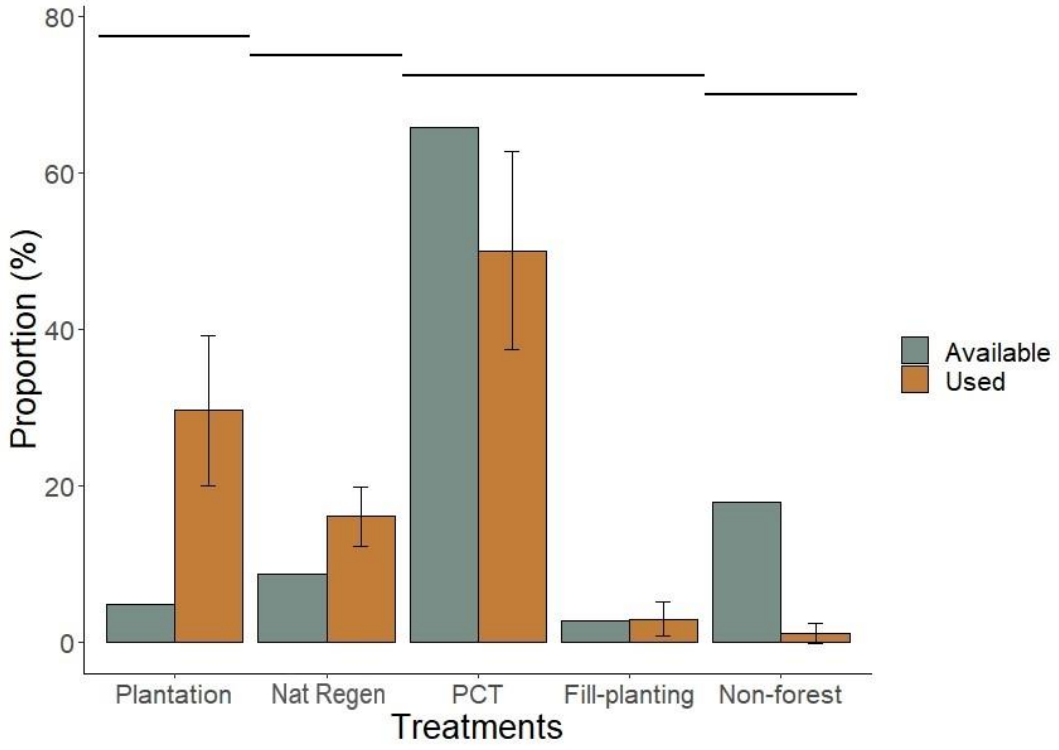

Figure 3.1: Available (landscape) and used (home range) habitats by nine female Bicknell's Thrush (*Catharus bicknelli*) during 2016 and 2017 breeding seasons (May – August) in north-central New Brunswick, Canada. Errors bars denote standard error. Categories joined by lines are not significantly different.

Table 3.1: Landscape (second order) habitat preference matrix of nine female Bicknell's Thrush (*Catharus bicknelli*) tracked during the breeding season in 2016 and 2017 in north-central New Brunswick, Canada. Significant differences designated by starred t-statistics, ordered in rank of preference with left and top ("Rank 1") being most preferred.

	Plantation	Nat Regen	PCT	Fill Planting	Non-forest
Plantation	*Rank 1*	2.15*	2.65*	2.51*	8.22*
Nat. Regen.		*Rank 2*	2.32*	2.06*	10.93*
PCT			*Rank 3*	0.34	5.36*
Fill Planting				*Rank 4*	4.35*
Non-forest					*Rank 5*

For males, compositional analyses using randomisation tests found non-random home range habitat selection ($\Lambda = 0.0622$, $p = 0.002$, Figure 2) versus landscape availability. Males ranked thinned habitat first, with non-forested the least preferred (Table 2), although pairwise comparisons found significance only between the non-forested and each of the other habitat types.

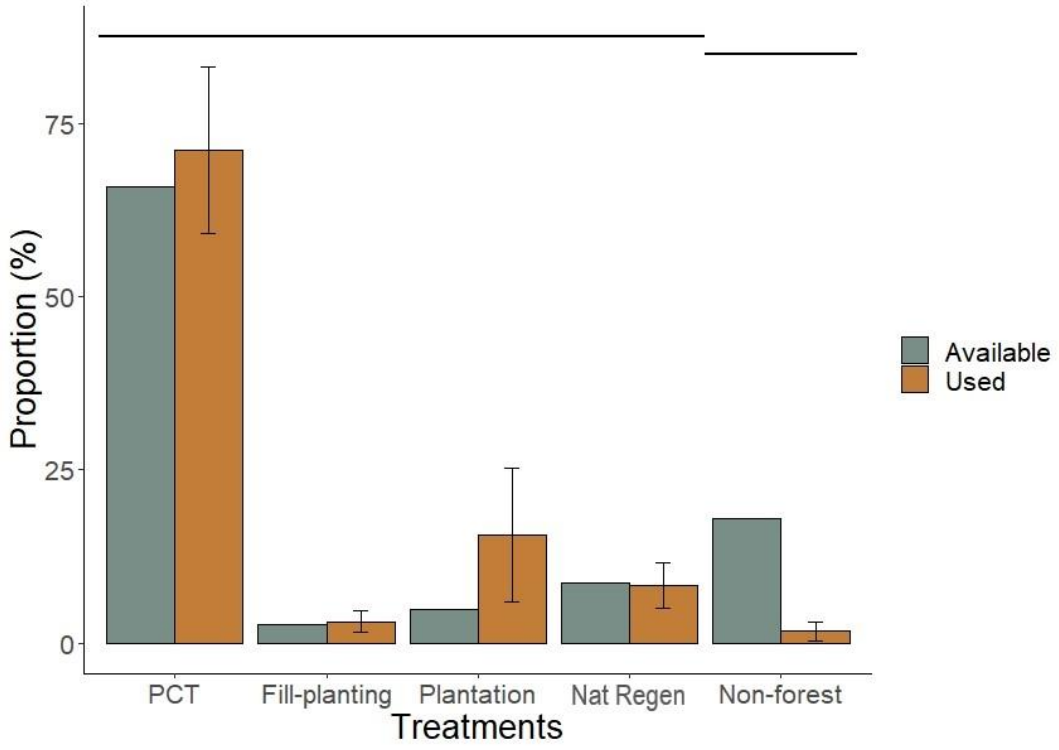

Figure 3.2: Available (landscape) and used (home range) habitats by 10 male Bicknell's Thrush (*Catharus bicknelli*) during 2016 and 2017 breeding seasons (May – August) in north-central New Brunswick, Canada. Errors bars denote standard error. Categories joined by lines are non-significant.

Table 3.2: Landscape (second order) habitat preference matrix of 10 male Bicknell's Thrush (*Catharus bicknelli*) tracked during the breeding season in 2016 and 2017 in north-central New Brunswick, Canada. Significant differences designated by starred mean differences between used and available log-ratios, ordered in rank of preference with left and top ("Rank 1") being most preferred.

	PCT	Fill-planting	Plantation	Nat. Regen.	Non-forest
PCT	*Rank 1*	0.27	0.32	0.38	2.62*
Fill-planting		*Rank 2*	0.051	0.11	2.35*
Plantation			*Rank 3*	0.062	2.29*
Nat. Regen.				*Rank 4*	2.23*
Non-forest					*Rank 5*

Third-order Selection

Females showed no preference in habitat selection within the home range (third-order selection) ($\Lambda = 0.785$, 2, $p = 0.337$, Figure 3.3); planted sites ranked first and thinned sites last but differences were not significant (Table 3.3). Four individuals selected for planted habitat with Manly ratios >1, two individuals selected for natural regeneration habitat, and five selected for thinned habitat (Table 3.4). An individual tracked two years in a row showed a marginal preference for natural regeneration sites the second year that was not found in the first year (Table 3.4, individual 2 and 10).

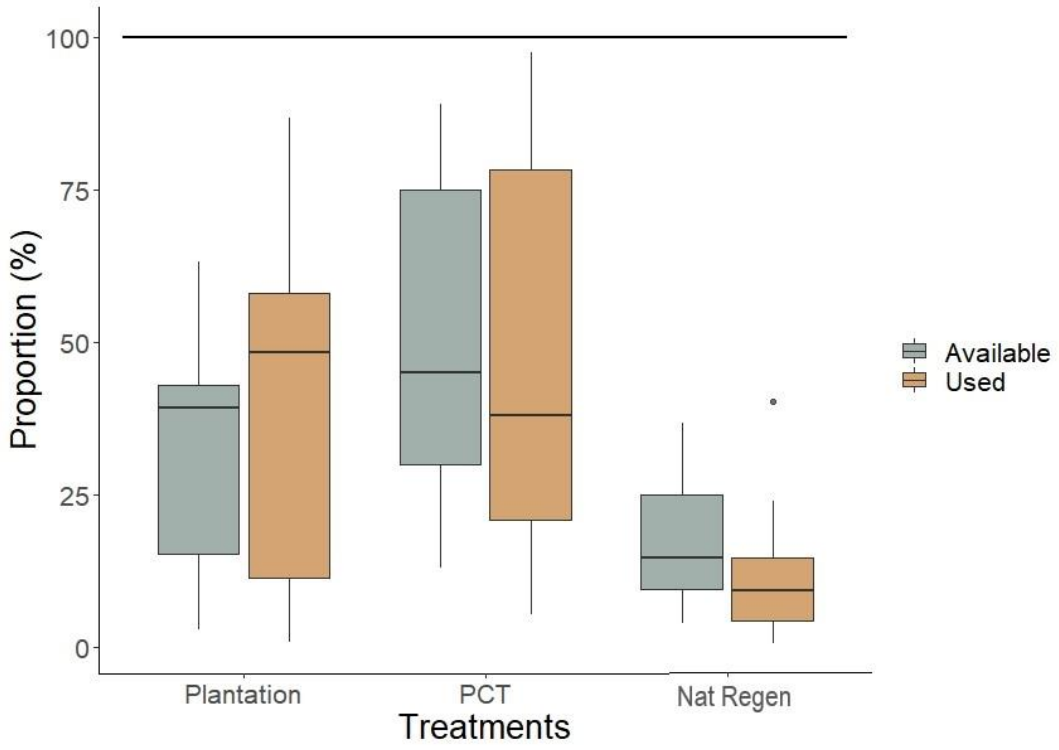

Figure 3.3: Available (home range) and used (proportion of relocations) habitat use by nine female Bicknell's Thrush (*Catharus bicknelli*) during 2016 and 2017 breeding seasons (May – August) in north-central New Brunswick, Canada. Errors bars denote standard error. Categories joined by lines are non-significant.

Table 3.3: Home range (third order) habitat preference matrix of nine female Bicknell's Thrush (*Catharus bicknelli*) tracked during the breeding season in 2016 and 2017 in north-central New Brunswick, Canada. Significant differences designated by starred t-statistics, ordered in rank of preference with left and top ("Rank 1") being most preferred.

	Plantation	PCT	Nat. Regen.
Plantation	*Rank 1*	0.124	1.175
PCT		*Rank 2*	0.621
Nat. Regen.			*Rank 3*

Table 3.4: Home range (third order) habitat selection ratios ("Manly ratios") of individual female Bicknell's Thrush (*Catharus bicknelli*) tracked during the breeding season in 2016 and 2017 in north-central New Brunswick, Canada. Stars designate the same female in different years, and numbers in parentheses are number of relocations.

Individual	Plantation	Nat. Regen.	PCT
1	1.523 (103)	0.879 (27)	0.593 (46)
2*	1.306 (132)	0.867 (56)	0.668 (45)
3	0.407 (27)	0.807 (17)	3.469 (61)
4	1.893 (64)	0.976 (11)	0.601 (45)
5	2.153 (65)	0.352 (3)	0.12 (4)
6	0.394 (66)	1.076 (132)	3.096 (136)
7	0.044 (5)	0.013 (1)	2.945 (278)
8	0.112 (2)	0.796 (8)	1.08 (242)
9	0 (0)	0.267 (5)	1.108 (205)
10*	7.341 (191)	1.003 (23)	0.113 (21)

Males also showed no habitat preference within the home range ($\Lambda = 0.9465127$, $p = 0.77$, Figure 3.4). Third order compositional analyses ranked planted sites most preferred and thinned sites least preferred but were not significantly different (Table 3.5). Four individuals selected for planted sites with Manly ratios >1, one for natural regeneration habitat, and five for thinned habitat (Table 3.6). One individual had all locations and home range within a thinned habitat patch (Table 3.6, individual 5).

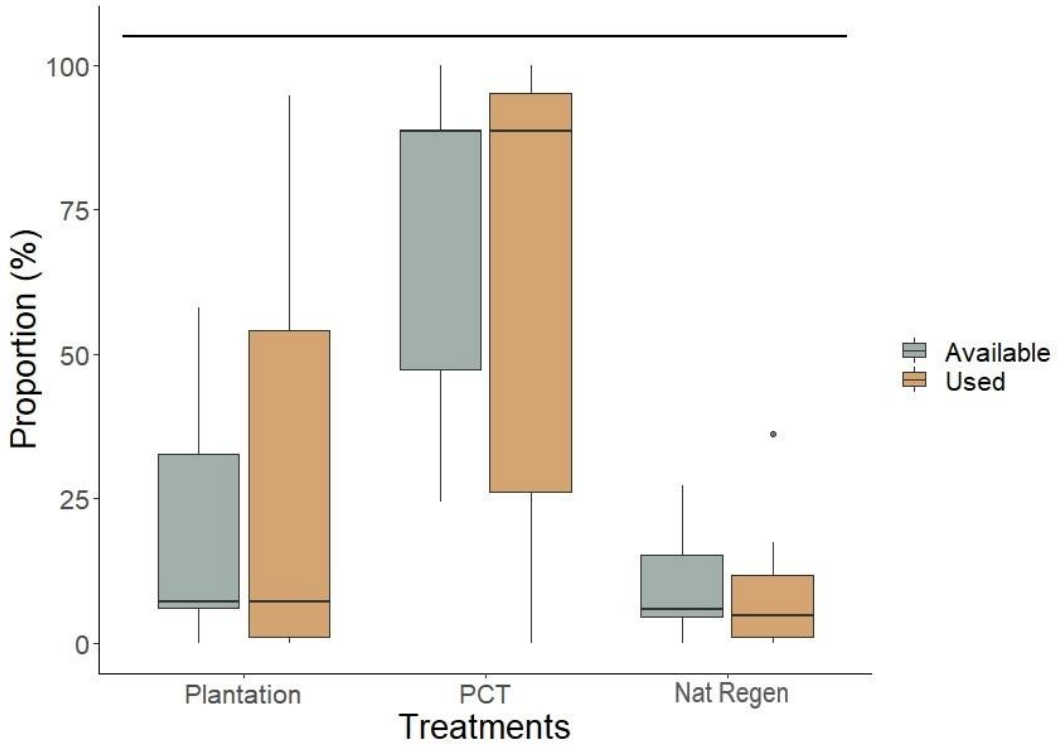

Figure 3.4: Available (home range) and used (proportion of relocations) habitats by 10 male Bicknell's Thrush (*Catharus bicknelli*) during 2016 and 2017 breeding seasons (May – August) in north-central New Brunswick, Canada. Errors bars denote standard error. Categories joined by lines are non-significant.

Table 3.5: Home range (third order) habitat preference matrix of 10 male Bicknell's Thrush (*Catharus bicknelli*) tracked during the breeding season in 2016 and 2017 in north-central New Brunswick, Canada. Significant differences designated by starred mean differences between used and available log-ratios, ordered in rank of preference with left and top ("Rank 1") being most preferred.

	Plantation	Nat. Regen.	PCT
Plantation	*Rank 1*	0.23	0.32
Nat. Regen.		*Rank 2*	0.082
PCT			*Rank 3*

Table 3.6: Home range (third order) habitat selection ratios ("Manly ratios") of individual male Bicknell's Thrush (*Catharus bicknelli)* tracked during the breeding season in 2016 and 2017 in north-central New Brunswick, Canada. Numbers in parentheses are number of relocations.

Individual	Plantation	Nat. Regen.	PCT
1	0 (0)	0 (0)	1.124 (20)
2	1.721 (18)	0 (0)	0 (0)
3	1.463 (22)	1.221 (15)	0.452 (8)
4	1.65 (26)	0.767 (8)	0.606 (12)
5	0 (0)	0 (0)	1 (74)
6	0 (0)	0.797 (1)	1.069 (18)
7	0 (0)	0.88 (1)	1.081 (22)
8	0 (0)	0.936 (1)	1.069 (19)
9	0 (0)	0 (0)	1.126 (28)
10	2.065 (47)	0.933 (6)	0.469 (21)

Discussion

Male and female Bicknell's Thrush showed different habitat preferences at the home range versus landscape level ("second-order" selection), where females showed significant differences in habitat preference, but males only avoided non-forested habitats. It is possible that the difference in number of relocations per individual between male and females could bias comparisons (Girard et al. 2002, Manly et al. 2002), which may be the case considering a habitat selection study in Quebec did not find any habitat differences between male and female home ranges (Aubry et al. 2011). Despite the potential for bias, the breeding ecology of Bicknell's Thrush could be causing the differences in habitat selection between the sexes in New Brunswick, and the differences in available habitat between the provinces could explain why this may be more apparent in New Brunswick than in Quebec. In New Brunswick, the difference in habitat selection between the sexes could be due to the polygynandrous breeding system of Bicknell's Thrush, where males visit and feed multiple nests (Goetz et al. 2003, Askanas 2008), overlapping several female home ranges (McFarland et al. 2008, Aubry et al. 2011, present study). In a heterogeneous habitat, while females may show habitat selection, male habitat use may reflect the habitat choices of several females within different habitats, resulting in habitat use which is mixed in nature. The different habitat choices of different females would contribute considerably to the lack of habitat discrimination shown by males. This may be more apparent in New Brunswick, as the available habitat in the present study was much different than in Quebec, with >60% of habitat treated with PCT in New Brunswick versus <30% in Quebec. The Quebec study also seemed to be characterized by a large unthinned area with about ten ~ 5 - 15 ha patches of thinned

habitat, whereas NB is characterized by forest blocks of mean size 5 ha with varying silviculture treatments throughout. Less complex habitat composition could simplify interpretation of habitat relationships (Mitchell and Powell 2008), with most individuals preferring the large amount of untreated habitat rather than the small patches of thinned habitat in Quebec. In New Brunswick, since patches are smaller and the landscape is more heterogeneous, habitat preferences of individuals in close proximity to one another may differ more than in Quebec, increasing the complexity of habitat of males that overlap several female home ranges.

It is no surprise that female Bicknell's Thrush preferred unthinned versus thinned and non-forested habitats at the home range vs landscape level in this system. Previous studies have identified Bicknell's Thrush habitat as thick, young, vigorously regenerating fir stands on mountain tops (Townsend et al. 2015). However, use of unthinned habitat was not uniform among all females; three of nine had more thinned habitat within their home ranges than was available within the landscape, and nearly all relocations of these three females were within thinned forest, suggesting that individuals were using only thinned habitat. However, it is unknown how successful individuals occupying thinned habitat were compared to individuals using unthinned habitat. Bicknell's Thrush tend to occupy habitat in clumps, encouraging shared feeding responsibilities (Goetz et al. 2003) and parentage. Individuals may use sub-optimal habitat to gain access to a group resource (males in this case). Groups of Bicknell's Thrush may inhabit large areas, especially if females maintain non-overlapping territories (although two females did have large overlap in the present study). When habitat is fragmented, individuals on the periphery of the group may be limited to sub-optimal habitat to maintain access to group benefits.

Previous studies have shown that thinning can have a negative impact on Bicknell's Thrush presence. Chisholm and Leonard (2008) described a steep decline of Bicknell's Thrush occurrence in three forest stands one year after thinning in New Brunswick. In Quebec, Aubry et al. (2011) found a preference for unthinned habitat, followed progressively by older thinned habitat and younger thinned habitat. Although the present study does rank thinned habitat below unthinned, three females used thinned habitat almost exclusively. These habitats had been thinned ~ 13 years prior and were ~27-year-old stands. Taken together, it is possible that although PCT has a direct and immediate effect on Bicknell's Thrush habitat use of a forest stand, that effect may change depending on time since treatment and composition of available habitats.

Surprisingly, females preferred plantations over natural regeneration at the home range vs landscape scale. Young conifer forest plantations can be characterized by uniform stand structure and relatively low tree mortality due to snow and ice damage, whereas forests growing from natural regeneration are characterized by an uneven stand structure, with the stand naturally self-thinning through mortality (Janas and Brand 1988). Female Bicknell's Thrush may be preferring plantations since the conifers are denser than in naturally regenerating forests. Interestingly, the planted stands within the study area were younger than those naturally regenerating, with plantations at age eight and nine years old and the mean age of naturally regenerating clear-cuts at 17 years old. In Quebec, Bicknell's Thrush detections were highest at stand ages between 20-30 years old and > 70 years old, peaking at a stand age of 25 years (Aubry et al. 2016). Planted sites may magnify stand characteristics that Bicknell's Thrush are looking for in habitat,

such as stem density, which may explain female Bicknell's Thrush preference for planted sites in New Brunswick.

Although movements during the breeding season can include mating, nest building, and predator avoidance/defence, while nests are active females are likely either brooding or feeding their young. Since all females had active nests while being tracked, most adult female relocations were probably associated with foraging for nestlings. Within their home ranges, Bicknell's Thrush showed no preference for habitat types, suggesting that there was no foraging preference among habitats. Considering all females had some thinned habitat within their home ranges, and at least half the female individuals used thinned habitat in their home range more than what was available in the landscape, thinned habitat is probably at least equal to unthinned habitat in terms of prey abundance. Indeed, studies have shown increases in biomass and abundances of insects immediately post-PCT, returning to pre-PCT levels after three years (Taki et al. 2010); shorter development time of spruce budworm (*Choristoneura fumiferana*) which could increase availability (Bauce 1996); and an increase in egg densities of balsam fir sawflies (*Neodiprion abietis*) in thinned stands (Ostaff et al. 2006). However, a meta-analysis by Verschuyl et al. (2011) of biodiversity response to thinning cautions against positive responses of invertebrates to thinning, as studies that had identified community responses (as distinct from single-species responses) from North America were lacking. Considering this, analysis of habitat preference within home range suggests that food availability is not limiting among habitat types, but future work on diet in industrial forests is necessary to confirm this.

Strong et al. (2004) suggest that nest predation ultimately limits Bicknell's Thrush productivity in the breeding season, as relationships between successful chick fledging and prey biomass within female home ranges were significant in years with low predation but not in years with high predation. As the present study suggests that females are selective in where they place their home ranges within the landscape but not in how they use habitat within their home ranges, a possible conclusion could be that females select their home ranges primarily based on available nesting habitat – i.e., dense, young conifers – to avoid predation. The American red squirrel (*Tamiasciurus hudsonicus*), Bicknell's Thrushes' main nest predator (Townsend et al. 2015), is ubiquitous throughout the landscape in New Brunswick. Indeed, over a quarter of false-nests placed by McKinnon (2009) were depredated, half of which were by members of the *Sciurdidae* family despite low numbers of squirrels observed during the field season. Although we also noted low numbers of red squirrel during our field season, we found the carcass of a tracked female Bicknell's Thrush within the den of a weasel (*Mustelidae sp.*), also a predator of false-nests from McKinnon's (2009) study. The den was in a pile of old wood, dead vegetation, and tree thinnings 50 meters away from several tracked Bicknell's Thrush nests. These piles of dead organic matter were common throughout the area and were likely leftover from forestry operations. Regardless of what type, the presence of a predator so near to a nesting site would be a strong driver to conceal nests in dense conifers. Since all females had contiguous and overlapping home ranges, females may select nest sites to conceal their nests from predators, and simply forage around their nest, increasing home range size (Chapter two) or recruiting males when food availability is low (Strong et al. 2004) or demands increase, as when chicks hatch. In

a heterogeneous landscape, this would encourage clumped occupancy around unthinned habitats, with nests concentrated within unthinned patches of forest.

Previous studies have identified PCT as an incompatible silviculture treatment to Bicknell's Thrush habitat, while also showing that Bicknell's Thrush prefer young forest that could be created by harvesting practices of the forestry industry. Despite low sample size, the present study illustrates this complex dynamic between Bicknell's Thrush and silviculture treatment, by showing that older, thinned habitat is used by Bicknell's Thrush – sometimes exclusively – and plantations may be preferred over natural regrowth. Although Bicknell's Thrush are selecting home ranges based on treatment, within the home range they show no such selection, suggesting nest-site selection may be important in selecting a home range within the landscape. Further studies on differences between nesting success and food availability in different types of habitats (e.g., unthinned vs. thinned), with chick and adult diet would help identify drivers of habitat selection in this species. Since Bicknell's Thrush use thinned and unthinned habitat similarly within home ranges, the practice of leaving unthinned patches during thinning may encourage some individuals to remain in the forest stand; however studies that follow Bicknell's Thrush presence before, during, and after thinning would be necessary to confirm this.

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CHAPTER 4 – MODELLING BICKNELL'S THRUSH (*CATHARUS BICKNELLI*) HABITAT USE IN REGENERATING INDUSTRIAL FORESTS

Introduction

The Bicknell's Thrush (*Catharus bicknelli*) is a threatened species in Canada (COSEWIC 2009) with the most restricted breeding range of all north American songbirds (Townsend et al. 2015). The species' breeding range includes the north-eastern United States, Quebec, northern Cape Breton, and New Brunswick (Townsend et al. 2015). Within New Brunswick, Bicknell's Thrush is restricted to the high elevations in the north-central and north-west of the province, where forested crown lands are managed by private forestry companies (Campbell and Stewart 2012). The relationship between Bicknell's Thrush and forestry is complicated, as Bicknell's Thrush are associated with mid-successional areas created naturally from fire, windthrow, snow, or insect damage (Ouellet 1993, Nixon et al. 2001). These natural disturbances are strongly managed and reduced by the province, limiting Bicknell's Thrush's contemporary habitat in New Brunswick to regenerating high elevation forests post-harvest (Nixon et al. 2001). Bicknell's Thrush are also sensitive to pre-commercial thinning (PCT), which reduces stem densities of young forest stands (15 – 20 years old) from > 5 000 trees/ha (but as high as 40 000 trees/ha) to between 2 000 and 3 500 trees/ha (Chisholm and Leonard 2008).

In New Brunswick, PCT was shown to reduce the occurrence of Bicknell's Thrush in forest stands one year post-treatment (Chisholm and Leonard 2008). However, McKinnon et al. (2014) suggested that small patches of dense habitat left within

treatment stands may allow Bicknell's Thrush to remain within the habitat, as they found nests located in unthinned stands < 500 m from stands treated with PCT. In Quebec, a habitat preference study of 42 Bicknell's Thrush annual breeding home ranges found a preference of unthinned habitat over two different-aged thinned stands, as well as a preference for stand edges, in habitat with a of mostly unthinned forest stands (Aubry et al. 2011). However, the field site in the present study was occupied by Bicknell's Thrush while it was considered old-growth (Mosseler et al. 2003) before a major windstorm event levelled the forest in 1994 (Gallant et al. 2014). Since then, Bicknell's Thrush has continued to occupy the area despite a drastic change in habitat and silviculture management, although numbers have seemed to be declining (Campbell and Stewart 2012). Indeed, in Chapter 2 and 3, I showed that several tracked females, captured in unthinned forests, occupied thinned habitat. With an apparent preference for stand edges, thinned habitat within home ranges, nest sites near or within thinned forests, and the use of ephemeral habitat, Bicknell's Thrush may be more resilient to a wider variety of high elevation industrial forest habitats than previously thought. Further, the effects found by Chisholm and Leonard (2008) may represent immediate effects of thinning on occupancy, with some individuals returning to thinned stands when sufficient regrowth has occurred – especially when ideal habitat is limited.

The present chapter aims to identify the effects of different forestry treatments (and in particular, pre-commercial thinning) on the habitat use of Bicknell's Thrush in the Christmas Mountains (47.20, -66.55) in north central New Brunswick, Canada, as well as the time since those treatments were conducted. Used habitat will be compared with available habitat within a modelling framework. Since Bicknell's Thrush prefer

unthinned forests over thinned, I predict that thinning would have a negative effect on Bicknell's Thrush habitat use, until those forests have regrown enough to have nesting habitat available. I also predict forests that were not thinned (naturally regenerating clear-cuts, planted sites, and windthrow) would have a positive effect on habitat use, until they had reached a stand age where Bicknell's Thrush would be less likely to occupy them (~30 years, Aubry et al. 2018).

Methods

Field Methods, Triangulation and Relocation Estimate

I used the same methods as Chapters 2 and 3 for collecting relocation data on Bicknell's Thrush. Bicknell's Thrush were captured via mist-nets, measured, banded and fitted with very high frequency (VHF) transmitters (Lotek Pip Ag376 and NTQB-3-2). Transmitters weighed between 2.8% and 3.7% of an individual's body weight. Individual relocations were then triangulated with three technicians in radio contact taking azimuths simultaneously for periods of 2 – 4 hours. For more detailed field methods, see methods Chapter 2.

Locations were estimated from azimuths and observer locations using the R Statistical Environment (R Core Team 2019) package 'razimuth' (Gerber et al. 2018). The package estimates locations using a hierarchical azimuthal telemetry model, fit using a specialized Markov chain Monte Carlo procedure. The posterior mode and 95% isopleth of the posterior draws from the Markov chain Monte Carlo were used as location and location error for each location estimate, based on 10 000 iterations.

Habitat Variables

Candidate variables came from the same dataset as Chapter 3. The most recent silviculture treatment, years since that treatment, and stand age (Table 1) were extracted from all three sources of data, following the same protocol as Chapter 3 (private silviculture dataset primary, the New Brunswick forest inventory database as the secondary, and the NBDERD silviculture history dataset as the tertiary dataset). I created 'available' locations by randomly selecting points throughout a potential habitat area, estimated as the area buffered 1000m around all home ranges, using the Create Random Points tool in ESRI's ArcGIS software at a ratio of three random locations for every one relocation. I extracted forest treatment, year since the treatment, stand age and elevation onto each relocation and available location (Table 4.1). I selected these variables as they represent forest habitat variables typically associated with Bicknell's Thrush (elevation and stand age) and the anthropogenic effects associated with the forest stand (forest treatment and year since that treatment). I did not include tree species composition since available data were too coarse for species-specific effects, and the habitat area is mainly uniformly balsam fir (*Abies balsamea*) at various ages. I randomly assigned available locations individual bird IDs at the same ratio as number of relocations per individual, so that each individual ID had the correct 1:3 ratio of use:available datapoints. Available locations were also assigned dates at the same ratio as relocations per individual bird ID (e.g., individual n has 5 relocations, with 2 relocations on date x and 3 on date y; available locations for that individual would number 15, with 6 on date x and 9 on date y). All geographic data manipulation for creating locations and appending data to relocations was done in ESRI's ArcMap version 10.7. Randomization of available

locations to individual numbers and dates was done in the R Statistical Environment (R Core Team 2019), using the base function *sample*.

Table 4.1: Variables used to model habitat use of Bicknell's Thrush (*Catharus bicknelli*) in north-central New Brunswick, Canada.

Variable	Description
Yr	Years since most recent silviculture treatment of harvest block.
Age	Stand age, calculated as years since most recent harvest (or windthrow) in block.
Treat:TI	Most recent treatment as pre-commercial thinning.
Treat:CC	Most recent treatment as clear-cut.
Treat:BP	Most recent treatment as plantation.
Treat:WIND	Most recent treatment as windthrow damage.
Treat:NF	Areas non-forested, including wetlands and roads.
Date.f	Date that the relocation was taken.
Ele	Elevation

Generalized Linear Mixed Models

To assess the effects of silviculture treatment on Bicknell's Thrush habitat use, I used a binomial generalized linear regression with a logit link to model Bicknell's Thrush use (1) and availability (0). Males and females were modelled separately. I used individual relocations as used habitat and random locations within the potential habitat (see Habitat Use) as available locations. I considered year since treatment (yr), treatment types (clear-cut [CC], pre-commercial thinning [TI], planting (including fill planting) [BP], windthrow [WIND], and non-forested [W]), elevation (ele) and stand age (age) as potential predictors with individual (indiv) as a random effect (Table 1). I accounted for temporal autocorrelation by including the date (date.f) of relocation as a random effect. Year since treatment, elevation, and stand age were scaled by their root mean square. I tested tolerance ($1 - R^2$) by running linear models of each numeric covariate against all other covariates. For any tolerances < 0.1, I identified colinear covariates by removing covariates until tolerance increased > 0.1 and did not include identified colinear covariates within the same candidate models. I then created candidate models and selected the best model by Akaike's Information Criterion corrected for small sample sizes (AICc, Hurvich and Tsai 1989). I considered candidate models within two ΔAIC from one another to have equal likelihood. Random variables that showed zero variance in all candidate models were subsequently removed from those models, and the candidate set was compared again. The variance inflation factors (VIF) were checked on best fit models for any predictors with VIF > 10. When VIF > 10 were identified, the covariates with the highest VIFs were removed until VIFs were < 10. Variables with VIF > 10 that were in interactions were not removed. If variables with VIF > 10 were identified, a

second set of candidate models was then created with offending covariates separated between models. All modelling was computed in the R Statistical Environment (R Core Team 2019), using the packages “lme4” (Bates et al. 2015) and “MuMIn” (Barton 2019).

Results

Relocations

Twenty Bicknell’s Thrush were tracked in this study: 10 females (five in 2016 and 2017), and 10 males (four in 2016 and six in 2017), with a total of 2463 relocations. Mean number of relocations of females in planted, clear-cut, fill-planted, thinned, and windthrown treatments were 72.8, 30.3, 11.3, 108.3 and 3.0 respectively (Figure 4.1), and 28.3, 5.3, 1.3, 24.7 and 2.7 for males (Figure 4.2). There were 7405 random available locations (see Chapter 3 for further details on available habitat). Median stand age was calculated as 20 years for relocations and 22 years for random locations, while median year since treatment was calculated as nine years for relocations and 13 years for random locations (Figure 4.3, Figure 4.4). The Pearson correlation coefficient between stand age and year since treatment was 0.51, while elevation had a Pearson correlation coefficient of -0.15 with stand age and -0.35 with year since treatment.

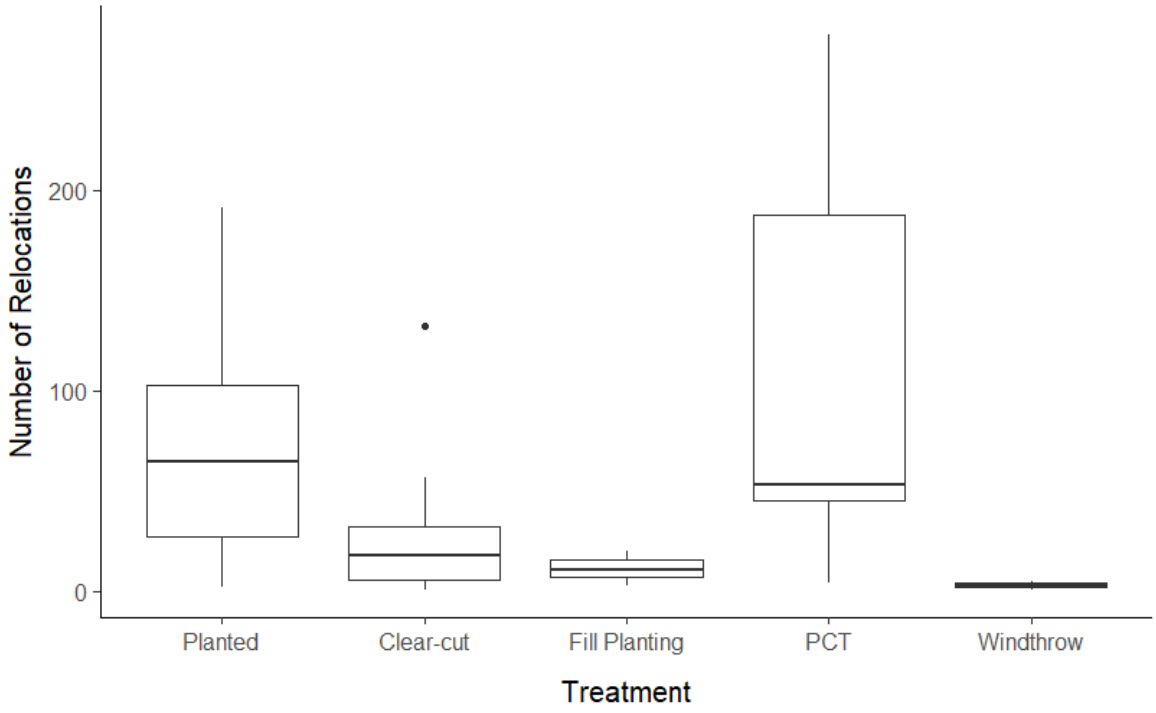

Figure 4.1: Relocations by treatments (planted, clear-cut, fill planting, pre-commercial thinning and windthrow) of female Bicknell's Thrush (*Catharus bicknelli*) tracked during the breeding seasons of 2016 and 2017 in north-central New Brunswick, Canada

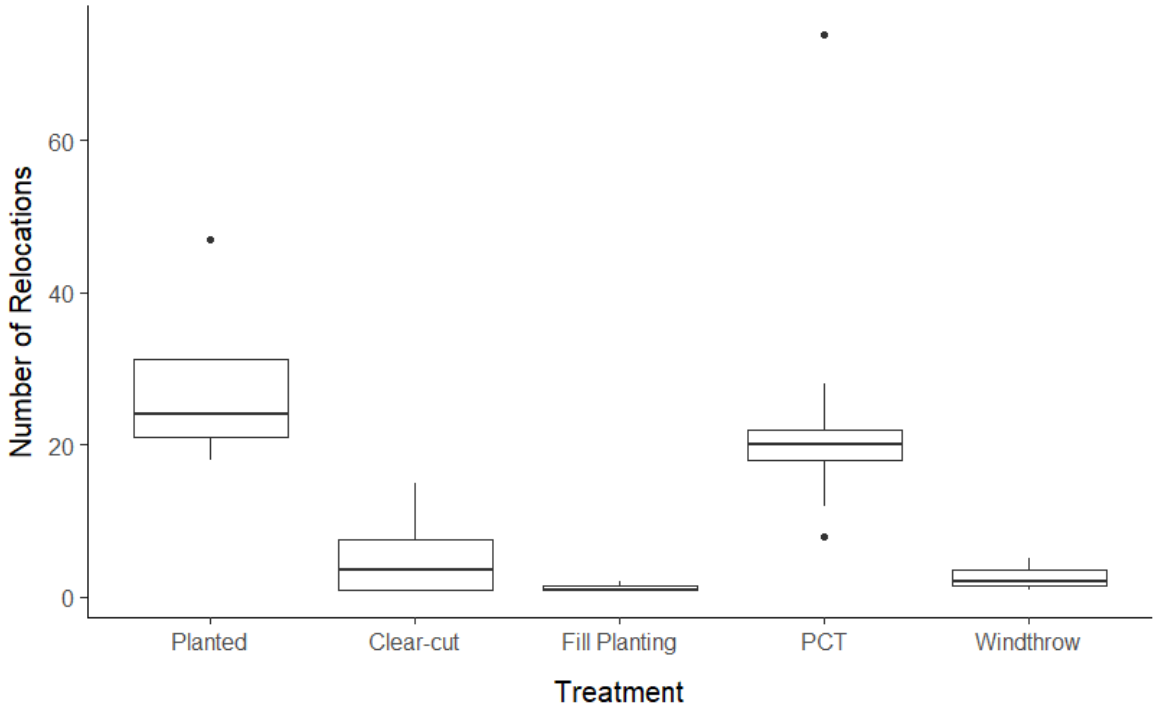

Figure 4.2: Relocations by treatments (planted, clear-cut, fill planting, pre-commercial thinning and windthrow) of male Bicknell's Thrush (*Catharus bicknelli*) tracked during the breeding seasons of 2016 and 2017 in north-central New Brunswick, Canada

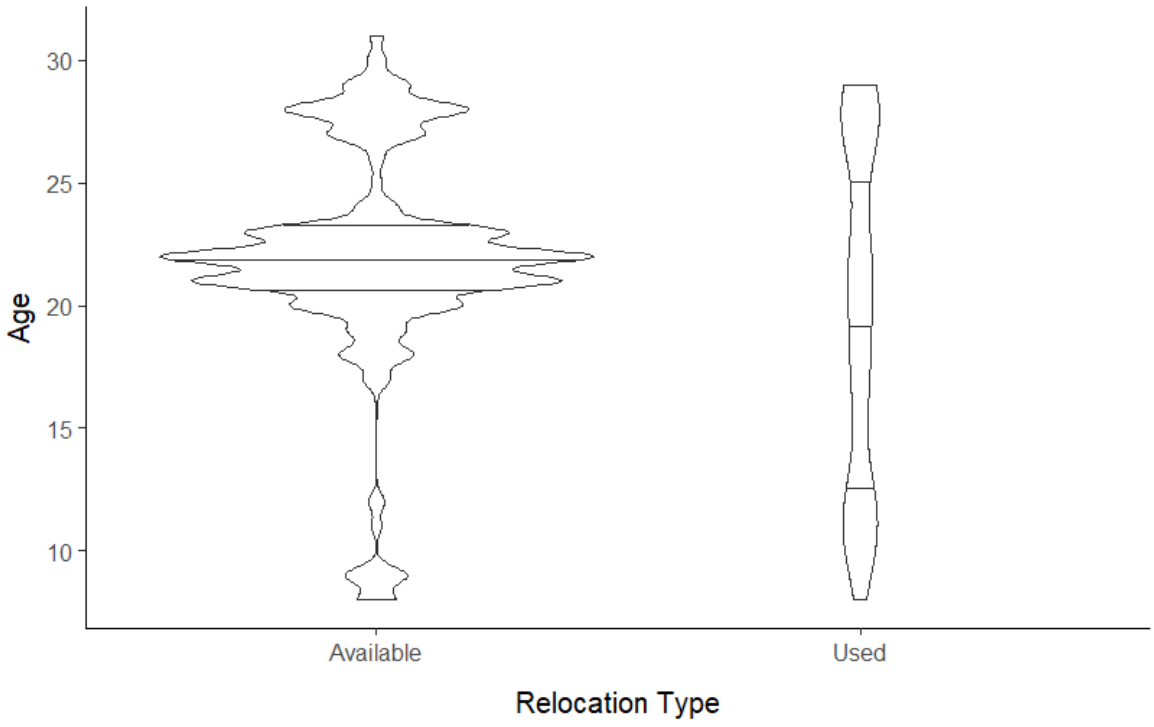

Figure 4.3: Frequency of datapoints at stand ages between used (= relocations) and available locations for stand age. Horizontal bars within violin represent separate quartiles (at 0.25, 0.5 and 0.75.)

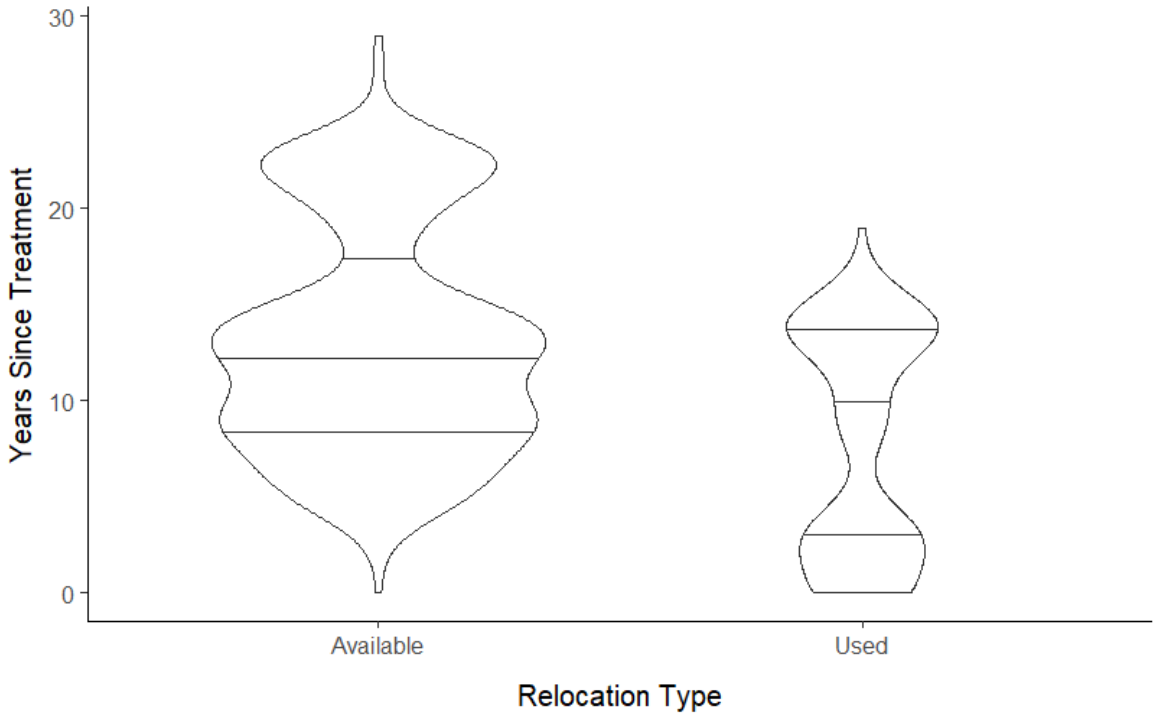

Figure 4.4: Frequency of datapoints at years since treatment between used (= relocations) and available locations for stand age. Horizontal bars within violin separate quartiles (at 0.25, 0.5 and 0.75.)

Generalized Linear Mixed Models

For both sexes all candidate models performed better than the null model (Table 4.2) and favoured more complex models. The top model for males (m1, table 4.3) included year since treatment (-); most recent silviculture treatments of clear-cut (+), PCT (-), non-forested (+), windthrow (+) and planted as the reference (intercept) variable (-); elevation (+); stand age (+) and the interactions between year since treatment and clearcut (-), year since treatment and pre-commercial thinning (+), year since treatment and non-forested (-) and year since treatment and windthrow (-).

One model for females (f1) received most of the AICc weight ($\omega_t = 1$). Model f1 (Table 4.4) included year since treatment (-); most recent silviculture treatments of clear-cut (+), PCT (-), non-forested (-), windthrow (+) and planted as the reference (intercept) variable (-); elevation (+); stand age (-) and the interactions between year since treatment and clearcut (-), year since treatment and pre-commercial thinning (+), year since treatment and non-forested (+) and year since treatment and windthrow (-).

Table 4.2: Model selection results using Akaike's Information Criterium (AICc), describing silviculture treatment characteristics (yr = year since treatment, age = stand age, CC = clear-cut, TI = pre-commercial thinning, BP = planted, WIND = windthrow, ele = elevation, indiv = individual number, date = date of relocation) of Bicknell's Thrush (*Catharus bicknelli*) during the breeding season (May – July) in 2016 and 2017 in north-central New Brunswick, Canada.

Model #	Explanatory Variables	Random Variables	K	AICc	ΔAICc	AICc ω_t
Males						
m1	yr × treat + ele + age	Indiv, date	14	508.68	0	1
m4	yr × treat + ele	Indiv, date	13	559.17	50.49	0
m7	yr + treat + ele + age	Indiv, date	10	584.23	75.55	0
m3	yr × treat + age	Indiv, date	13	641	132.32	0
m6	age × treat + ele	Indiv, date	13	675. 32	166.64	0
m10	age × ele + treat	Indiv, date	10	678.75	170.07	0
m5	treat + ele + age	Indiv, date	9	685.09	176.4	0
m2	yr + ele	Indiv, date	5	703.26	194.58	0
m9	treat + ele	Indiv, date	8	705.61	196.93	0
m8	ele + age	Indiv, date	5	745.07	236.39	0
m.null	1	Indiv, date	3	1057.17	548.48	0
Females						
f1	yr × treat + ele + age	Indiv, date	14	3253.95	0	1
f4	yr × treat + ele	Indiv, date	13	3508.97	255.02	0
f3	yr × treat + age	Indiv, date	13	4482.25	1228.3	0
f7	yr + treat + ele + age	Indiv, date	10	6000.95	2747	0
f6	age × treat + ele	Indiv, date	13	6617.64	3363.69	0
f2	yr + ele	Indiv, date	5	6724.01	3470.05	0
f10	age × ele + treat	Indiv, date	10	6742.34	3488.39	0
f5	treat + ele + age	Indiv, date	9	6914.22	3660.26	0
f9	treat + ele	Indiv, date	8	6923.09	3669.14	0
f8	ele + age	Indiv, date	5	7300.58	4046.63	0
f.null	1	Indiv, date	3	9119.73	5865.78	0

Table 4.3: Parameter estimates (β) on the logit (used habitat) scale from the best model (m1) used to predict male Bicknell's Thrush (*Catharus bicknelli*) habitat use with standard deviations and 95% confidence intervals (LCI, UCI). Continuous parameters (year since treatment [yr], stand age [age], elevation [ele]) were scaled by their root-mean-square. Treatments include clear-cut with no further treatments (CC), pre-commercial thinning (TI), windthrow (WI), non-forested (NF) and planted (intercept term).

	β	LCI	UCI	z-value	p-value
(Intercept)	-54.03	-66.97	-41.08	-8.18	< 0.05
yr	-8.27	-10.53	-6.01	-7.17	< 0.05
treatCC	13.6	-262.25	289.44	0.1	0.92
treatTI	-11.77	-14.31	-9.23	-9.09	< 0.05
treatNF	38.02	-210.07	286.11	0.3	0.76
treatWIND	15.27	-288.82	319.36	0.1	0.92
ele	43.85	32.36	55.33	7.48	< 0.05
age	9.48	6.65	12.31	6.56	< 0.05
yr:treatCC	-72.46	-426.75	281.82	-0.4	0.69
yr:treatTI	8.3	6.03	10.57	7.17	< 0.05
yr:treatNF	-30.93	-289.7	227.85	-0.23	0.81
yr:treatWIND	-16.38	-220.94	188.18	-0.16	0.88

Table 4.4: Parameter estimates (β) on the logit (used habitat) scale from the best model (m1) used to predict female Bicknell's Thrush (*Catharus bicknelli*) habitat use with standard deviations and 95% confidence intervals (LCI, UCI). Continuous parameters (year since treatment [yr], stand age [age], elevation [ele]) were scaled by their root-mean-square. Treatments include clear-cut with no further treatments (CC), pre-commercial thinning (TI), windthrow (WI), non-forested (NF) and planted (intercept term).

	β	LCI	UCI	z value	p-value
(Intercept)	-23.45	-26.67	-20.23	-14.28	< 0.05
yr	-24.47	-26.64	-22.3	-22.15	< 0.05
treatCC	107.85	79.48	136.23	7.45	< 0.05
treatTI	-19.44	-20.8	-18.07	-27.93	< 0.05
treatNF	-31.23	-191.68	129.22	-0.38	0.7
treatWIND	18.4	-156.38	193.17	0.21	0.84
ele	37.51	34.35	40.67	23.27	< 0.05
age	-8.17	-9.27	-7.08	-14.69	< 0.05
yr:treatCC	-177.27	-224.43	-130.11	-7.37	< 0.05
yr:treatTI	36.97	34.25	39.69	26.65	< 0.05
yr:treatNF	25.68	-101.78	153.14	0.39	0.69
yr:treatWIND	-3.61	-188.24	181.01	-0.04	0.97

Discussion

Both male and female Bicknell's Thrush habitat use was explained by models with the same explanatory variables (Table 4.3 and Table 4.4), which is unexpected when considering males showed less preference than females in compositional analysis (Chapter 3), and tend to overlap home-ranges (and therefore their habitat) with multiple females (Chapter 2, Collins 2007, McFarland et al. 2008, Aubry et al. 2011). The retained variables in the final model reflect a slightly more complex dynamic between age and treatment than compositional analysis found in Chapter 3. The habitat types of windthrow (WIND) and non-forested (NF) were retained in the top models, however large confidence intervals including zero suggest the effects are not important. These two variables probably suffered from a lack of sufficient samples (Figure 4.1 and Figure 4.2). Despite stand age and year since treatment of some treatments (e.g., clear-cut) being similar, both age-type terms (year since treatment and stand age) were retained in the top models, suggesting that not only is age of the stand important but also how long since a treatment has occurred. However, this only applies to thinned habitat since stand age is equal to time since treatment for windthrow, clearcut and planted treatments. The final models of both sexes also included interaction terms between years and the most recent treatments, suggesting that Bicknell's Thrush are responding differently over time, depending on treatment.

The strong (compared with the scaled continuous variables of stand age and year since treatment) positive effect of elevation is unsurprising considering Bicknell's Thrush are high elevation specialists. Although previous studies have strongly suggested that Bicknell's Thrush require young, dense forests in their breeding habitat (Townsend et al.

2015), these choices are apparently made after a landscape-wide site at an elevation level has been selected by an individual, as individuals still prefer higher elevations even within a high elevation landscape. Interestingly, male and female habitat use was influenced by stand age differently: females were less likely to be present in older forests, and males more likely, despite all being tracked within the same area. Stand age, at high elevations relative to the surrounding landscape, may have a more flexible influence on habitat use, similarly to a recent study on Bicknell's Thrush in Quebec (Aubry et al. 2018), where the interaction between a positive stand age estimate and a negative stand age by elevation interaction was interpreted as a lower effect of stand age at higher elevations.

The most recent treatment of clear-cut had a positive effect compared with planted sites on both male and female Bicknell's Thrush, although the confidence interval around the estimate for males suggests the effect is doubtful for that sex. The difference between the two treatments is surprising considering females seemed to prefer planted sites in compositional analysis (Chapter 3). However, the interaction between clear cut and time since treatment amplifies the negative effect of year when the area has been clear cut. This may indicate that Bicknell's Thrush prefer naturally regenerating forests, but the structure of uniform, densely planted trees in plantations may encourage individuals to remain in planted sites longer. Areas post clear-cut are essentially "natural regrowing forests," and in the highlands of New Brunswick, have similar species composition as planted sites (Erdle and Pollard 2002). Planted sites are characterized by slightly less (~2%) balsam fir (*Abies balsamea*), more (~5%) black spruce (*Picea mariana*), a reduction of about half (~5%) in white spruce (*P. glauca*) and the loss of red

spruce (*P. rubens*), when compared to natural forests in the same ecoregion (Erdle and Pollard 2002). Bicknell's Thrush have been associated predominantly with balsam fir and red spruce (Erskine 1993, Ouellet 1993, Nixon et al. 2001, Connolly et al. 2002, McKinnon et al. 2014), so they may more readily inhabit stands with both tree species.

Unsurprisingly, pre-commercial thinning had a negative effect compared to planted sites for both sexes. Several authors have found PCT to decrease the suitability of habitat to Bicknell's Thrush (Chisholm and Leonard 2008, Aubry et al. 2016, Aubry et al. 2018). However, areas treated with PCT also reduced the negative effect of year since treatment to near zero in males (Table 4.3) and reversed the effect to a positive in females (Table 4.4). Both clear-cuts and planted sites maintain negative effects of year since treatment, whereas PCT forests increase likelihood of use beyond the negative effects of years since treatment. I interpret this positive effect over time to mean that older PCT sites are more likely to support Bicknell's Thrush than sites immediately post-thinning.

Pre-commercial thinning is an intensive disturbance that significantly alters forest stand structure (Ker 1981) and has both immediate and longer-term impacts on Bicknell's Thrush. In young, dense coniferous habitat, nests are often concealed in between several nearby trees 2-4 meters high (Townsend et al. 2015); and in habitat with stem densities up to 35 000/ha (Aubry et al. 2011), the likelihood of a thinning technician discovering a nest (and therefore ceasing to cut) while operating is low. Detecting Bicknell's Thrush is made more difficult because they typically call or sing only before dawn and after sunset (Ball 2000), and a single visit is rarely enough to detect the species (Nixon et al. 2001). PCT should therefore not be conducted during the breeding season because technicians are unlikely to detect either the birds or their nests. Further, immediately after thinning,

the habitat is unsuitable as trees between 5 - 10 cm in diameter (or 2 - 7 m in height) are spaced 2 - 4 meters apart, with little understory growth.

However, considering Bicknell's Thrush are more likely found in forests up to 30 years old and 70 years and older (Aubry et al. 2018), individuals may re-occupy areas once thinned habitat has regrown to satisfy forest structure requirements of the species. In Maine, Weiskittel et al. (2009) found that PCT increased crown widths of red spruce and balsam fir by 95.6 and 75.1% twenty-five years after thinning, as well as crown ratio (height of crown/tree height) to increase by 43.2 and 58.1% compared to control plots that had no PCT treatment. Further, Pitt and Lanteigne (2008) found that in New Brunswick, crown areas rapidly increased during early stand development (10-20 years after thinning) in balsam fir and red spruce at elevations between 300 and 450 meters, with a high degree of canopy layering. Combined with a 10% increase in number of branches between one and two meters above breast height (2.3 – 4.3 meters, Weiskittel et al. 2009), these properties may indicate characteristics that encourage Bicknell's Thrush occupancy as thinned forests age.

New Brunswick, and in particular the present field site, contains more thinned habitat than in Quebec and Vermont (McFarland et al. 2008, Aubry et al. 2011, Chapter 3) where previous radio-tracking studies were conducted. With substantially more thinned habitat (less "optimal" habitat), an alternative explanation to individuals using thinned forests could be that a lack of preferred habitat is forcing individuals to use sub-optimal areas. Yet, Bicknell's Thrush inhabit the landscape in a clumped pattern (Townsend et al. 2015), and recent work by Aubry et al. (2018) has suggested that the species leaves substantial potential habitat unoccupied. Further studies that examine the

effects of PCT on nest success of individuals nesting in pre-commercially thinned habitat would help to identify if birds nesting in these areas are incurring negative effects associated with the habitat.

A drawback of the current study is the young age of the forest currently occupied by tracked individuals. Indeed, most studies in New Brunswick (Nixon et al. 2001, Chisholm 2005, McKinnon 2006, Chisholm 2008, Askanas 2008, Mckinnon et al. 2014) have worked on Bicknell's Thrush in young, typically post-harvest, forests, following the windthrow of 1994. Actually, much of New Brunswick's forest is "post harvest" forest; however, the high elevation area surrounding the current study site was comprised of 60 – 80 year old balsam fir until the windthrow event in 1994 (Morrison 2001). Birds Canada's first Maritime Breeding Bird Atlas, conducted between 1988 and 1990, suggests that Bicknell's Thrush (then identified as a subspecies of Gray-Cheeked Thrush, *Catharus minimus*) occupied this high elevation area pre-blowdown (Erskine 1993). In Quebec, Aubry et al. (2018) showed older forests were occupied by Bicknell's Thrush more frequently than not. With current monitoring focused on typical, young forested habitats, the occupancy and use of older, high elevation forests (e.g., Mount Carleton or the Freeze Lakes) of Bicknell's Thrush in New Brunswick would be an important research topic for this species.

By modelling habitat use of Bicknell's Thrush according to forestry treatments, elevation and time, I found that these predictors affect Bicknell's Thrush similarly to previous studies (Hill and Lloyd 2017, Aubry et al. 2018). Elevation seems to have the strongest effect on habitat use of the species, with the likelihood of use decreasing as both stand age and time since the most recent treatment increases (but limited to young

forests). Further, I identified that Bicknell's Thrush may inhabit pre-commercially thinned habitats as these forests age. It may seem obvious that forests regrow into space freed up by thinning as the stand ages, however current management still assumes Bicknell's Thrush will not inhabit forests treated with PCT regardless of age. Silviculture managers should still be cautious when prescribing pre-commercial thinning to areas that are within Bicknell's Thrush potential habitats, but conservation managers may want to reassess the suitability of older forests at high elevations for this species.

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CHAPTER 5 – DETERMINING NEST SUCCESS AND NEST SITE HABITAT IN BICKNELL'S THRUSH (*CATHARUS BICKNELLI*)

Introduction

Bicknell's Thrush (*Catharus bicknelli*) is a threatened (COSEWIC 2009) songbird that nests in high elevation coniferous forests in north-eastern United States and eastern Canada (Townsend et al. 2015). In New Brunswick (NB), Bicknell's Thrush nest at high elevations in the north-central and north-western parts of the province in industrial forests (Nixon et al. 2001). In these industrial forests, Bicknell's Thrush come into direct contact with anthropogenic effects of silviculture such as tree harvesting (in the form of clear-cutting in NB) and pre-commercial thinning (McKinnon et al. 2014). The direct effects of these silviculture treatments are obvious, with the reduction of habitat in the short term from clear-cutting and reduced habitat suitability from pre-commercial thinning (Townsend et al. 2015). However, Bicknell's Thrush seemingly prefer young forests (5-25-year-old, Ouellet 1993, Connolly et al. 2002), so clear-cuts actually create habitat as regrowth occurs. Pre-commercial thinning of forests, on the other hand, has been assumed to permanently decrease habitat suitability for Bicknell's Thrush, as it greatly reduces stem density (Chisholm and Leonard 2008, Aubry et al. 2011). One hypothesis to explain Bicknell's Thrush preference for thick forests is that they increase nest protection. A previous study in NB has shown that individuals select nest sites with high densities of young conifer stems compared with random plots, and yet almost half (44%) of habitat within 500 meters from nests was thinned (McKinnon et al. 2014). Further, research has shown preferences for forest edges in Bicknell's Thrush nests (McFarland et

al. 2008), and thinned forest occurs within Bicknell's Thrush home ranges in Quebec (Aubry et al. 2011) and in NB (McKinnon et al. 2014), with some authors suggesting that thinned forests might be used by Bicknell's Thrush as long as patches of unthinned forest are available, presumably for nesting (McKinnon et al. 2014). However, no studies have reported nesting success at these sites.

Assessing productivity of a bird species in a specific habitat is important when determining suitability of that habitat for that species, especially when density or abundance estimates of individuals may not correlate with productivity (Van Horne 1983). One method of determining success is monitoring nests until young have fledged or the nest has failed, with regular visits to check on growth. These repeated visits are labour intensive, and despite being shown to have little effect on nest success in songbird nests (Ortega et al. 1997, Skagen et al. 1999, Weidinger 2008), especially in areas with high human traffic (Mayer-Gross et al. 1997, Weidinger 2008), the risk of attracting predators to human activities (Gutzwiller at al. 2002) and the creation of open spaces in thick regrowth around Bicknell's Thrush nests suggests an alternative may be more appropriate in this system. Different tactics have been used to reduce observer effects on nests, such as remote monitoring via video (Thompson et al. 1999) and nest temperature (Weidinger 2006). Remotely monitoring nest behaviours with temperature has been used for over 60 years (Howell and Dawson 1954, Zerba and Morton 1983, Joyce et al. 2001), however the miniaturization of technology has allowed low-cost, low-impact temperature recording devices to be used instead of bulky tools that sometimes require partial destruction of clutches (e.g., Zerba and Morton 1983). The use of temperature loggers to measure survival of songbird nests has been validated (Weidinger 2006), and I use them

here to evaluate success of Bicknell's Thrush nests. iButtons, small (17 mm) temperature data loggers, have been used successfully for detecting incubation and predation events (Hartmann and Oring 2006). The small size, long battery life, and large storage space of iButtons allow nests to be monitored remotely and greatly reduce disturbance to nests.

The goal of this chapter is to compare nest site habitat with surrounding habitat of nests found within an industrial forest in north-central New Brunswick, describe nest placement associated with differently treated forests, and report nesting success of Bicknell's Thrush. I hypothesize that nests will be found in dense, young forests untreated with PCT with higher stem densities than random plots and will be more successful in these habitats.

Methods

Field Methods

I used the same methods as chapters 2, 3 and 4 for capturing and radiotracking birds. Birds were captured in mistnets, measured, banded and tagged with VHF radio transmitters (Lotek Pip Ag376). Tags weighed between 2.8 and 3.7% of the individual's body mass and were attached via the backpack method (Rappole and Tipton 1991). Transmitters were assumed to have negligible effect on behaviour (Townsend et al. 2012). Females were tracked to nests while incubating eggs or young. Care was taken as signal strength of transmitters increased (i.e., distance to nest decreased) to not accidentally flush or disturb the nest without locating it. Once found, the nest's location, number of eggs or young, age of young, and nest support structures (tree species, placement on tree and nest height) were recorded.

Changepoint Analysis and Nest Success Determination

In 2017, technicians determined nesting stage using small temperature data loggers (TDL; Thermochron iButtons, model # DS1921G-F5, 17.35 mm in diameter by 5.89 mm height, 4.5 grams) wrapped in black nylon cloth to blend in with the nest materials. Technicians placed TDLs in nest cups in the corner of cup, next to eggs or young, and attached it to the nest with wire that went through the cup and locked on the outside to keep the logger from being removed (Figure 5.1, Walters et al. 2016). Technicians collected TDLs when the female had either begun incubation at another location (determined by radiotracking) or after 30 days of deployment (exceeding a Bicknell's Thrush nesting period, Townsend et al. 2015). To obtain a corresponding measurement of ambient temperature, technicians placed TDLs in trees within 5 meters from nests at similar height and shade. Loggers recorded temperature (± 0.5 ºC) every twenty minutes until memory reached capacity (>30 days of recording).

Figure 5.1: Bicknell's Thrush (*Catharus bicknelli*) nest viewed from above with four eggs and iButton temperature logger.

I estimated nest vacancy date by determining a change point in both variance and mean using the "changepoint" package (Killick and Eckley 2014) in the R Statistical Environment (R Core Team 2019) of the time and temperature data offloaded from iButtons. Using the *cpt.meanvar* function, I looked for a single changepoint in both mean and variance of nest temperature using the "At Most One Change" (AMOC) method and a modified Bayes Information Criterion (MBIC, Zhang and Siegmund 2007). I plotted temperature of each nest and its associated ambient temperature recorded by time with the changepoint to verify changepoints represented when nest temperature began to parallel to ambient temperature (i.e., nest temperature = ambient temperature and an empty nest).

Nest success was determined similar to Weidinger (2006), where potential fledging dates were estimated by adding potential fledging age to estimated age of nest occupants. In Bicknell's Thrush, incubation and fledging periods range from 9-14 days each, with mean clutch sizes between 3-4 (Wallace 1939). For nests that contained eggs, my calculation of earliest potential fledging age depended on the number of eggs present, where nests that had 3 or 4 eggs could hatch within one to nine days, and nests with fewer than three eggs would be nine plus a day for each egg up to three. I then added an additional nine days for chick brooding. For nests that contained chicks, I first visually estimated chick age (1 – 3 days, 4 – 6, days, 7 – 9 days, 9 – fledge). With estimated chick age, I subtracted the lowest chick age within the age classification range from the potential fledging age (nine days), which gave the number of days until earliest potential fledging date. Nest fate was classified as survived or failed dependent on nest vacancy date determined by TDLs occurring before or after the earliest potential fledging date. I

estimated a hatching date range by subtracting fledging period ranges back from nest vacancy date on successful nests.

Nest Site Habitat Variables

Nesting habitat variables were sampled after nests were vacated by birds (when possible) or when recovering iButtons from active nests. Methods used were similar to McKinnon et al. (2014). I counted number of trees of each species within a 5 m radius of each nest or center point, while visually estimating average canopy height to the nearest meter of the sample plot. Both Chisholm and Leonard (2008) and McKinnon et al. (2014) were conducting their studies in younger forests with smaller diameter trees, and used size classes of 0 - 2.5 cm, >2.5 cm – 5 cm, and >5 cm. I deviated from these previous size classes because a third of the nests found were in older forest stands with much different age classes than young forest which would not have been captured with McKinnon et al.'s (2014) or Chisholm and Leonard's (2008) methods. Additionally, McKinnon et al. (2014) found no significant effects of tree size in their model. I classified trees into three size classes: small (0-8cm), medium (8.1-16cm), and large (>16cm). A plot 100m away in a randomly selected direction was surveyed and paired with each nest. Paired plots that were selected in obvious non-nesting habitat (i.e., roads) were reselected by drawing a new azimuth from the nest plot.

Nest Habitat Modelling

To assess nesting habitat, I used a binomial generalized linear regression with a logit link to model Bicknell's Thrush nesting sites (1) and random plots (0) described in Habitat Variables. I considered stem density (dens), proportion of balsam fir (*Abies*

balsamea) small, medium, large and total balsam fir (p.bf.s/m/l/t), proportion deciduous species (p.dec), canopy height (canopy), and density of large trees (d.lg) as potential predictors, with individual (tag.num) as a random effect. All variables were calculated from vegetation plot data collected in the field (see Habitat Variables). All numeric covariates (except tag.num) were scaled by the root mean square.

I used the same model selection framework in this chapter as Chapter 4, but conducted model averaging for models of similar AIC. For model averaging, I selected the top models within 95% cumulative model weight and identified their full average weights and significance using the model.avg function from the "AICcmodavg" package. All modelling was computed in the R Statistical Environment (R Core Team 2019), using the packages "lme4" (Bates et al. 2015), "MuMIn" (Barton 2019), and "AICcmodavg" (Mazerolle 2019).

Results

Nest Placement and Fate

I monitored seven Bicknell Thrush nests from five females with TDLs in the summer of 2017. I was unable to analyze two of the seven nests which were second attempts late in the season and were not followed to their conclusion. Of the five nests analyzed, two were with eggs and three with chicks. All seven changepoints calculated reflected points where nests returned to ambient temperature (Figures 5.2 – 5.7). I classified four nests as successful breeding attempts (Table 5.1).

Four of five female Bicknell's Thrush nested in thinned habitat (Table 5.2). One female whose nest failed, moved from thick regrowth post-clear cut to thinned habitat.

Nests were found between one and two meters from the ground and were mostly between two to four trunks of young balsam fir (Table 5.2).

Table 5.1: Estimated success of Bicknell's Thrush (*Catharus bicknelli*) nests monitored in north-central New Brunswick, Canada during the 2017 breeding season. Success was determined by comparing vacancy date (calculated as a changepoint in the mean and variance of nest temperature) to earliest potential fledging date.

Nest	Indiv. Tag #	Date Found	Number of Young					Earliest potential fledging date	Nest Vacancy Date	Success / Fail
			Eggs	1-3d chick	4-6d chick	7-9d chick	>9d chick			
A	85055	June 27	-	-	-	2	-	June 28	July 2	Success
B	85046	June 27	3	-	-	-	-	July 6	July 1	Fail
C	85048	June 28	-	2	-	-	-	July 4	July 9	Success
D	85047	June 28	4	-	-	-	-	July 7	July 12	Success
E	85023	June 28	-	4	-	-	-	July 4	July 5	Success
F	85048	July 13	4	-	-	-	-	July 22	n/a	n/a
G	85046	July 20	-	2	-	-	-	July 26	n/a	n/a

Table 5.2: Nest structure and general habitat characteristics of Bicknell's Thrush (*Catharus bicknelli*) nests in north-central New Brunswick, Canada during the 2017 breeding season. Diameter at breast height (DBH) and tree height were measured on trees that nests were directly attached to. Nests by the same individual are represented by stars.

Nest	Fail / Success	Treatment – Year	Nest Support Characteristics			
			Tree Spcs	DBH/Height	Loc. on Tree	Nest Height
A	Success	Thinned – 2004	Balsam fir (*Abies balsamea*)	5 cm/ 2.5 m	Between three trunks	1.8 m
B*	Fail	Clearcut – 1995	Red spruce (*Picea rubens*)	10 cm/5 m	Between two branches	1 m
C**	Success	Thinned – 2003	Balsam fir (*Abies balsamea*)	5 cm/3 m	Between three trunks	1.5 m
D	Success	Thinned – 2003	Balsam fir (*Abies balsamea*)	10 cm/5 m	Between two branches	1.5 m
E	Success	Planted – 2008	Balsam fir (*Abies balsamea*)	5 cm/2.5 m	Between two trunks	2 m
F**	n/a	Thinned – 2003	Balsam fir (*Abies balsamea*)	5 cm/2.5 m	Between four trunks	1.5 m
G*	n/a	Thinned – 2003	Red spruce (*Picea rubens*)	10 cm/5 m	On single branch	1.5 m

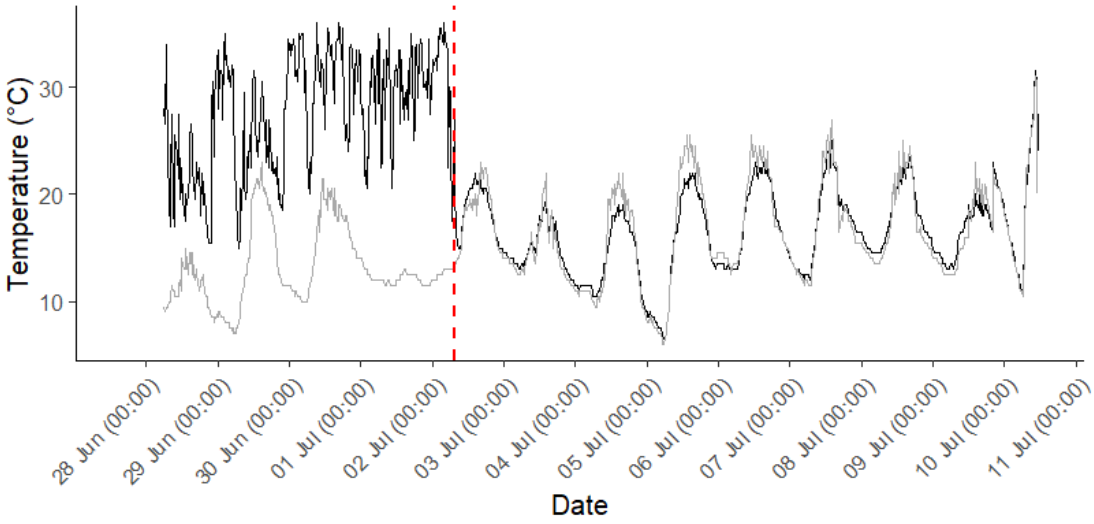

Figure 5.2: Temperature of Bicknell's Thrush (*Catharus bicknelli*, female 85055, nest A) nest and ambient environment found in north-central New Brunswick, Canada during the 2017 breeding season. Nest temperature was recorded using Thermochron iButtons placed within the nest cup as well as on a tree at similar height and shade as the nest 5 meters away. Dashed, vertical red line indicates time that nest was vacated, calculated as a mean and variance changepoint.

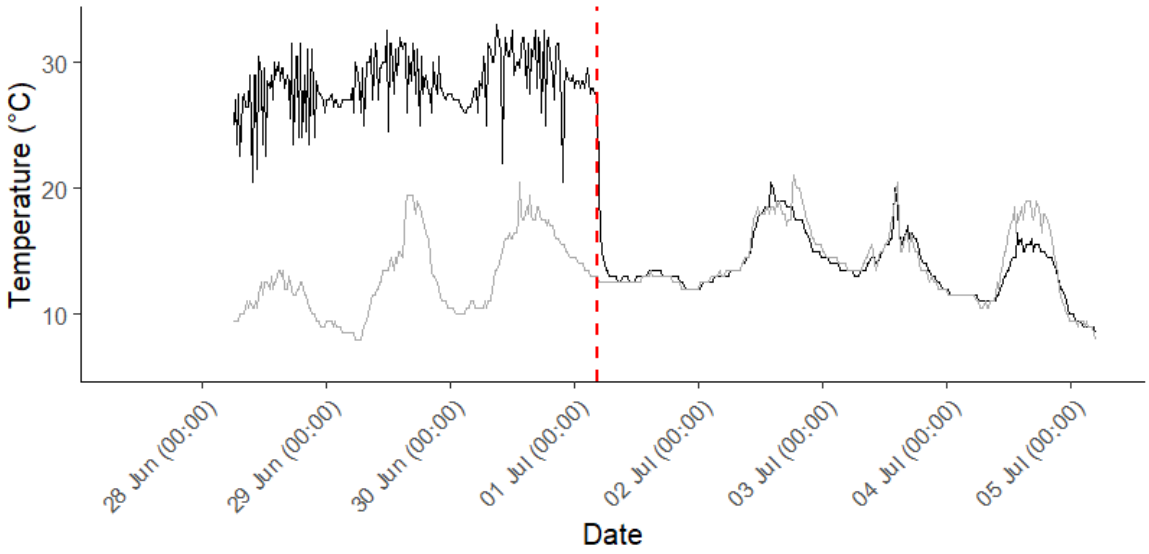

Figure 5.3: Temperature of Bicknell's Thrush (*Catharus bicknelli*, female 85046, nest B) nest and ambient environment found in north-central New Brunswick, Canada during the 2017 breeding season. Nest temperature was recorded using Thermochron iButtons placed within the nest cup as well as on a tree at similar height and shade as the nest 5 meters away. Dashed, vertical red line indicates time that nest was vacated, calculated as a mean and variance changepoint.

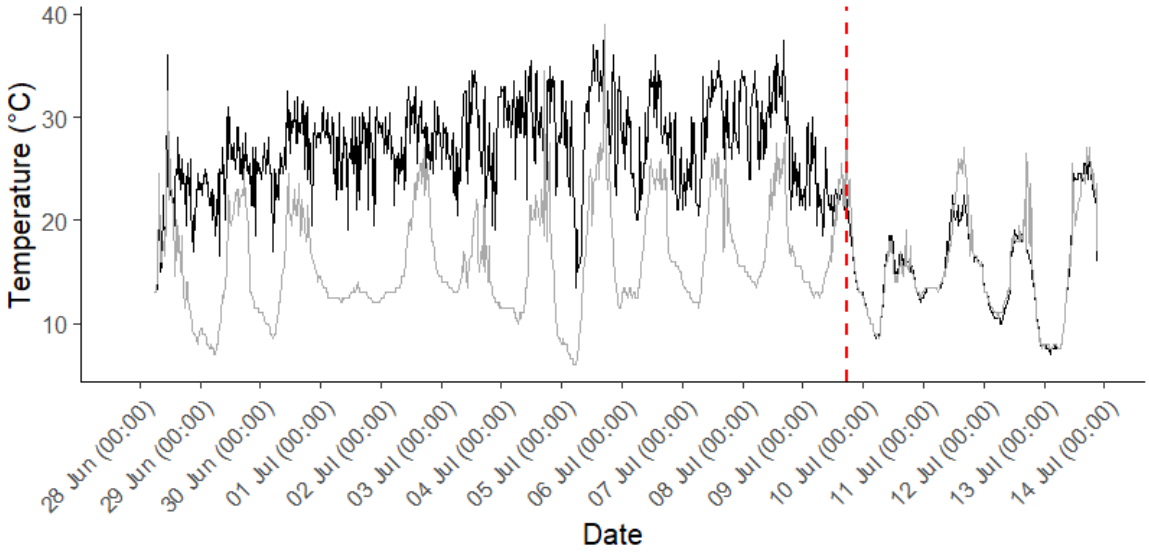

Figure 5.4: Temperature of Bicknell's Thrush (*Catharus bicknelli*, female 85048, nest C) nest and ambient environment found in north-central New Brunswick, Canada during the 2017 breeding season. Nest temperature was recorded using Thermochron iButtons placed within the nest cup as well as on a tree at similar height and shade as the nest 5 meters away. Dashed, vertical red line indicates time that nest was vacated, calculated as a mean and variance changepoint.

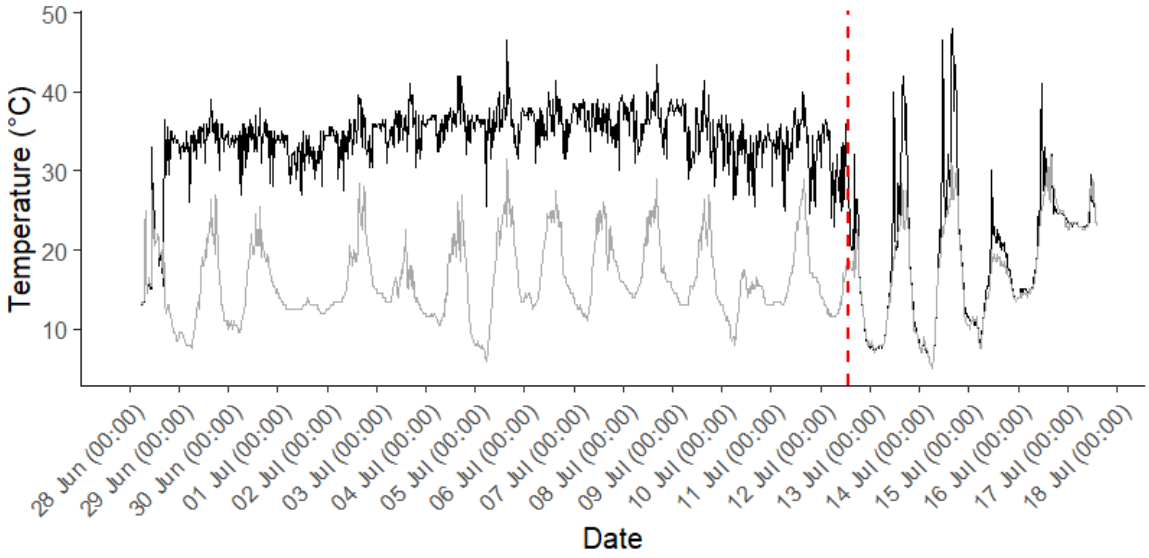

Figure 5.5: Temperature of Bicknell's Thrush (*Catharus bicknelli*, female 85047, nest D) nest and ambient environment found in north-central New Brunswick, Canada during the 2017 breeding season. Nest temperature was recorded using Thermochron iButtons placed within the nest cup as well as on a tree at similar height and shade as the nest 5 meters away. Dashed, vertical red line indicates time that nest was vacated, calculated as a mean and variance changepoint.

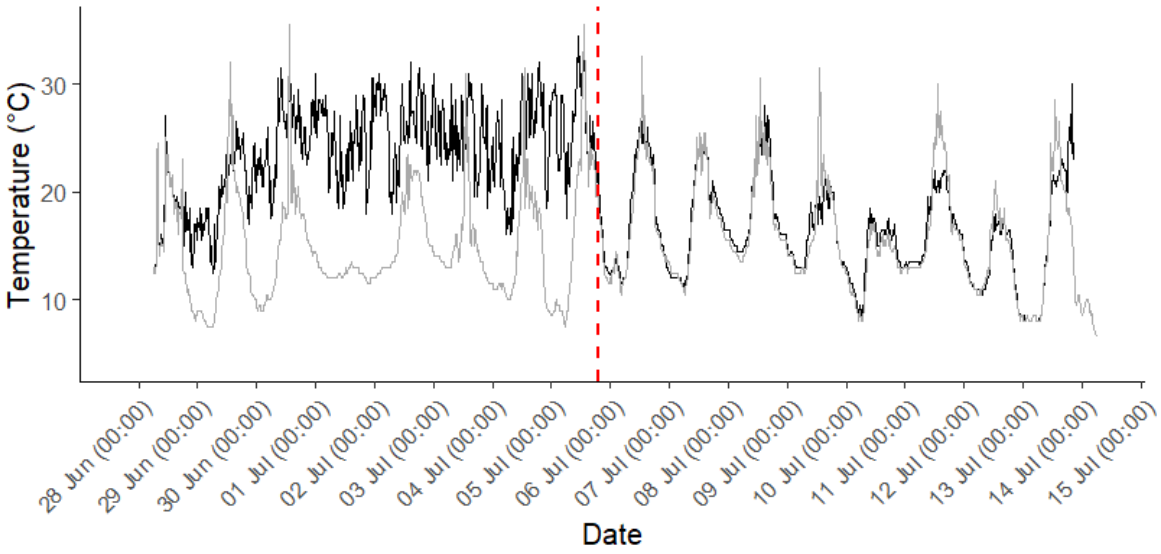

Figure 5.6: Temperature of Bicknell's Thrush (*Catharus bicknelli*, female 85046, nest E) nest and ambient environment found in north-central New Brunswick, Canada during the 2017 breeding season. Nest temperature was recorded using Thermochron iButtons placed within the nest cup as well as on a tree at similar height and shade as the nest 5 meters away. Dashed, vertical red line indicates time that nest was vacated, calculated as a mean and variance changepoint.

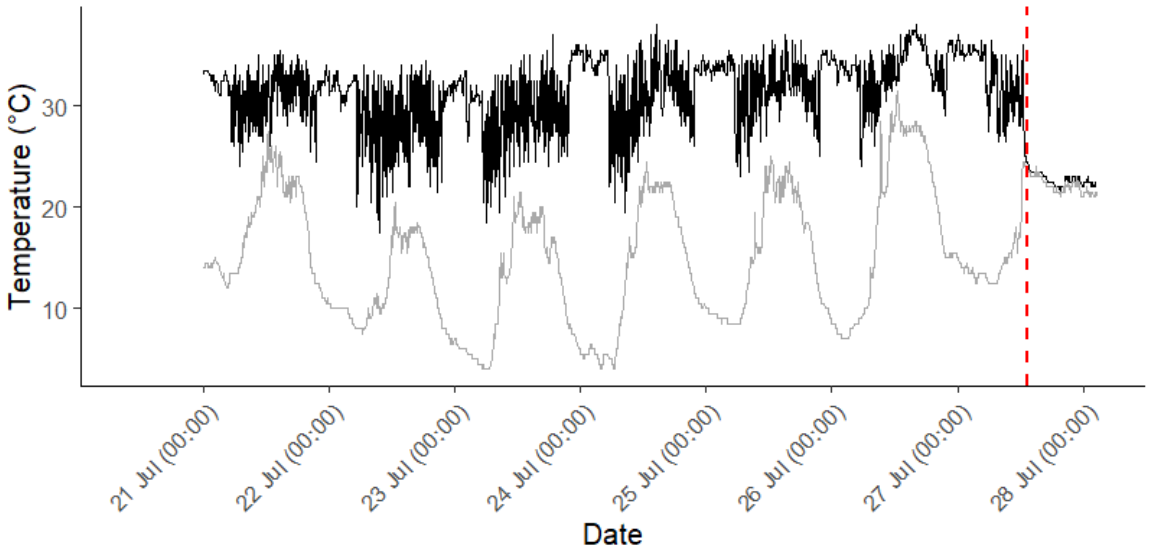

Figure 5.7: Temperature of Bicknell's Thrush (*Catharus bicknelli*, female 85048, nest F) nest and ambient environment found in north-central New Brunswick, Canada during the 2017 breeding season. Nest temperature was recorded using Thermochron iButtons placed within the nest cup as well as on a tree at similar height and shade as the nest 5 meters away. Dashed, vertical red line indicates time that nest was vacated, calculated as a mean and variance changepoint.

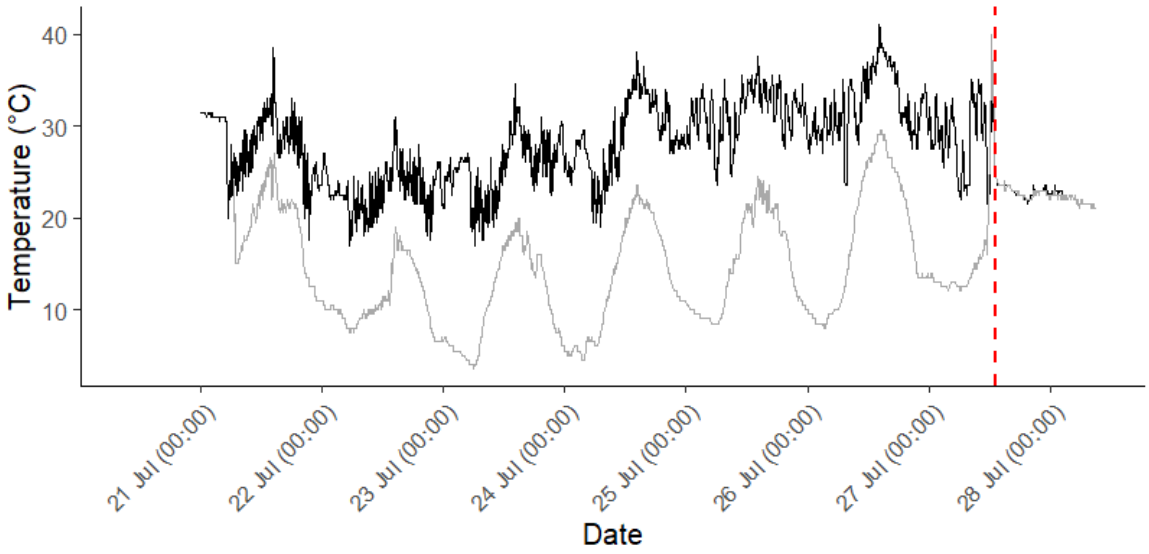

Figure 5.8: Temperature of Bicknell's Thrush (*Catharus bicknelli*, female 85046, nest G) nest and ambient environment found in north-central New Brunswick, Canada during the 2017 breeding season. Nest temperature was recorded using Thermochron iButtons placed within the nest cup as well as on a tree at similar height and shade as the nest 5 meters away. Dashed, vertical red line indicates time that nest was vacated, calculated as a mean and variance changepoint.

Nest Site Habitat

Five out of eight candidate models received substantial AIC weight ($\omega t > 0.05$, Figure 5.9, Table 5.3), and were all within two ΔAIC units of the best model. All but one model supported stem density as a predictor, three models supported some form of proportion of balsam fir, and only one model included proportion deciduous (Figure 5.9, Table 5.3). In the model with lowest AIC, nest presence was best modelled by an intercept term, stem density, proportion of large balsam fir trees, and the density of large trees, all non-significant (Table 5.4), with a residual deviance of 29.959 on 22 degrees of freedom. The null model, including just an intercept term, had a deviance of 36.044 on 25 degrees of freedom. Full model averaging showed no significance for any predictor (Table 5.5).

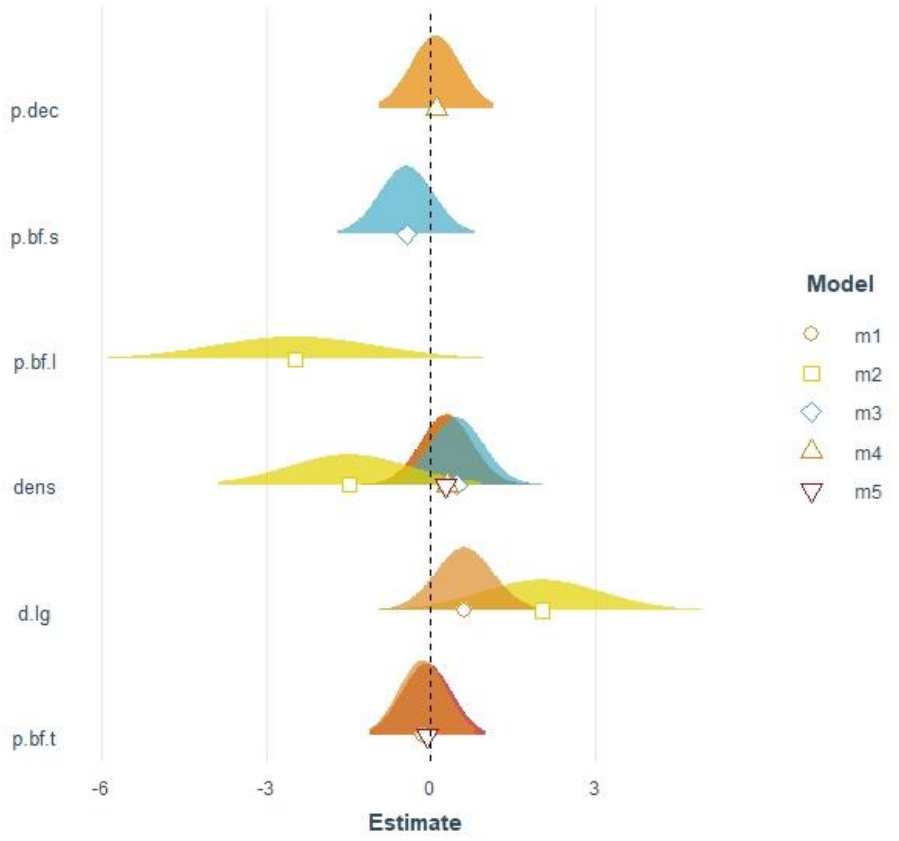

Figure 5.9: Variable summary plot of models describing nesting characteristics (p.dec = percent deciduous, p.bf.s = percent small balsam fir (< 8 cm), p.bf.l = percent large balsam fir (*Abies balsamea*) (> 16 cm), dens = stem density, d.lg = density of large stemmed trees (> 16 cm), p.bf.t = percent of total balsam fir) of Bicknell's Thrush (*Catharus bicknelli*) with model weight > 0.05.

Table 5.3: Model selection results using Akaike's Information Criterion (AICc), describing nest patch characteristics (p.dec = percent deciduous, p.bf.s = percent small balsam fir (< 8 cm), p.bf.l = percent large balsam fir (> 16 cm), dens = stem density, d.lg = density of large stemmed trees (> 16 cm), p.bf.t = percent of total balsam fir) of Bicknell's Thrush during the breeding season (May – July) in 2016 and 2017 in north-central New Brunswick, Canada. Models with > 0.05 model weight (ωt) are shown.

Name	Model	ΔAICc	ω_t	K
m1	dens + p.bf.l + d.lg	0	0.27	5
m2	p.bf.t + d.lg	0.63	0.20	4
m3	dens + p.bf.s	1.05	0.16	4
m4	dens + p.dec	1.72	0.11	4
m5	dens + p.bf.t	1.74	0.11	4

Table 5.4: Parameter estimates (β) on the logit (presence) scale from the best model (m1) used to predict Bicknell's Thrush nest presence with standard deviations (SE) and 95% confidence intervals (LCI, UCI).

Parameter	β	SE	LCI	UCI
(Intercept)	6.1523	4.35	-3.25	15.56
dens	-0.9289	0.69	-2.43	0.57
p.bf.l	-16.2077	9.77	-38.72	6.31
d.lg	8.1895	4.40	-5.19	21.57
Observations		26		
R^2 (Tjur)		0.218		

Table 5.5: Parameter estimates of model averages for models predicting the presence of Bicknell's Thrush (*Catharus bicknelli*) nests using habitat patch characteristics surrounding nests and a paired patch 100m away in a random direction.

Parameter	Estimate	Standard Error	Adjusted Standard Error	z-value	*p*	Sum of Weights	N containing models
(Intercept)	2.59655	4.44895	4.5801	0.567	0.571	-	-
dens	-0.31725	0.73375	0.75315	0.421	0.674	0.8	4
p.bf.l	-7.03936	10.29356	10.53146	0.668	0.504	0.63	2
d.lg	4.05796	4.82217	4.93606	0.822	0.411	0.43	1
p.bf.t	-0.14328	1.07998	1.13716	0.126	0.9	0.3	2
p.bf.s	-0.35092	1.29366	1.33731	0.262	0.793	0.16	1
p.dec	0.04557	0.66034	0.69552	0.066	0.948	0.11	1

Discussion

Surprisingly, most of the nests found during the breeding season of 2017 were in habitat that had been thinned 10-15 years prior. The 80% nest success rate within these habitats suggest that Bicknell's Thrush may not be incurring a breeding disadvantage when nesting within thinned forest. However, one female that had been estimated as having fledged her young successfully started another brood shortly after her success. Since nest success is calculated by comparing nest vacancy and earliest possible fledging, it is possible that the first nest had been depredated before or around fledging date and was mis-identified as successful. It is impossible to determine if her young were depredated after fledging, but it is likely considering Bicknell's Thrush tend not to have more than one brood per breeding season (Townsend et al. 2015). Regardless, female Bicknell's Thrush choosing older, thinned habitat for nesting is not necessarily surprising when considering previous work by McFarland et al. (2008), who found 57 – 62% of nests within 100 meters of an edge to be within the 10 meters closest to the forest edge, and Aubry et al. (2011) who showed that Bicknell's Thrush were not edge averse. Within thinned habitat in the present field site, the forest is segmented into "lanes" of open, unforested areas with vigorous conifer growth on either side. These alternating lanes and thick forest could mimic edge effects throughout the thinned forest stand, providing easy access to thick cover for nests. Similarly, McKinnon et al. (2014) came to a related conclusion, suggesting a matrix of thinned and unthinned habitat may be enough to support Bicknell's Thrush breeding in industrial forests as an average of 44% of home ranges around nests contained thinned habitat. In this system, Bicknell's Thrush may

prefer dense forest for nest cover immediately around their nest but prefer to have easy access to that nest in the form of proximity to edges.

Predators account for most nest failures of forest songbirds (Ricklefs 1969, Martin 1995); however, the effects of silviculture on predation rates, especially related to edge effects, are unclear (King and DeGraaf 2000, Bourque and Villard 2001 Barber et al. 2001), and seem to vary depending on predator abundance and diversity (Carignan and Villard 2002). Although a very small sample size, these results indicate that at least some individuals nesting in thinned habitats can fledge successfully. Further studies that identify predator abundance and fledge success over multiple years in differing forest habitats that are characteristic of industrial forests would be able to identify whether Bicknell's Thrush are commonly successful in PCT forests.

Unlike McKinnon et al. (2014), I found no pattern or significant predictors for Bicknell's Thrush nest site selection within an industrial forest. One factor that may have influenced these results is the homogeneous forest within treatment blocks where random comparison plots were selected. Although the current study was unable to show any significant predictors of nest site selection, previous research in New Brunswick has identified increases in total tree density and decreases in proportion of deciduous trees within patches as predictors for Bicknell's Thrush nests (McKinnon et al. 2014). Stem density may be particularly important for Bicknell's Thrush nesting in young forests, as most nests found in 2017 (5/7 nests) were constructed between 3-4 balsam fir trees within ~15 cm of one another with dbh ~ 5 cm. Those found in thinned forests in 2017 were either constructed similarly (4/5 nests), or between two branches of a large balsam fir of diameter at breast height >15 cm – similar to most (73/105 nests) nests found in Vermont

(Townsend et al. 2015). High stem densities, or older trees that provide cover and structure for nesting, are likely factors limiting Bicknell's Thrush nest site selection.

Changepoint analysis clearly identified shifts in temperature from occupied nest temperatures to environmental temperatures in all five nests that were followed to vacancy and identified logger removal in the final two nests (Figures 5.2 – 5.8). Using temperature loggers to identify nest vacancy and success is not a novel method, but using changepoint analysis, to my knowledge, has not been used for this purpose. Further, changepoint analysis could be useful in identifying on-off bouts of incubation if temperature logging frequency is high. However, ground-truthing, in the form of observation *in-situ* or through video recordings, would be necessary to determine the accuracy of any results on precise behaviour.

Nest monitoring of forest-dwelling bird species is a fundamental measure in identifying productivity, population health, and habitat suitability (Martin and Geupel 1993). For Bicknell's Thrush, nest monitoring is made challenging by several factors including the cryptic nature of the species, the difficulty in searching large areas of terrain within their preferred dense forest habitats and visually locating nests within those habitats, and the increased risk of creating predator cues due to repeated disturbance of the immediate surroundings of nests. I have shown here that by using low-cost, miniaturized temperature loggers, breeding success can be easily assessed with minimal disturbance to nests. In addition, when combined with radio-tracking studies, Bicknell's Thrush nests can be easily found and monitored with little effort from researchers. Unlike video recording, temperature data can be analyzed quickly either using change point analyses used here or visually as in other studies (e.g., Weidinger 2006). Combined with

video recordings, temperature signatures of different events (such as fledging, incubation patterns or predation event) may be ground-truthed to allow deeper understanding of nest failures and successes. Despite validation with other species,, a camera study combined with the use of temperature loggers in nests is still warranted if using TDLs to estimate more precise behaviours (such as on-off bouts or egg hatching).

Despite previous studies finding negative effects of PCT (Chisholm et al. 2008, Aubry et al. 2018), this small sample study suggests that Bicknell's Thrush are nesting and can fledge successfully in thinned habitat within this industrial forest system. Further, nest sites compared with random plots of nests found in 2016 and 2017 breeding seasons, similarly to McKinnon et al. (2014), found little evidence for nest habitat selection. Two different nesting strategies (between trunks of young balsam fir and between branches of older red spruce) may have contributed to the lack of strong predictors in modelling. Research programs and studies that are sampling or surveying for Bicknell's Thrush in industrial forests should examine older thinned forests for Bicknell's Thrush occurrence, especially if near unthinned forests stands.

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CHAPTER 6 – GENERAL DISCUSSION

Thesis Summary

In this thesis, I examined space use by Bicknell's Thrush (*Catharus bicknelli*) within a high elevation industrial forest system that had experienced a substantial change in habitat via a windstorm in 1994. By tracking individuals throughout two breeding seasons, I estimated home range sizes as well as habitat associations throughout the breeding season. In chapter two, I used home range sizes and overlap to determine a population estimate within a revised potential habitat model as well as within an occurrence area that has historically had consistent Bicknell's Thrush presence. These data provide an alternative measure for Bicknell's Thrush population in New Brunswick, as well as showing that Bicknell's Thrush may substantially overlap home ranges during the breeding season. In chapter three, I assessed habitat selection at the landscape scale using compositional analysis, which showed that females preferred planted sites over natural regrowth and thinned habitats, but males did not show any preference except for an avoidance of non-forested habitat, suggesting females are the more selective sex. In chapter four, I modelled Bicknell's Thrush presence with different silviculture treatments, elevation, stand age, and years since treatment. I found that elevation had a strong positive relationship with Bicknell's Thrush presence, a negative relationship with both variables associated with time (stand age and years since treatment), and negative relationships with all treatments except untreated clear-cuts. I also surprisingly found that an interaction between treatments and time since treatments showed a relationship where pre-commercially thinned forests could increase probability of Bicknell's Thrush

presence as time since the treatment increases. Finally, my fifth chapter reported nest survival estimated using nest temperature and changepoint analysis, and assessed nest site selection using a modelling framework. These data, although limited, suggest that Bicknell's Thrush are nesting within older thinned habitat and successfully fledging young. All these data, taken together, suggest Bicknell's Thrush in New Brunswick can use most habitats at high elevations, including older thinned forests, and remain within the area despite drastically changing from old-forest habitat that was available pre-blowdown to a heavily managed industrial forest.

Orientation Within an Industrial Forestry Landscape

Bicknell's Thrush had larger home ranges, especially females, than in previous studies conducted in both Vermont (Collins 2007, McFarland et al. 2008) and Quebec (Aubry et al. 2011). Further, some females overlapped home ranges considerably with other females, which has not been found in other parts of the range (McFarland et al. 2008, Aubry et al. 2011). Several factors can influence changes in home range size, such as food availability, conspecific density, and predation (McLoughlin and Ferguson 2000).

In Vermont, predation was the main factor in breeding success for Bicknell's Thrush, where nests were predicted to have only 19% success following years of high cone production, an indicator of high red squirrel (*Tamiasciurus hudsonicus*) abundance (McFarland et al. 2008), a known predator of both nests and adults in songbirds. When predation is high, individuals may show predator avoidance behaviour, higher vigilance, or require habitat with more cover (McLoughlin and Ferguson 2000) and a larger home range in New Brunswick may indicate lower abundances of predators within the habitat.

This may not be the case, however, as predators did not seem absent within the field site. One female was depredated during tracking and subsequently found in an American marten (*Martes americana*) den less than a hundred meters away from several Bicknell's Thrush nests in a forest plantation. McKinnon (2006) found evidence of egg predation by both squirrels (Sciuridae) and American marten (*Martes americana*) in the study area. Additionally, although limited in sample size, at least one of seven tracked Bicknell's Thrush nests was depredated in 2017.

Conspecific density is unlikely to play a major role in home range size of Bicknell's Thrush, since males do not defend territories, and both sexes have home ranges with high overlap (McFarland et al. 2008, Aubry et al. 2011, Chapter 2). Bicknell's Thrush home range size in New Brunswick may be more influenced by prey availability, as females already adjust number of male breeders according to available food (Strong et al. 2004). When females select home ranges and nest sites, they are bound to their nest as a central location within their foraging area (i.e., central place foraging, Orians and Pearson 1979). When prey are not as abundant as expected within habitats, females would expand their foraging area, especially if other alternatives are unavailable (such as a low number of available males, Askanas 2008). Although thinned habitat, which is the majority of available habitat within this system, has shown an increased diversity and biomass in invertebrates in other systems (Baucé 1996, Ostaff et al. 2006, Taki et al. 2010, Verschuyl et al. 2011), this relationship may not hold true within a high elevation industrial landscape in New Brunswick (Verschuyl et al. 2011).

Compositional analysis showed female Bicknell's Thrush chose home ranges within the landscape, with planted sites preferred the most, followed by natural

regenerating clear-cuts, then thinned sites and fill plantings, and finally non-forested. Contrastingly, males showed no selection among these habitats except that they avoided non-forested land. This relationship suggests that females are the sex choosing home ranges, and potentially, nest sites – evidence that has not been shown for this species (COSEWIC 2009). Bicknell's Thrush have a polygynandrous mating system, where males visit multiple nests (Goetz et al. 2003), which may also contribute to lack of habitat selection by males. Considering predators have a high influence on nest productivity in other parts of their range (McFarland et al. 2008) and in birds in general (Martin 1992), female Bicknell's Thrush would be expected to prefer home ranges with thick habitat (e.g., planted and regenerating clear cut sites). However, most nests found in 2017 were located within older thinned habitat, so micro-habitat characteristics or perceived predator abundances after females select a home range may play a role in actual nest selection. The lack of habitat selection within the home range implies that individuals forage unpreferentially in habitats within their home ranges. Selection within the home range might suggest that some habitats are more important for foraging (Rolstad et al. 2000), and the lack of selection in Bicknell's Thrush may indicate an adequate food supply for foraging individuals. Bicknell's Thrush have already been shown to use alternative measures to secure additionnal feeding for nestlings in the form of additional male feeders (Strong et al. 2004), although additional male feedings in New Brunswick do not actually reduce the female's workload (Askanas 2008). Planted, thinned, and naturally regenerating clear-cut forests in this area are possibly not limiting in available food sources here, however this needs to be explored further.

The greatest surprise is the extent of use of thinned habitat in this system. All other research on thinned habitat has shown negative effects on this species (Chisholm 2005, Chisholm and Leonard 2008, Aubry et al. 2011, Aubry et al. 2016, Aubry et al. 2018). Despite preferring thinned habitat less than unthinned in compositional analysis, Bicknell's Thrush still nested within and used forests pre-commercially thinned 13-14 years before. This is reflected in the top model of chapter 4, where thinned habitats are more likely to have Bicknell's Thrush as time since the treatment increases. Preferring other habitats over thinned forest, but increasing likelihood of presence in older PCT habitat could be explain by the large amount of PCT habitat within the area (>60%) compared with other studies (<30%, Aubry et al. 2011). However, most nests monitored in thinned habitat during the 2017 season seemed to have successfully fledged. Unfortunately, modelling nesting habitat immediately around nests compared with plots 100 m away found no conclusive effects of stem density or composition of trees surrounding the nest, contrary to McKinnon et al. (2014) finding a positive effect of total tree density and a negative effect of proportion of deciduous trees. Most nests were found between four young, closely spaced balsam fir trees, but surrounding habitat varied from dense unthinned to older thinned forest. Despite the direct, immediate effects of PCT on Bicknell's Thrush habitat, data shown here suggests that these habitats may be re-inhabitted as the treated stands grow.

Population Estimate and Decline

The population estimated here is likely inflated from the true population found in New Brunswick as it considers the potential habitat to be saturated with Bicknell's

Thrush. However, it is striking that the estimate is similar to previous estimates by Campbell and Stewart (2012), despite assuming a much smaller potential habitat due to a much higher elevation cut off (~350 m, Lambert et al. 2005, to 575 m, used here, Campbell 2017). With Bicknell's Thrush using a wider diversity of high elevation forests than previously reported (chapters 3, 4 and 5) and elevation presenting as a strong predictor for presence in chapter 4, it is possible that decreases in Bicknell's Thrush in New Brunswick represent abundances at lower elevations decreasing, rather than habitat loss through silviculture. Alternatively, the effects of global warming on high elevations are magnified, and a decrease of only 1°C has been predicted to reduce Bicknell's Thrush habitat by half (Rodenhouse et al. 2008). Since the population of Bicknell's Thrush in New Brunswick represents the lowest elevation at which this species breeds (other than island or coastal habitats), any effects of global warming should present here first. Studies that examine how Bicknell's Thrush populations have declined within a global warming context, either alternatively or additively to silviculture treatment effects, may help explain the observed drop in population observed by Birds Canada (Campbell and Stewart 2012).

Further Research

This thesis highlights the use of habitat by Bicknell's Thrush in industrial systems during the breeding months, but does not follow individuals into the post-breeding. As a species seemingly isolated on mountain tops, post-breeding dispersal may be important for individuals to explore potential breeding habitat. Further, identifying habitat use when individuals are not bound to a nest may shed light on how nest site selection influences

habitat preference (Vitz and Rodewald 2006). Most important, however, is determining the likelihood of Bicknell's Thrush re-inhabiting areas that have been harvested or thinned but have grown enough to support breeding groups. The post-breeding movement and dispersal of individuals is crucial in identifying if enough movement occurs for this to happen. Finally, one female, tracked in both 2016 and 2017 (individual #85023), nested in the same young fir tree both years; and several males were recaptured in the same area (within 100 meters) in both years. It is possible that experienced breeders may rely more on site fidelity from previous years rather than assessments of habitat when returning to the breeding grounds. When thinning or harvest occurs after the breeding season, returning Bicknell's Thrush must rely on correctly identifying appropriate habitat without prior knowledge from previous breeding seasons as their habitat no longer exists. Understanding how these birds deal with habitat loss, through multi-year studies after disturbances, would improve our understanding of how resilient this species is to industrial use.

The differences between thinned and unthinned habitat have been highlighted several times throughout this thesis with regards to predators (King and DeGraaf 2000, Bourque and Villard 2001 Barber et al. 2001, Carignan and Villard 2002) and food availability (Baucé 1996, Ostaff et al. 2006, Taki et al. 2010, Verschuyl et al. 2011). Further studies on what Bicknell's Thrush are feeding on and providing to their young, as well as the presence of predators, in high elevation industrial forests is a logical next step to identifying what influences success when nesting in these habitats.

Suggestions for Management

Forestry

This thesis demonstrates that Bicknell's Thrush still use thinned habitat within their home ranges, sometimes nesting within it (after several years of regrowth), suggesting that the idea of leaving small patches of unthinned habitat within thinned area may improve Bicknell's Thrush occurrence within industrial forests. However, these practices should not replace current best management practices, such as not thinning during the breeding season (May through August). Forest managers should also be wary of neglecting as potential habitat high elevation forests that do not meet the typical, young, dense forests associated with Bicknell's Thrush. Evidence in other parts of the range has identified Bicknell's Thrush using old (+70 years) forests (Aubry et al. 2018), and thinned forests occupied by Bicknell's Thrush in the present study can be as old as 25 years and may continue to be occupied until harvest. Management guidelines should describe potential Bicknell's Thrush habitat not only as young, vigorous regrowth but high-elevation forests of any age, including areas that have been thinned. Treatments and disturbance in these habitats should be delayed until at least after the breeding season (May – mid-August), which would decrease the reliance on identifying if Bicknell's Thrush are absent from a forest stand. Alternatively, if Bicknell's Thrush are occuring in "less than ideal" habitats due to high site fidelity, then providing ideal habitat either through thinning/harvesting smaller patches of forest or providing undistrubed forest throughout the treated stand to allow returning birds the following year a place to nest.

Conservation

Bicknell's Thrush is currently monitored only by Birds Canada through the Mountain Bird Watch 2.0 program, which is limited to monitoring the species sufficiently intensively to detect a minimum 3% annual trend over 30 years. Mountain Bird Watch does this by revisiting sites that have a high probability of Bicknell's Thrush presence, but has little capacity to identify areas that historically had Bicknell's Thrush, but were thinned or harvested and did not have them in the immediate years after. Further, unless thinning or harvest within the potential habitat areas are adequately surveyed for Bicknell's Thrush through multiple visits prior to harvest, prescribed treatments should be delayed at least until after the breeding season is over. Conducting monitoring for both of these scenarios would improve understanding of the effects of harvest on the population of Bicknell's Thrush in New Brunswick, and a framework that assesses and manages thinning and harvests with clear guidelines for silviculture companies would improve the sustainability of the population and provide clarity to forest management planners who operate within the potential habitat area.

Synopsis

This thesis improved population estimates, estimated home ranges, identified habitat use and reported nesting success of Bicknell's Thrush in north-central New Brunswick. I calculated a population for Bicknell's Thrush in New Brunswick by using an unconventional method of calculating number of possible home ranges within an area of occurrence, increasing accuracy of previous estimates. I showed that females choose habitat within the landscape while males do not, supporting the finding that males overlap

with several females for breeding, and reflecting the very different habitats chosen by different individual females. I also showed that within an industrial forest landscape, Bicknell's Thrush successfully use thinned habitat that had previously only been shown to reduce likelihood of presence. These habitats apparently did not reduce success, as nests found within the habitats had fledged. Finally, I showed how nest temperature, in combination with radio tracking, can be used to easily track nest success in Bicknell's Thrush with reduced effort and disturbances from nest visits. This thesis will improve conservation of Bicknell's Thrush within New Brunswick by encouraging conservation managers to re-examine high elevation habitats previously assumed not to support this species.

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