

**ASSESSING THE IMPACTS OF MOOSE-INDUCED HABITAT CHANGE
ON A FOREST BIRD COMMUNITY**

by

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ABSTRACT

Forest songbirds are sensitive to habitat disturbances that result in changes to forest structure and composition. In Newfoundland, Canada, browsing by hyper-abundant, non-native moose (*Alces alces*) has caused failed regeneration across extensive areas of forest following disturbance. I examined the impact of these habitat changes at multiple spatial scales on forest bird occurrence and species richness within Gros Morne National Park based on point counts that incorporated both silent intervals and intervals during which black-capped chickadee (*Poecile atricapillus*) mobbing calls were broadcast. Early successional bird species were more likely to occur with increased failed regeneration on the landscape. Some forest habitat generalists were less likely to occur with increased failed regeneration cover at the local scale. Comparing detection probabilities across silent and playback intervals for 17 species, I found that playbacks increased detection rates for seven species, and either had no effect or decreased detection rates for the remaining ten species.

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1. Introduction and overview

1.1. Herbivore impacts on forest bird communities

Wild ungulates directly influence the structure, species composition and successional trajectory of vegetation communities through selective browsing (Côté et al. 2004).

Herbivores influence ecosystems by decreasing plant biomass through browsing or grazing. Large herbivores may also indirectly impact other animals that occupy the same habitat via broader changes to vegetation community composition and landscape structure such as altered vegetation cover in both the canopy and understory of a forest (Van Wieren and Bakker 2008). In some instances this may include either degradation or outright loss of habitat (e.g. van der Wal 2005). For birds, habitat loss contributes to the decline of populations worldwide (Bird Life International 2004). The mechanism behind these declines, attributable to habitat loss, is the prevention of individuals from meeting foraging, singing or nesting requirements. In turn, altered behaviour can have repercussions for survival and reproductive success (King et al. 1996, Smith et al. 2008).

Effects that browsing by large herbivores have on various aspects of bird biology include potential impacts on individuals (e.g. reproductive success or breeding density) and communities (e.g. overall abundance and species diversity). Individuals may be affected by changes in prey availability (Bailey and Whitman 2003), reproductive success (Pedersen et al. 2007) or direct competition for resources (Leathwick et al. 1983). At the community level, changes in bird diversity in response to browsing are variable. Regional species diversity may increase due to the increased heterogeneity of habitat (Ogada et al.

2008), or increased productivity due to biogeochemical alterations (Feeley and Terborgh 2006). However, extirpation of specialists – particular riparian habitat specialists – have also been observed following habitat alteration due to increased ungulate herbivory (Berger et al. 2001).

Changes to vegetation caused by ungulate browsing can affect foraging by birds, which in turn can have implications for the ability of those birds to provide for their young, and ultimately affects reproductive success (Pedersen et al. 2007). Specifically, Pederson et al. (2007) found that great tit (*Parus major*) nests near feeding areas with high moose (*Alces alces*) densities in Norway produced 1.3 fewer fledglings compared to those nests on unbrowsed plots. In addition to moose reducing the total arthropod biomass near high density areas, this decline in reproductive output may have been partially attributable to decreased birch (*Betula spp.*) canopy cover, an important feeding substrate for songbirds, as a result of selective browsing by moose (Pedersen et al. 2007). Black-tailed deer (*Odocoileus hemionus columbianus*) browsing was also associated with lower reproductive success of songbirds in the forests of the Queen Charlotte Islands, British Columbia (Martin et al. 2008). These songbirds, dependent on understory vegetation for feeding and nesting, demonstrated declines in nesting success that were primarily attributed to increased nest predation as a result of removal of vegetation by deer (Martin et al. 2008).

Many studies on the cascading effects of wild herbivore browsing on ecosystems focus on deer over-abundance (Côté et al. 2004). In North America, black-tailed deer

introduced to the Haida Gwaii archipelago in British Columbia had a negative impact on songbird abundance and alpha diversity. Species dependent on understory vegetation were most affected by the changes brought about by deer (Allombert et al. 2005). These effects were likely because of a decline in food resources and suitable nesting micro-habitat. Atypically large populations of white-tailed deer maintained by supplemental feeding, in combination with high densities of introduced elk (*Cervus canadensis*) and mouflon sheep (*Ovis musimon*) had similar impacts on bird communities of deciduous forests within a wildlife research preserve in Pennsylvania (Casey and Hein 1983). Specifically, species associated with understory growth such as black-and-white warbler (*Mniotilta varia*) were absent from heavily browsed plots, whereas bark-foraging species like red-breasted nuthatch (*Sitta canadensis*) were abundant. More recently, exclosures in areas of Virginia with high densities of white-tailed deer showed increases in bird abundance but not diversity (McShea and Rappole 2000). In particular, it seems richness and abundance of intermediate canopy nesting species decline with increased deer density (DeCalesta 1994). However, one study reported no effect of deer presence on abundance or diversity of forest songbirds, though changes in species composition were evident (DeGraaf et al. 1991).

Deer over-abundance is prevalent beyond North America. Sika deer (*Cervus nippon*) populations in Japan have decreased species richness and abundance of understory nesters and foragers, but not cavity-nesters or bark gleaners, an effect attributed to reduced cover of nesting sites (Hino, 2000, Hino, 2006). In Europe, native roe (*Capreolus capreolus*) and fallow deer (*Dama dama*), along with introduced Muntjac

deer (*Muntiacus reevesi*), have caused declines among species that nest in low vegetation, presumably due to reduced availability of suitable habitat for nesting (Perrins and Overall 2001). This result is supported by the review of Gill and Fuller (2007) who showed that the abundance of woodland bird species that use the understory is increased when deer are excluded. The primary factors cited are reduced food and nest site availability, as well as increased nest failure due to exposure to predators of the remaining nest sites.

1.2. Moose in Newfoundland

Six moose were introduced to the island of Newfoundland (111,390 km²): two in 1878 and four in 1904 (Pimlott 1953). The population has grown dramatically since that time because of the abundance of available habitat and absence of natural predators; black bears occupy the island and prey on young moose, however, they are unlikely to influence moose density (Zager and Beecham 2006). Densities are particularly high in the national parks on the island; there are 0.7 and 3.0 moose/km² in Terra Nova and Gros Morne National Parks, respectively, where, in addition to the absence of natural predators, hunting is prohibited (Gosse et al. 2011; note that hunting has been allowed in these parks over the past two years). In comparison, typical moose densities are <0.5/km² across the range in North America (Crête and Daigle 1999). The foraging activities of moose and other non-native herbivores (varying from non-native rodents to introduced slugs) have the capacity to change forest stand structure and landscape composition (Connor et al. 2000, McLaren et al. 2004, Gosse et al. 2011). Specifically, intense moose browsing changes the successional trajectory of balsam fir (*Abies balsamea*) forests by impeding the growth of advanced regeneration balsam fir saplings (Connor 2004). With

an absence of forest fires on the west coast of Newfoundland, the main type of natural forest disturbance in Newfoundland is infestation by hemlock looper (*Lambdina fiscellaria*) and spruce budworm (*Choristoneura spp.*; Thompson et al. 2003). These insect disturbances are the basis for the influence of moose browsing activities on forest succession. Although advanced regenerating saplings would normally enable forest stands to recover following these disturbances, in Gros Morne National Park (GMNP), samples collected from 200 m long transects within 15 mature balsam fir stands across three ecoregions in 2008 indicated that the stem density of woody plants >0.3 m tall declined from approximately 20 400 stems/ha in 1977 (a period of low browsing intensity) to 15 100 stems/ha, largely due to browsing by moose (Whitaker and Gallant, Parks Canada unpubl. report). The consequence of reduced recruitment of saplings into mature tree age classes is the creation of open areas dominated by grasses and ferns known as “moose meadows”. Remote sensing analysis has revealed that 45% of 95 km² previously categorized as regenerating forest (i.e. disturbed or regenerating stands) in GMNP were converted to moose meadows, compared with 26.6% believed to be regenerating successfully (Taylor and Sharma 2010).

One consequence of the creation of moose meadows is the loss of a local seed source to aid further forest regeneration in these open habitats; having fewer mature trees in a stand limits seed production (Hulme 1996). In addition to fewer trees reaching seed-producing stage, in GMNP there is increased pre-dispersal predation pressure exerted by non-native red squirrels (*Tamiasciurus hudsonicus*) on those trees that are still present and able to produce seeds (Boa-Antwi 2009). Additionally, Noel (2004) showed that, for

those individuals that do become established, seedling mortality from non-native slugs and small mammals is also increased. Overall, degraded seedbed quality, limited sapling recruitment, and browsing by moose are causing drastic changes to the landscape in Newfoundland. It is predicted that with continued intense browsing pressure, area of forest cover in GMNP will decrease and grassland cover will increase (Zhu et al. 2010). Further, white birch (*Betula papyrifera*) and mountain maple (*Acer spicatum*) are expected to decrease under continued intense browsing. With hardwood trees such as white birch and maple comprising a low proportion of total stems in these overbrowsed systems, this leads to increased browse intensity on balsam fir (Connor et al. 2000).

Parks Canada considers a species to be hyper-abundant if its local density clearly exceeds the upper range of natural variability characteristic of the particular ecosystem, and it has a demonstrated impact on ecological integrity (Nugent et al. 2010). Based on this definition, moose in GMNP are considered hyper-abundant.

1.3. Bird survey techniques

A reliable survey method is required to assess how intense browsing and the amount of degraded habitat impacts bird distribution and abundance in the landscape. Point counts, a common technique used to survey birds, are a special case of the line transect survey. In point count surveys, an observer censuses birds present at a given site (Ralph et al. 1995). However, birds present are not always observed, which leads to biased estimates of bird distribution and abundance (MacKenzie et al. 2006). Distance from observer, singing rate

and volume, weather and observer differences all influence whether a bird is detected (Alldredge et al. 2007).

Different survey protocols and data analysis methods have been developed to estimate and correct for imperfect detection rates. For example, distance sampling estimates detection probability as a function of distance from the observer, assuming that individuals 0 m from the observer are always detected while those further from the observer are less likely to be detected as the distance increases (Buckland 2001). Double observer methods use differential detections between two observers in a single point count to estimate the rate at which species present are not detected (Nichols et al. 2000). Similarly, using patterns of detection and non-detection across repeat visits has been employed to determine detection probabilities (MacKenzie et al. 2002). As an alternative to calculating detection rates, researchers have modified point count protocols to maximize detection rates through the broadcasting of vocalizations such as the mobbing calls of the black-capped chickadee (*Poecile atricapillus*; Turcotte and Desrochers 2002, Mitchell and Donovan 2008).

The black-capped chickadee, a year-round resident of boreal and temperate forests across North America, is known for its diverse vocalizations (Foote et al. 2010). Within its repertoire, chickadees use variations on the *chick-a-dee-dee-dee* call to alert conspecifics to the presence of possible threats (Templeton et al. 2005) and potentially to draw them together to mob the predator (Odum 1942; Lucas and Freeburg 2007). Heterospecific attraction to black-capped chickadee mobbing calls also has been noted

for a variety of species (Hurd 1996; Desrochers and Hannon 1997). Therefore, researchers have attempted to exploit this response in an attempt to increase the rate at which observers detect birds during point count surveys by broadcasting chickadee mobbing call recordings during the point count. This approach has been successful for boreal forest birds during winter (Turcotte and Desrochers 2002) but had mixed results when tested on breeding birds in a temperate forest (Mitchell and Donovan 2008).

1.4. Thesis objectives and outline

Modifications to habitat associated with the browsing activities of hyper-abundant moose are recognized as a major change to the forest landscape of GMNP (Connor et al. 2000, McLaren et al. 2004, Gosse et al. 2011); however, the cascade of effects on other wildlife affiliated with this altered landscape has not yet been investigated. I studied forest songbird communities present across a range of successional stages to assess the influence that moose-altered forest regeneration has on the abundance and diversity of those forest birds. To conduct this work, I used a modified point count technique that incorporated the use of chickadee mobbing calls broadcast as part of the protocol. In Chapter 2, I assess the value of this modified approach for censusing songbirds by comparing point count detection rates with and without the use of mobbing call playback. I then present data in Chapter 3 that quantify the relationship between songbird assemblages and moose-induced change at multiple spatial scales. This is followed by Chapter 4, where I summarize and discuss my overall findings.

1.5. Co-authorship statement

I conducted this research independently but with input from Dr. Ian Warkentin, my graduate supervisor, and Dr. Darroch Whitaker, a member of my supervisory committee. I was responsible for initiating the study design in consultation with Drs. Warkentin and Whitaker and completed data collection with the assistance of three field technicians who were under my supervision: Etienne Cardinal, Jeff Siddall, and Simon Octavio Valdez.

I completed the data analyses and interpretation with guidance from Drs. Warkentin and Whitaker and wrote the manuscripts that constitute the chapters of this thesis. I revised the manuscripts included in this thesis (chapters 2 & 3) based on the advice and comments of Drs. Warkentin and Whitaker (co-authors of those manuscripts), as well as comments provided by committee members and journal reviewers. The second chapter, Rae LF, Whitaker DM & Warkentin IG, Variable effect of chickadee mobbing call playback on detection probability of boreal forest birds, has been accepted for publication by the Journal of Field Ornithology. The third chapter, Rae LF, Whitaker DM & Warkentin IG, Multiscale impacts of forest degradation through browsing by hyper-abundant moose (*Alces alces*) on songbird assemblages, has been published in the peer-reviewed journal Diversity and Distributions (2014, 20:382-395). As such, there is some necessary repetition of material between the general introduction and manuscript chapters, and formatting differences among chapters which reflect the journal to which the manuscript was submitted.

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2. Variable influence of mobbing call playback broadcast on bird detection probability

2.1. Abstract

Modification of the point count survey method to include playback of songbird mobbing calls in an attempt to increase detection probabilities has met with mixed success. We compared detection probabilities for boreal forest songbirds using traditional point count methods and counts using broadcasts of the mobbing calls of Black-capped Chickadees (*Poecile atricapillus*) in an attempt to increase detection probability. We conducted 594 point counts during the 2010 breeding season in Newfoundland, Canada. Each point count consisted of an 8-min silent observation period followed by an 8-min broadcast of Black-capped Chickadee mobbing calls. Occupancy model results showed that response to playback broadcast varied across species, with detection probabilities higher for seven of 17 species during the silent portions of point counts and three species more likely to be detected during playback intervals. For all species, the number of visual detections increased during periods of playback and, averaged across species, individuals were >6 times more likely to be seen during the playback period than during the silent period. Differences in detection probability among observers were apparent during both silent and playback periods. We suggest that using playback of chickadee mobbing calls during point count surveys of common boreal forest songbird species may be most beneficial when visual detection is important. However, playback may also be useful for species-specific surveys during periods when birds are less likely to be vocal or for studies of less common species with chronically low detection probabilities. A combined silent and

playback approach could also be useful, although observer and species differences should be accounted for if comparing data across species or studies.

Keywords: Black-capped Chickadee (*Poecile atricapillus*), boreal forest, detectability, occupancy modeling, point count

2.2. Introduction

Birds are considered important indicators of ecosystem health because their diversity and varied requirements for habitat features that provide for nesting, foraging, and escape cover make them sensitive to a broad range of stressors (O'Connell et al. 2000, Hart et al. 2012, Rae et al. 2014). A prerequisite to using birds as indicators is a survey technique that accurately quantifies abundance or relative abundance and distribution. Commonly employed survey methods that provide density or abundance data include line transects (Burnham et al. 1980), territory mapping (Svensson 1979), and standardized mist-netting surveys (Peach et al. 1996). Line transects, of which point counts are a special case, are perhaps the most widely used technique because they allow relatively rapid assessment of birds in sampling areas of various sizes (Goetz et al. 2010, Millington et al. 2011). In general, point count surveys involve at least one observer taking a census of individuals seen or heard at the site of interest over a standardized time period (Ralph et al. 1995), but there is high variability in survey protocol depending on study-specific considerations and constraints.

A common criticism of the point count method is its tendency to underestimate abundance or occurrence due to imperfect detection of individuals present in the surveyed area (MacKenzie et al. 2002). This issue can be addressed by employing statistical methods to estimate rates of detection, such as occupancy modeling (MacKenzie et al. 2006), double observer surveys (Nichols et al. 2000), or distance sampling (Buckland 2001). These approaches aim to correct observed abundance based on detection rates and generate true population size, density, or occupancy estimates (Pollock et al. 2002). Point

count surveys have also been modified by some researchers to include playback of recorded bird songs or calls in an attempt to increase detection rates. Species-specific surveys of songbirds have taken advantage of response to playback of the target species' vocalizations with mixed success (Sliwa and Sherry 1992, Kubel and Yahner 2007, Jakob et al. 2010). Where a mixed species assemblage of birds is being surveyed, interspecific attraction to the calls of a single species may be exploited. For example, the predator mobbing call of Black-capped Chickadees (see Table 2-1 for scientific names of bird species) is often used for multi-species sampling because it attracts a variety of species (Hurd 1996). Broadcasting mobbing calls triggers a range of behaviors in responding birds, including joining in to produce mobbing calls, increased call rate, and movement towards the source of the call. Further, Betts et al. (2005) showed that, for two species of wood warblers, individuals will move up to 175 m, but not beyond territory boundaries, in response to broadcast of chickadee mobbing calls.

Chickadee mobbing calls can also increase visual detections of survey species (Gunn et al. 2000). Such observations potentially enable the resighting of marked individuals or confirmation of breeding activity through observation of behaviors such as mate guarding, carrying nesting material, or food to provision an incubating female or nestlings, strengthening links between species presence and reproductive success (Gunn et al. 2000). Although visual detections may be necessary for evidence of breeding, auditory detections are particularly important in dense vegetation where even birds attracted close to the observer may not be visible. Playbacks may influence auditory detections by encouraging a vocal or mobbing response. However, playbacks could also

decrease the detection of some birds through masking of vocalizations of birds with short or quiet songs and calls and because some species may become furtive on hearing mobbing calls, even if attracted to the sound source.

The generality of species attraction to Black-capped Chickadee mobbing calls suggested by Gunn et al. (2000) has been challenged by Mitchell and Donovan (2008), who found increased detection rates for 14 species, decreased rates for 20, and varied responses for seven species at a study site in Vermont. To further investigate responses to the broadcast of chickadee mobbing calls in a boreal forest context, we conducted point count surveys with silent and playback intervals to examine the hypothesis that playback broadcast during point counts consistently increases detection probability in widely separated parts of the range for a particular species. We took a mark-recapture approach to modeling occupancy which also allowed us to determine detection rates for each species while controlling for differences in detection rates across habitats.

2.3. Methods

2.3.1. Study area

Research was conducted in Gros Morne National Park (GMNP; 1805 km²), on the west coast of insular Newfoundland, Canada (49°29'N, 57°40'W). Using ArcGIS 9.2 (ESRI 2008), we identified 3485 random points that met the following criteria: located in a forest stand at least 1 ha in size, >20 m from the edge of the stand, and >300 m from the nearest neighboring point (see Rae et al. 2014 for further details). Of the points that met these criteria, 607 were chosen for sampling based on accessibility by foot given the

constraints of topography and proximity to trail or roadway. Stands were dominated by balsam fir (*Abies balsamea*), with varying amounts of white birch (*Betula papyrifera*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*) comprising <50% of canopy trees. Prior to sampling, each site was classified by forest type using the 1995 Forest Resource Inventory (FRI) for GMNP and similar numbers of regenerating, mature, and disturbed forest sites were visited. Regenerating stands were <20 years old and characterized by a high density of saplings <5 cm diameter at breast height (dbh) whereas mature stands of forest had experienced some natural thinning and had a lower density of stems, which were typically >5 cm dbh. Disturbed sites were formerly forested stands that failed to regenerate following insect kills or small-scale domestic forest harvest due to intense browsing pressure by moose (*Alces alces*; Gosse et al. 2011). These open areas, known as moose meadows, were typically 15 to 25 years post-disturbance and dominated by grasses, ferns, non-palatable woody shrubs, a low density of white spruce and mature white birch, and typically retained a large amount of coarse woody debris.

2.3.2. Survey method

From 3 June to 8 July 2010, four trained observers conducted point counts of forest birds (Ralph et al. 1995). Points were each visited once and counts took place between 0.5 h before sunrise and 10:30 NST. Surveys were not conducted during periods of rain or high wind (> 25 km/hr). Each count consisted of four contiguous 2-min silent listening intervals followed by four 2-min intervals of Black-capped Chickadee predator mobbing calls broadcast using Foxpro FX3 game callers (Foxpro, Lewistown, PA). The game callers have two speakers that broadcast in opposite directions. During the survey, game

callers were placed on the ground ~2 m from the observer. The volume control was set to the same level for each survey, and at this level the average volume measured every 0.1 s for 38 s at 1 m from the caller was 81.5 dB and average peak volume per 0.1 s was 92.7 dB. The recording was made during spring 1997 at Riley Brook, New Brunswick, by presenting a group of chickadees with a taxidermic mount of a Northern Saw-whet Owl (*Aegolius acadicus*) and included at least three individuals producing emphatic mobbing calls with 3 to 15 “dee” notes, indicative of response to small predators (Templeton et al. 2005). Black-capped Chickadees are found in boreal and temperate forests across North America (Foote et al. 2010) and abundant in our study area. A count of all birds detected was recorded for each 2-min interval, as well as the type of observation (i.e., auditory or visual) when a bird was first detected during that interval. Where necessary, habitat for a point was reclassified based on visual assessment of vegetation within 50 m of the point count center to correct for any errors in the initial classification made using the 1995 FRI map. We classified habitat as open or closed canopy forest, or non-forest (formerly forested habitat that failed to regenerate to its former state).

2.3.3. Data analysis

For each species detected at >25% of survey points, we built a set of occupancy models to compare detection probabilities between silent and playback point count intervals (MacKenzie et al. 2006). Analyses were based on 4-occasion occupancy models. Because the raw point count surveys consisted of eight intervals, consecutive pairs of 2-min intervals for each treatment type were combined to create four 4-min intervals: A, B, C, and D (i.e., original silent intervals 1 and 2 were combined, as were silent intervals 3 and

4, and so on for all playback intervals, creating four 4-min intervals or occasions); the highest number of observations for a species within each original pair of 2-min intervals was retained for inclusion in the model to represent the count for each combined interval. These models, similar to closed-population mark-recapture models, use maximum likelihood to estimate both the probability of site occupancy (ψ) and the probability of species detection at a site, given that it is present (p) (pg. 94 of Mackenzie et al. 2006). We built models to represent competing hypotheses to describe the influence of point count treatment (silent versus playback) and habitat (open or closed canopy, and non-forest) on detection probability (Table 2-2; Mitchell and Donovan 2008). We fixed detection probabilities for intervals A and B, and C and D to be equal to reduce the number of estimated parameters for silent and playback portions from two to one for each period. Detection of an individual during the playback period may have been influenced by whether it was observed during previous intervals. While we did not test for this directly, our results are not indicative of a bias in favour of increased detections during the playback portion due to previous detections. Given the flight speeds of songbirds (25–50 km/h; e.g., Evans and Drickamer 1994), responsive birds within the audible range of the broadcasts would have been able to travel to the survey point well within these time periods. Detection rates are expected to vary across habitat types (Bibby and Buckland 1987, McShea and Rappole 1997), so we included the site habitat factor variable to test this idea in a playback context and to control for differences in occupancy throughout the study area to meet a model assumption that occupancy is equal across all sites. We did not include observation type (i.e., auditory or visual) because initial visual contact data

were too sparse. We did, however, make qualitative comparisons between auditory and visual detections based on mean values for each interval type. Because observer differences may affect detection probability during traditional point count surveys (Allredge et al. 2007), we also built models to include observer (model 7; Table 2-2), as well as interactions between observer and point count treatment (full interaction: model 10; partial interactions: models 8 and 9; Table 2-2). Testing for observer effects was not part of the original study design, so observer models were added to the original set of models as a separate *post-hoc* analysis.

We used an information theoretic framework to compare the set of models for each species (Burnham and Anderson 2002). Models were ranked based on Akaike's Information Criterion corrected for small sample sizes (AIC_c), a measure of model likelihood that is penalized based on increasing model complexity (i.e., number of parameters estimated). The lowest AIC_c value indicates the most parsimonious model. The numerical difference between a given model and the most parsimonious model in the set (ΔAIC_c), along with Akaike weight (ω_i), indicates relative support for a given model. We used a limit of $\Delta AIC_c < 2$ for reporting of top model results, which is a commonly used threshold that includes only those models for which there is reasonable support (Burnham and Anderson 2002). However, we used model averaging, where weighted average parameter estimates are calculated across all models based on the individual model weights (ω_i), in our reporting of detection and occupancy rates (Burnham and Anderson 2002). All analyses were carried out using program MARK (v. 6.1; White and

Burnham 1999) via package RMark (v. 2.1.3; Laake and Rexstad 2008) for R (v. 2.13.1; R Development Core Team 2004).

2.4. Results

We observed 65 bird species across the 607 points sampled, with 17 species present at >25% of sites; these most common species were included in the occupancy modelling process (Table 2-3). Because of technical problems during 13 surveys, only 594 sites were included in occupancy models. Estimated occupancy probabilities ranged from 0.08 (Mourning Warblers in closed-canopy forest) to 0.98 (White-throated Sparrows in non-forest habitat), and detection probabilities from 0.19 (Boreal Chickadees during playback period) to 0.94 (White-throated Sparrows during silent period).

The influence of playbacks and habitat on detectability of the 17 most common species in our sample was highly varied. For five species, the only model identified in the top model set ($\Delta AIC_c < 2$) was that reflecting the influence of playback on detectability (model 5; Table 2-3). For three species, detectability was higher during silent periods (American Robins, Fox Sparrows, and Hermit Thrushes; Fig. 2-1) whereas detectability during silent periods was lower for two other species (Black-and-white Warblers and Black-capped Chickadees; Fig. 2-1).

With the exception of White-throated Sparrows (see below), model sets for the remaining 12 species reflected a more complex interacting influence of treatment and habitat on detectability (Table 2-3). The null model, reflecting no impact of treatment or habitat (model 1), was included in the set of best models for three species (Golden-crowned Kinglets, Mourning Warblers, and Yellow-rumped Warblers), indicating little

influence of chickadee mobbing call playback or habitat on detection probability (Table 2-3). However, in all three cases, the null model was the weakest of those included in the top model set, with one or more other models providing stronger explanations for the patterns exhibited. Similarly, the model reflecting an effect of habitat on detectability (model 2) was included among the two to five models in the top model set for three species. It was the best model (Table 2-3) for Magnolia Warblers (detections lowest in non-forests) and Yellow-rumped Warblers (detections lowest in open canopy forest), and the second-highest value for Golden-crowned Kinglets (lowest detections in non-forest).

We found support for models with interactions between treatment and habitat for all species except Mourning Warblers and the five species listed above that were influenced solely by treatment. However, top model sets for another nine species also included the treatment-only model (model 5; Table 2-3). Five of these latter nine species clearly had higher detection probabilities during silent periods (Black-throated Green Warblers, Northern Waterthrushes, Ruby-crowned Kinglets, Swainson's Thrushes, and Yellow-bellied Flycatchers), whereas Boreal Chickadees were more likely to be detected during playback (Fig. 2-1). For the remaining species (Golden-crowned Kinglets, Mourning Warblers, and Yellow-rumped Warblers), we found no clear difference in detection probability between treatment periods based on graphical assessment of model-averaged parameter estimates (Fig. 2-1).

Evidence of an interaction effect was demonstrated by the presence of models 3, 4, or 6 in the model set. White-throated Sparrows were the only species where detectability was modified by habitat uniquely for each treatment (only model 6 in top

model set, Fig. 2-1), with detection probability lower for all habitats during playback, but most markedly for closed-canopy forest. For three of the remaining 10 species whose model sets included interactive models, we found habitat differences in detection probability only during the silent period (model 3; Fig. 2-1). Detection probabilities in the silent period were lower in closed-canopy forests for Ruby-crowned Kinglets, and highest in open-canopy forests for Swainson's Thrushes and Yellow-bellied Flycatchers. Similarly, for three species, there were habitat differences in detection probability during the playback period only (model 4; Fig. 2-1). Detection probabilities during the playback period were higher in open-canopy forests for Boreal Chickadees, and lowest in closed-canopy forests for Northern Waterthrushes and Yellow-rumped Warblers. We found some evidence for habitat effects in silent and playback periods for Black-throated Green Warblers (models 3 and 4; Fig. 2-1). However, although detection probabilities during the silent period were higher than during the playback period, habitat differences were minor. For the final three species, we found evidence of an interactive habitat effect during both silent and playback periods (model 6; Fig. 2-1). Detection probabilities were consistently lower in open-canopy forests for Blackpoll Warblers, and consistently lower in non-forest for Golden-crowned Kinglets and Magnolia Warblers. For all species where there was evidence of a habitat effect, except Boreal Chickadees and Golden-crowned Kinglets, detection probabilities were higher during the silent period.

Overall, we had 6095 detections during the silent period, with 97% ($N = 5931$) made by ear and 6% ($N = 355$) visually. In contrast, of 5457 detections during playback, 84% ($N = 4557$) were by ear and 37% ($N = 2042$) were visual detections. The sum of

detection types are greater than 100% for each category because individuals were often detected both by ear and visually. For all species, we had more auditory than visual detections regardless of interval. Visual detection rates increased during the playback period for all species and, for all except three species (Black-capped Chickadees, Boreal Chickadees, and Golden-crowned Kinglets), auditory detections decreased during playback (Fig. 2-2). By contrast, 467 and 20 Black-and-white Warblers were observed by sound and sight, respectively, during silent periods. However, during playback periods, 383 individuals were heard and 307 were observed visually.

When we conducted our *post-hoc* tests to determine potential observer effects, we found that either the observer differences model (model 7) or one of the three interactive models (models 8, 9, and 10) was included in the top model set for 14 species (among these, Black-throated Green Warblers included the null model as part of this set). For the remaining three species (Golden-crowned Kinglets, Mourning Warblers, and Yellow-rumped Warblers), no observer differences were detected. The fully interactive model was included in the top model set for eight species, implying not only that observers differed in their ability to detect birds, but that this effect differed between the silent and playback periods for a given observer (model 10; American Robins, Black-capped Chickadees, Hermit Thrushes, Magnolia Warblers, Northern Waterthrushes, Ruby-crowned Kinglets, Swainson's Thrushes, and White-throated Sparrows). We also found an interactive effect of observer and playback treatment during the silent period for five species (model 8; Black-and-white warblers, Blackpoll Warblers, Black-throated Green Warblers, Boreal Chickadees, and Magnolia Warblers) and during the playback period

for four species (model 7; Fox Sparrows, Hermit Thrushes, Northern Waterthrushes, and Yellow-bellied Flycatcher). In general, the direction of effect of playback treatment was consistent across observers for a particular species, but the magnitude of the effect varied. For one observer (obs2), detection probability was higher during playback than the silent period for four species (American Robins, Blackpoll Warblers, Hermit Thrushes and Magnolia Warblers), whereas the opposite effect of playback was apparent for the other three observers. Similarly, for another observer (obs3), the effect of playback treatment on detection probability was not consistent with that of the other three observers (higher during the silent period for Black-throated Green Warblers and lower for the other observers, and higher during playback for Magnolia Warblers and Ruby-crowned Kinglets and lower for the other observers).

2.5. Discussion

Our results show that the effect of broadcasting the mobbing calls of Black-capped Chickadees during point count surveys varied among species. Detection rates increased for Black-and-white Warblers and, not surprisingly, the two chickadee species. However, we found no effect of call broadcast on detection probabilities of Golden-crowned Kinglets, Mourning Warblers, and Yellow-rumped Warblers, a limited habitat-mediated effect on Blackpoll Warblers, Magnolia Warblers, and White-throated Sparrows, and a discernible negative effect on detection probabilities for eight species (American Robins, Black-throated Green Warblers, Fox Sparrows, Hermit Thrushes, Northern Waterthrushes, Ruby-crowned Kinglets, Swainson's Thrushes, and Yellow-bellied Flycatchers).

The outcomes we observed are likely related to how individual species respond to threats from predators. Specifically, species that do not exhibit aggressive behavior toward predators would not be easily observed during playback. For example, female Swainson's Thrushes respond to predators by silently flushing from the nest or freezing in place, depending on breeding stage, and males move quietly throughout their territories and deliver single "whit" call notes (Mack and Yong 2000). In contrast, Black-and-White Warblers aggressively protect their territories against intrusion (Kricher 2014), likely contributing to their increased detectability during playback. Still, participation in mobbing behaviour does not necessarily mean detection rates will increase with playback. For example, Golden-crowned Kinglets responded to broadcast of the mobbing calls of Black-capped Chickadees during the fall migration period (Nocera et al. 2008, Nocera and Ratcliffe 2010), whereas we found no evidence of a response.

The most common goal of using playback during point counts is to increase the likelihood of detecting individuals present within the survey area. Our results demonstrate that this goal was achieved for some, but not all, species. Consequently, understanding the nature of response to playback by individuals of target species is critical for effective use of this technique. Clearly, this becomes more difficult where investigators aim to census individuals of all species present in a survey area using point counts augmented with mobbing call playback. Differences in responses of different species to playback must be accounted for because, without such knowledge, our ability to interpret data collected for multiple species using playback may be limited. If the effect of playback is measured and occupancy or abundance is adjusted to account for

response to playback, then comparisons could even be made between counts within a study and with counts in other studies where standardized occupancy or abundance surveys were conducted. Where response to playback is deemed of interest, an approach that includes both silent and playback periods may be most effective in providing comparable data from the silent period, but also enhancing detection of some species with the use of playback, as we did in our study.

We consistently observed an increase in visual detections across species during playback compared with silent periods (Fig. 2-2), and Gunn et al. (2000) reported similar results during playback surveys of birds in coniferous forests in Quebec and New Brunswick. This increase in visual detections provides a greater opportunity to observe evidence of breeding, such as mate guarding, carrying nesting material, or carrying food to provision an incubating female or nestlings. All of these would help to confirm the breeding status (i.e., breeders vs. non-breeders) of responding birds. However, this does not always help estimate reproductive success (Doran et al. 2005). Playback may also be useful in studies requiring visual observations of birds, such as resighting surveys of marked individuals. In contrast to the increase in visual detections, we had fewer audio detections during playback periods than during silent periods for all species except Black-capped Chickadees, Boreal Chickadees, and Golden-crowned Kinglets (Fig. 2-2). This decline in auditory detections between treatments was apparent regardless of the effect that the playback broadcast had on species-specific detection probability. We believe that auditory detections were generally lower during the playback portion of the point count because the sound from the broadcast interfered with detection of at least some

individuals that were vocalizing, but not visible to observers. Also, chickadee mobbing calls may cause some species to be less vocal (e.g., Hermit and Swainson's thrushes; D. Whitaker, pers. observ.), perhaps in an effort to remain undetected when investigating a potential threat.

Ten of our focal species were also focal species in Mitchell and Donovan's (2008) study of the effect of playback on songbird detection probabilities in temperate forests of Vermont. In that study, the only habitat effect of playback was an increased detection probability for Hermit Thrushes. In contrast, we found a negative response to playback for Hermit Thrushes. Overall, however, results reported by Mitchell and Donovan (2008) were similar to ours, suggesting that species' responses to playback may be relatively consistent throughout their ranges. Further, although more regional and seasonal studies are needed to confirm their finding, Nocera et al. (2008) showed that Neotropical migrant birds responded to chickadee mobbing calls during migration, even in areas outside the normal range of Black-capped Chickadees.

Habitat-specific responses to playback were apparent for most of our focal species. Detection probabilities were generally higher in open-canopy and non-forest habitats, likely due to increased visibility. As suggested by Mitchell and Donovan (2008), birds also tend to have higher detection probabilities in habitats where they are typically found. For example, Magnolia Warblers, normally associated with dense, regenerating forest, were one of the few species in our study with higher detection probabilities in closed-canopy forest habitat. This may occur because birds are less likely to be territorial outside of their core habitat, and most species are more furtive when off territory, perhaps

to remain undetected by conspecifics during forays related to extrapair mating or intraspecific brood parasitism (Whitaker and Warkentin 2010). However, where there was a clear response to playback (positive for three species, negative for eight), this effect was evident regardless of habitat.

One of the assumptions of occupancy models is that occupancy remains constant across observation intervals (i.e., no immigration or emigration within the surveyed area; MacKenzie et al. 2006). To meet this assumption, we used all detections within an unlimited radius of point count centers. Using an unlimited radius count allowed us to include all individuals that could have potentially been responding to the mobbing call during both silent and playback periods. However, because detection probability decreases with increasing distance from the observer (Alldredge et al. 2007), birds attracted toward the point count center by playback broadcast, but not arriving because they have stopped at a territory boundary, may not have been detected. For example, Betts et al. (2005) found that Black-throated Blue (*Setophaga caerulescens*) and Black-throated Green warblers moved up to 175 m in response to playbacks, but not beyond their territory boundaries. As noted by Mitchell and Donovan (2008), this issue could be managed by incorporating a distance sampling approach (Buckland 2001) or by simply using only one of either silent or playback point counts in a given study. The distance moved by individuals responding to playbacks could also be an issue when using playbacks in studies designed to assess habitat relationships because birds may move between habitat types in response to playback. Thus, if studying habitat use, playbacks may be better suited for assessments at the landscape scale than at finer scales.

We could not test for temporal (i.e., seasonal) differences in response to playback in this study because each site was only visited once during the breeding season. Costs associated with predation vary throughout the breeding season; as such, responses to mobbing calls are likely not constant across breeding stages and this may be a useful topic for future research. However, because previous studies have documented species response to playback at various stages throughout the year, including fall migration (Nocera and Ratcliffe 2009) and winter (Turcotte and Desrochers 2002; see below also), we do not believe that variation in species responsiveness to playback during point count surveys had a large impact on our results.

Although our study was not specifically designed to assess observer effects, *post-hoc* tests identified differences among observers in the likelihood of detecting a particular species depending on the point count interval (silent versus playback). Detection probability varied among observers for Fox Sparrows, Hermit Thrushes, Northern Waterthrushes, and Yellow-bellied Flycatchers. In each case, detection probability was higher during the silent observation period than during playback, but was less consistent among observers while mobbing calls were broadcast. Fox Sparrows and Hermit Thrushes are furtive species that occupy the forest understory (Weckstein et al. 2002, Dellinger et al. 2012) and, as a result, visual detection is less likely, potentially reducing the effectiveness of playback. Similarly, Yellow-bellied Flycatchers have an abrupt, short-duration call (Gross and Lowther 2011) which makes them difficult to detect by ear, and perhaps even more difficult to detect with the added noise of the playback broadcast. In contrast, observers more consistently detected Black-and-white Warblers,

Blackpoll Warblers, Black-throated Green Warblers, Boreal Chickadees, and Magnolia Warblers during playback than during silent periods, but again the impact of playback on detection probability also varied among observers. For this latter group, the increase in visual detections (attributable to more aggressive defense of territory, e.g., Black-and-white Warblers; Kricher 2014) may have contributed to a higher detection probability during playback, although an explanation for the lack of consistency among observers is less apparent. We also identified two observers for whom the effect of playback differed from the rest of the group for several species. Although the observers trained together initially and worked closely together through the season, some apparently found it easier to detect certain species during playback. As with traditional point counts (Alldredge et al. 2007), observer differences can vary when playback is used and should be considered as a covariate when estimating detection probability and abundance or occupancy.

We built models to assess detection probability for a suite of the most common species of songbirds in our study area, i.e., ~20% of the species we observed, including two resident species (Black-capped and Boreal Chickadees). Our results (Table 2-1) support the suggestion of Turcotte and Desrochers (2002) that mobbing calls can be used to increase detection rates for resident species (similar to findings by Mitchell and Donovan 2008). Therefore, we suggest that broadcast of chickadee mobbing calls may be a valuable addition to point count surveys of boreal forest birds, and particularly resident species, if preceded by a silent observation period, as has been recommended for surveys in other biomes (Dettmers et al. 1999).

Playbacks may also be valuable for surveys conducted during non-breeding periods when detection probabilities are chronically lower because birds are more likely to be silent (Nocera and Ratcliffe 2009). Based on 285 point count surveys conducted in GMNP over three winters, >4.5 times as many birds were detected during playback than during the preceding silent point count period (D. Whitaker, unpubl. data). Further, all nine regularly occurring winter resident species (including Red-breasted Nuthatches, Golden-crowned Kinglets, Gray Jays, and three species of woodpeckers; see Table 2-1) were observed at least 1.5 times more often during playback portions of winter point count surveys than during the preceding silent period.

Finally, most species we observed were absent from >75% of sites, and 27 (or 47%) of these less common species were detected more often during the playback portion of point counts (Table 2-1). Thus, along with surveying resident species, broadcast of mobbing calls during point counts should be considered as an option for rare species, species with chronically low detection probabilities, or for periods when birds are less vocal and more likely to have lower baseline detection probabilities (e.g., during winter). In all cases, investigators conducting surveys where visual detection is important should consider using broadcast of mobbing calls.

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Table 2-1: Overall species prevalence, observations during silent and playback treatment intervals and as a percent of total sites surveyed (n=594) and observations expressed as a ratio of playback to silent detection types from point counts conducted in the 2010 breeding season throughout Gros Morne National Park, Newfoundland, Canada.

Scientific Name	Common Name	Migratory Status	Prevalence (%)	Treatment		Ratio (Playback: Silent)
				Silent (%)	Playback (%)	
<i>Empidonax alnorum</i>	Alder Flycatcher	Migrant	2.1	1.6	1.3	0.8
<i>Corvus brachyrhynchos</i>	American Crow	Resident	0.5	0.0	0.5	0.0
<i>Carduelis tristis</i>	American Goldfinch	Migrant	1.0	0.3	1.0	3.0
<i>Setophaga ruticilla</i>	American Redstart	Migrant	9.1	5.8	7.6	1.3
<i>Turdus migratorius</i>	American Robin*	Migrant	50.2	33.8	37.6	1.1
<i>Mniotilta varia</i>	Black-and-White Warbler*	Migrant	64.1	44.8	56.0	1.3
<i>Setophaga castanea</i>	Bay-breasted Warbler	Migrant	0.8	0.0	0.8	0.0
<i>Picoides arcticus</i>	Black-backed Woodpecker	Resident	0.3	0.3	0.3	1.0
<i>Poecile atricapillus</i>	Black-capped Chickadee*	Resident	41.7	12.2	39.0	3.2
<i>Vireo solitarius</i>	Blue-headed Vireo	Migrant	5.4	3.5	4.1	1.2
<i>Cyanocitta cristata</i>	Blue Jay	Migrant	0.8	0.5	0.5	1.0
<i>Setophaga striata</i>	Blackpoll Warbler*	Migrant	29.7	24.9	19.6	0.8
<i>Poecile hudsonicus</i>	Boreal Chickadee*	Resident	27.8	8.4	25.4	3.0
<i>Certhia americana</i>	Brown Creeper	Migrant	1.3	1.2	0.7	0.6
<i>Setophaga virens</i>	Black-throated Green Warbler*	Migrant	38.1	27.5	32.5	1.2
<i>Branta canadensis</i>	Canada Goose	Migrant	0.2	0.0	0.2	0.0
<i>Spizella passerina</i>	Chipping Sparrow	Migrant	0.5	0.5	0.2	0.3
<i>Gavia immer</i>	Common Loon	Migrant	0.2	0.0	0.2	0.0
<i>Corvus corax</i>	Common Raven	Resident	3.6	1.8	2.3	1.3
<i>Geothlypis trichas</i>	Common Yellowthroat	Migrant	7.6	7.2	5.4	0.8
<i>Junco hyemalis</i>	Dark-eyed Junco	Migrant	8.7	5.1	7.2	1.4
<i>Picoides pubescens</i>	Downy Woodpecker	Resident	5.4	1.2	4.9	4.3
<i>Passerella iliaca</i>	Fox Sparrow*	Migrant	16.0	13.7	9.2	0.7
<i>Regulus satrapa</i>	Golden-crowned Kinglet*	Migrant	18.6	12.4	14.2	1.1
<i>Catharus</i>	Gray-cheeked	Migrant	0.8	0.5	0.7	1.3

<i>minimus</i>	Thrush					
<i>Perisoreus canadensis</i>	Gray Jay	Resident	9.2	4.8	7.1	1.5
<i>Picoides villosus</i>	Hairy Woodpecker	Resident	5.8	2.3	4.6	2.0
<i>Catharus guttatus</i>	Hermit Thrush*	Migrant	17.1	11.5	11.2	1.0
<i>Empidonax minimus</i>	Least Flycatcher	Migrant	0.3	0.3	0.3	1.0
<i>Melospiza lincolnii</i>	Lincoln's Sparrow	Migrant	11.9	9.4	7.9	0.8
<i>Setophaga magnolia</i>	Magnolia Warbler*	Migrant	56.5	44.3	49.1	1.1
<i>Falco columbarius</i>	Merlin	Resident	0.5	0.3	0.2	0.5
<i>Zenaidura macroura</i>	Mourning Dove	Migrant	0.2	0.0	0.2	0.0
<i>Geothlypis philadelphia</i>	Mourning Warbler*	Migrant	20.6	16.3	17.1	1.1
<i>Setophaga coronata</i>	Yellow-rumped Warbler*	Migrant	44.6	28.0	37.1	1.3
<i>Colaptes auratus</i>	Norther Flicker	Resident	2.3	1.2	1.6	1.4
<i>Parkesia noveboracensis</i>	Northern Waterthrush*	Migrant	33.8	28.5	23.4	0.8
<i>Contopus cooperi</i>	Olive-sided Flycatcher	Migrant	3.1	2.6	2.3	0.9
<i>Seiurus aurocapilla</i>	Ovenbird	Migrant	4.1	3.3	2.8	0.9
<i>Setophaga palmarum</i>	Palm Warbler	Migrant	0.5	0.5	0.3	0.7
<i>Pinicola enucleator</i>	Pine Grosbeak	Resident	4.0	2.5	2.3	0.9
<i>Carduelis pinus</i>	Pine Siskin	Resident	1.0	0.8	0.7	0.8
<i>Haemorhous purpureus</i>	Purple Finch	Resident	3.1	2.3	1.6	0.7
<i>Sitta canadensis</i>	Red-breasted Nuthatch	Resident	4.0	1.0	3.5	3.5
<i>Regulus calendula</i>	Ruby-crowned Kinglet*	Migrant	48.3	33.6	41.5	1.2
<i>Vireo olivaceus</i>	Red-eyed Vireo	Migrant	0.2	0.2	0.0	0.0
<i>Passerculus sandwichensis</i>	Savannah Sparrow	Migrant	0.3	0.3	0.2	0.5
<i>Melospiza melodia</i>	Song Sparrow	Migrant	0.2	0.0	0.2	0.0
<i>Melospiza georgiana</i>	Swamp Sparrow	Migrant	1.8	1.5	0.7	0.4
<i>Catharus ustulatus</i>	Swainson's Thrush*	Migrant	37.9	26.0	28.2	1.1
<i>Oreothlypis peregrina</i>	Tennessee Warbler	Migrant	8.9	7.6	6.4	0.8
<i>Tachycineta bicolor</i>	Tree Swallow	Migrant	0.3	0.3	0.0	0.0

<i>Gallinago delicata</i>	Wilson's Snipe	Migrant	2.5	1.6	1.5	0.9
<i>Cardellina pusilla</i>	Wilson's Warbler	Migrant	7.7	5.8	5.9	1.0
<i>Troglodytes hiemalis</i>	Winter Wren	Migrant	5.1	4.4	3.8	0.9
<i>Zonotrichia albicollis</i>	White-throated Sparrow*	Migrant	56.7	48.9	39.0	0.8
<i>Loxia leucoptera</i>	White-winged Crossbill	Resident	4.9	3.8	2.1	0.6
<i>Empidonax flaviventris</i>	Yellow-bellied Flycatcher*	Migrant	49.8	42.5	37.2	0.9

*Species that were included in occupancy models

Table 2-2: Candidate set of models provided by Mitchell and Donovan (2008) that were used to test hypotheses about the influence of habitat type and playback of mobbing calls of Black-capped Chickadees on detection probability of songbirds during point count surveys during the 2010 breeding season in Gros Morne National Park, Newfoundland.

Model	Hypothesis	Full model	Parameters	Structural model for p
1	p is constant	$\Psi_{(habitat)}, p_1=p_2=p_3=p_4$	4	β_0
2	p is affected by habitat	$\Psi_{(habitat)}, p_1=p_2=p_3=p_4(habitat)$	6	$\beta_0 + \beta_1(nf) + \beta_2(oc)$
3	p is affected by habitat and p is modified by habitat during playback treatment	$\Psi_{(habitat)}, p_1=p_2, p_3=p_4(habitat)$	7	$\beta_0 + \beta_1(silent) + \beta_2(PB:nf) + \beta_3(PB:oc)$
4	p is affected by habitat and p is modified by habitat during silent treatment	$\Psi_{(habitat)}, p_1=p_2(habitat), p_3=p_4$	7	$\beta_0 + \beta_1(PB) + \beta_2(silent:nf) + \beta_3(silent:oc)$
5	p is affected by treatment	$\Psi_{(habitat)}, p_1=p_2, p_3=p_4$	5	$\beta_0 + \beta_1(silent)$
6	p is affected by habitat and p is modified by habitat uniquely for each treatment	$\Psi_{(habitat)}, p_1=p_2(habitat), p_3=p_4(habitat)$	9	$\beta_0 + \beta_1(silent:nf) + \beta_2(silent:oc) + \beta_3(PB:nf) + \beta_4(PB:oc) + \beta_5(PB:cc)$
7	p is affected by observer	$\Psi_{(habitat)}, p_1=p_2=p_3=p_4(observer)$	6	$\beta_0 + \beta_1(obs1) + \beta_2(obs2) + \beta_3(obs3)$
8	p is affected by observer and p is modified by observer during playback treatment	$\Psi_{(habitat)}, p_1=p_2, p_3=p_4(observer)$	7	$\beta_0 + \beta_1(silent) + \beta_2(PB:obs1) + \beta_3(PB:obs2) + \beta_4(PB:obs3)$
9	p is affected by observer and p is modified by observer during silent treatment	$\Psi_{(habitat)}, p_1=p_2(observer), p_3=p_4$	7	$\beta_0 + \beta_1(PB) + \beta_2(silent:obs1) + \beta_3(silent:obs2) + \beta_4(silent:obs3)$
10	p is affected by observer and p is modified by observer uniquely for each treatment	$\Psi_{(habitat)}, p_1=p_2(observer), p_3=p_4(observer)$	10	$\beta_0 + \beta_1(silent:obs1) + \beta_2(silent:obs2) + \beta_3(silent:obs3) + \beta_4(PB:obs1) + \beta_5(PB:obs2) + \beta_6(PB:obs3) + \beta_7(PB:obs4)$

nf=non forest
oc=open canopy forest
cc=closed canopy forest
silent=silent treatment
PB=playback treatment
 ψ = site occupancy
p = detection probability

Table 2-3: Top models ($\Delta AIC_c < 2$) describing the influence of habitat type and playback of the mobbing calls of Black-capped Chickadees on detection probability of songbirds during point count surveys during the 2010 breeding season in Gros Morne National Park, Newfoundland, including a list of model parameters estimated (see Table 2 for model descriptions). Where a difference between treatments was observed, the direction of the effect ($>$ [silent detection probability is greater than playback] or $<$ [playback detection probability is greater than silent]) is indicated^a.

Species	Model	Description	k	AIC _c	ΔAIC_c	Weight
American Robin	5	$P_{\text{silent}} > P_{\text{playback}}, \Psi_{\text{habitat}}$	5	2745.94	2.58	0.67
Black-and-white Warbler	5	$P_{\text{silent}} < P_{\text{playback}}, \Psi_{\text{habitat}}$	5	2644.11	2.86	0.68
Black-capped Chickadee	5	$P_{\text{silent}} < P_{\text{playback}}, \Psi_{\text{habitat}}$	5	1999.66	3.47	0.75
Blackpoll Warbler	6	$P_{\text{silent:habitat}} > P_{\text{playback:habitat}}, \Psi_{\text{habitat}}$	9	1664.35	0.53	0.43
	4	$P_{\text{silent}} > P_{\text{playback:habitat}}, \Psi_{\text{habitat}}$	7	1664.88	2.23	0.33
Black-throated Green Warbler	5	$P_{\text{silent}} > P_{\text{playback}}, \Psi_{\text{habitat}}$	5	1964.15	1.87	0.52
	4	$P_{\text{silent}} > P_{\text{playback:habitat}}, \Psi_{\text{habitat}}$	7	1966.02	1.89	0.20
	3	$P_{\text{silent:habitat}} > P_{\text{playback}}, \Psi_{\text{habitat}}$	7	1966.03	3.80	0.20
Boreal chickadee	5	$P_{\text{silent}} < P_{\text{playback}}, \Psi_{\text{habitat}}$	5	1393.79	0.34	0.46
	4	$P_{\text{silent}} < P_{\text{playback:habitat}}, \Psi_{\text{habitat}}$	7	1394.13	3.23	0.39
Fox sparrow	5	$P_{\text{silent}} > P_{\text{playback}}, \Psi_{\text{habitat}}$	5	1465.66	2.72	0.71
Golden-crowned kinglet	4	$P_{\text{silent}} < P_{\text{playback:habitat}}, \Psi_{\text{habitat}}$	7	1076.16	0.93	0.29
	2	$P_{\text{habitat}}, \Psi_{\text{habitat}}$	6	1077.08	1.19	0.18
	5	$P_{\text{silent}} < P_{\text{playback}}, \Psi_{\text{habitat}}$	5	1077.34	1.33	0.16
	6	$P_{\text{silent:habitat}} < P_{\text{playback:habitat}}, \Psi_{\text{habitat}}$	9	1077.49	1.50	0.15
	1	$P_{\text{intercept}}, \Psi_{\text{habitat}}$	4	1077.65	2.85	0.14
Hermit Thrush	5	$P_{\text{silent}} > P_{\text{playback}}, \Psi_{\text{habitat}}$	5	1869.37	3.89	0.77
Magnolia Warbler	2	$P_{\text{habitat}}, \Psi_{\text{habitat}}$	6	2429.61	0.84	0.52
	6	$P_{\text{silent:habitat}}, P_{\text{playback:habitat}}, \Psi_{\text{habitat}}$	9	2430.45	3.83	0.34
Mourning Warbler	5	$P_{\text{silent}} > P_{\text{playback}}, \Psi_{\text{habitat}}$	5	1262.14	0.22	0.43
	1	$P_{\text{intercept}}, \Psi_{\text{habitat}}$	4	1262.37	3.60	0.38
Northern Waterthrush	5	$P_{\text{silent}} > P_{\text{playback}}, \Psi_{\text{habitat}}$	5	2114.59	1.00	0.52
	4	$P_{\text{silent}} > P_{\text{playback:habitat}}, \Psi_{\text{habitat}}$	7	2115.58	3.30	0.32
Ruby-crowned Kinglet	3	$P_{\text{silent:habitat}} < P_{\text{playback}}, \Psi_{\text{habitat}}$	7	2603.80	0.64	0.50
	5	$P_{\text{silent}} > P_{\text{playback}}, \Psi_{\text{habitat}}$	5	2604.44	3.71	0.36
Swainson's Thrush	5	$P_{\text{silent}} > P_{\text{playback}}, \Psi_{\text{habitat}}$	5	2385.13	0.61	0.48
	3	$P_{\text{silent:habitat}} > P_{\text{playback}}, \Psi_{\text{habitat}}$	7	2385.74	3.31	0.35
White-throated Sparrow	6	$P_{\text{silent:habitat}} > P_{\text{playback:habitat}}, \Psi_{\text{habitat}}$	9	2296.09	24.36	1.00
Yellow-bellied Flycatcher	3	$P_{\text{silent:habitat}} > P_{\text{playback}}, \Psi_{\text{habitat}}$	7	2460.15	3.84	0.46
Yellow-rumped Warbler	2	$P_{\text{habitat}}, \Psi_{\text{habitat}}$	6	2207.28	0.87	0.33
	5	$P_{\text{silent}} < P_{\text{playback}}, \Psi_{\text{habitat}}$	5	2208.16	1.19	0.21
	4	$P_{\text{silent}} < P_{\text{playback:habitat}}, \Psi_{\text{habitat}}$	7	2208.47	1.36	0.18
	1	$P_{\text{intercept}}, \Psi_{\text{habitat}}$	4	2208.64	3.34	0.17

^aObserver effects (models 7, 8, 9, and 10; see Table 2-2) were not included in this comparison as they were examined *post-hoc*.

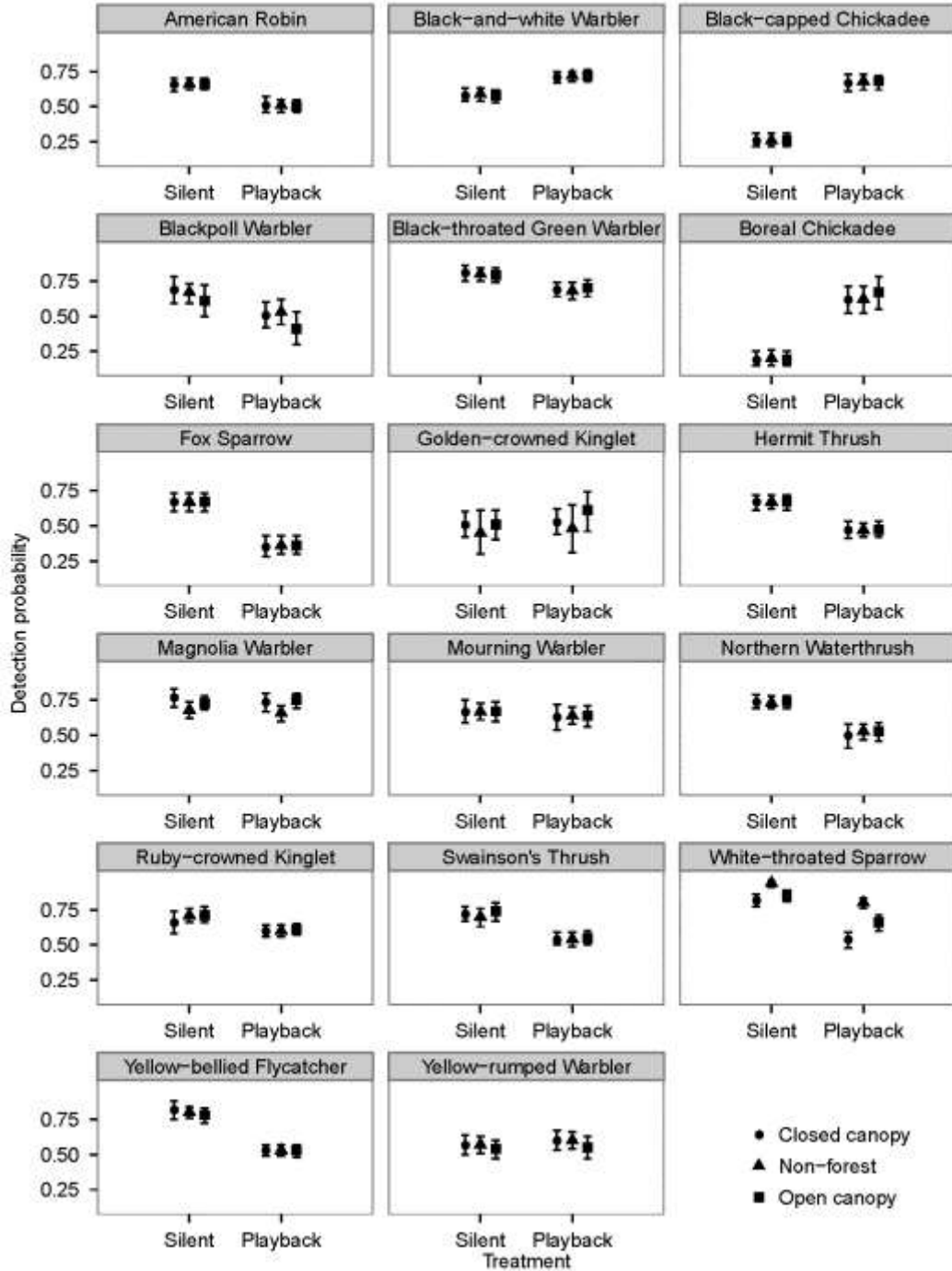


Figure 2-1: Model averaged parameter estimates (\pm SE) from 4-occasion occupancy models comparing detection probability across silent and playback intervals of point counts in different habitat types within Gros Morne National Park during the 2010 breeding season.

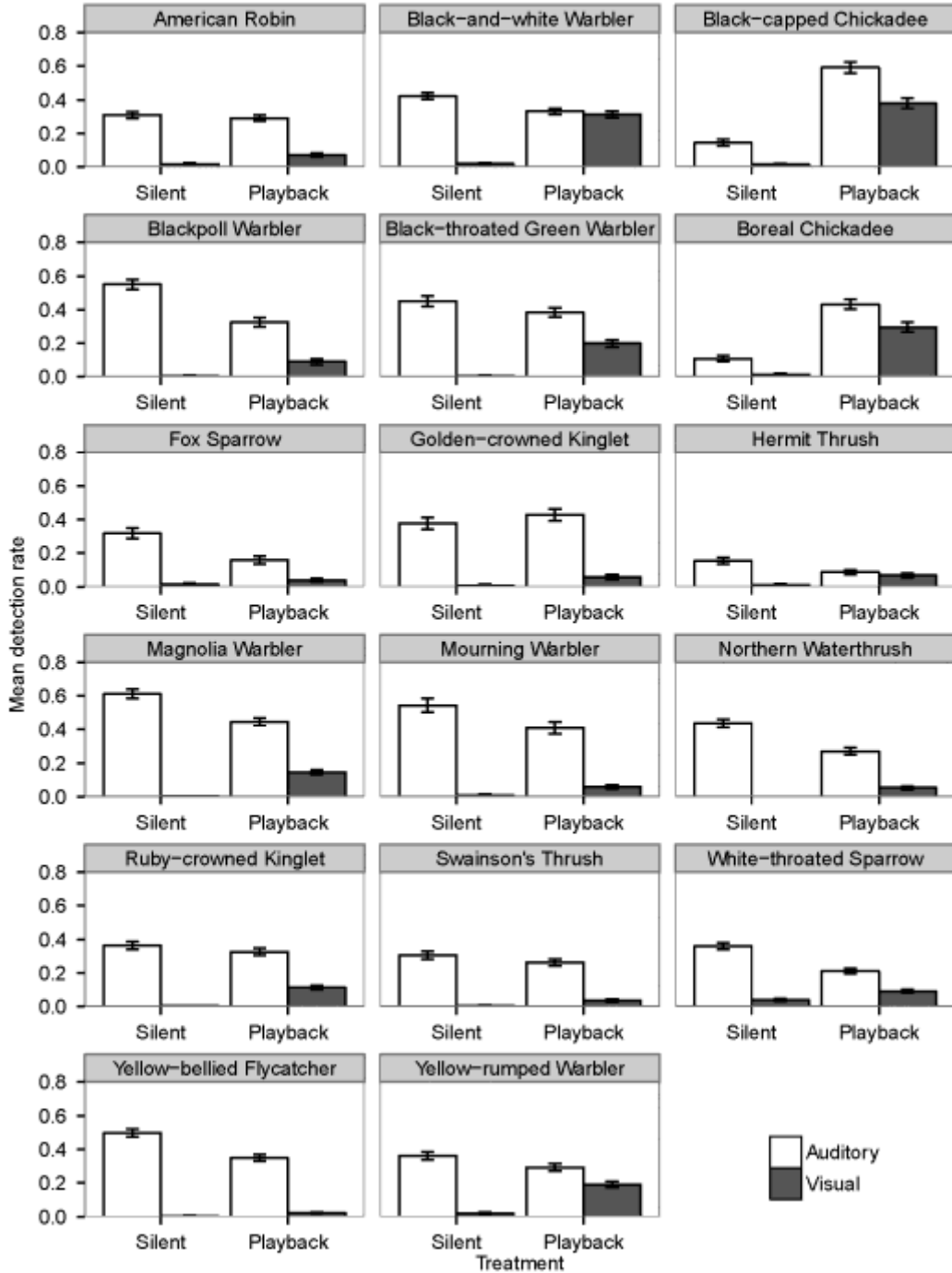


Figure 2-2: Mean number of visual and auditory detections across 8 minute silent and 8 minute playback portions of point count treatments within Gros Morne National Park during the 2010 breeding season.

3. Multiscale impacts of forest degradation through browsing by hyper-abundant moose (*Alces alces*) on songbird assemblages

3.1. Abstract

Aim

Songbirds are sensitive to changes in forest structure and composition at various spatial scales, particularly during the breeding season. Habitat degradation associated with herbivore browsing may contribute to declines in songbird populations. Here, we evaluate songbird responses to herbivore-induced habitat change at multiple spatial scales.

Location

In Gros Morne National Park (GMNP), Newfoundland, Canada, browsing by hyper-abundant moose (*Alces alces*) has changed forest structure by reducing understory cover and converting regenerating stands to open areas dominated by grasses and shrubs.

Methods

We conducted point count surveys to measure bird occurrence throughout GMNP during the 2010 breeding season. Using vegetation information from ground plots and remote sensing, we characterized habitat at three scales: local, neighborhood and landscape. Following a two-step procedure to model species occurrence with habitat, the most important habitat factors within each scale were retained for cross-scale modeling.

Results

Cross-scale models revealed patterns in the association of songbird habitat assemblages with moose-altered habitats. Early successional species such as mourning warbler (*Geothlypis philadelphia*) were positively associated with moose-browsed habitat at the landscape scale. Forest interior specialist (e.g. black-throated green warbler, *Setophaga virens*) and generalist species (e.g. boreal chickadee, *Poecile hudsonicus*) were negatively associated with moose-browsed habitat at the neighborhood scale. Local songbird species richness was independent of moose-browsed habitat at any scale.

Main conclusions

The influence of intense browsing on forest songbirds varies by species but has the potential to extend beyond the area of immediate impact. Continued intense browsing and resulting forest alteration could cause declines in forest specialists and generalists, but may increase populations of early successional species. To maintain bird assemblages characteristic of the region we recommend management actions that lower moose density in areas with hyper-abundant populations such as GMNP to maintain forest structure and regeneration comparable to that present prior to the introduction of moose.

Keywords: bird-habitat modeling, boreal forest, moose (*Alces alces*), multiscale, overabundance, songbirds

3.2. Introduction

Changes to forest structure may influence the ability of bird populations to persist (Urban & Smith, 1989; Holmes & Sherry, 2001; Millington et al., 2011). In particular, birds are sensitive to disturbances which modify canopy height and density (Marshall & Cooper, 2004), understory structure and composition (Heyman, 2010), and amount of forest cover in the surrounding landscape (Costello et al., 2000). Where these changes occur in breeding habitat, they can lead to reduced survival or productivity that result in population declines, or complete avoidance of modified habitat altogether (Schmiegelow & Mönkkönen, 2002). The effects of such changes to habitat structure and composition may be expressed at multiple spatial scales (Johnson, 1980; Luck, 2002; Taylor & Krawchuk, 2005). For example, bird distribution can be strongly related to local habitat characteristics such as stem density (DeGraaf et al., 1998), while changes to the composition and configuration of cover types at regional levels also can influence populations (McGarigal & McComb, 1995; Drapeau et al., 2000). In general, habitat selection is thought to follow a nested hierarchical pattern, with different factors influencing habitat use at different scales (Lawler & Edwards, 2006; Whitaker & Warkentin, 2010).

Disturbances that alter vegetation structure in temperate and boreal forests result from natural processes such as fire, windthrow, and insect infestation (Kurz et al., 1995) or from anthropogenic activities such as timber harvesting (Schneider et al., 2003). A third category of disturbance is grazing or browsing by herbivores (Weisberg & Bugmann, 2003; Nuñez et al., 2009) which can influence the structure of forest stands but

may also change habitat composition at the landscape scale (Alverson & Waller, 1997; McLaren et al., 2004; Beschta & Ripple, 2008). Habitat change resulting from browsing by large mammalian herbivores has been demonstrated to result in cascading impacts on birds (Martin et al., 2010).

Consequences of browsing for forest birds include reduced prey availability (Bailey & Whitman, 2003), decreased reproductive success (Pedersen et al., 2007), decreased body condition (Holt et al., 2013), and increased direct competition for resources (Leathwick et al., 1983). Ultimately, altered forest regeneration following grazing or browsing may lead to reduced occupancy by some species due to habitat degradation (Millington et al., 2011). At the community level, high ungulate browsing pressure has been associated with greater regional avian species diversity because of increased habitat heterogeneity (Ogada et al., 2008) or enhanced food resources linked to biogeochemical alterations that heighten plant productivity (Feeley & Terborgh, 2006). However, the extirpation of habitat specialists, such as riparian associated gray catbirds (*Dumetella carolinensis*) and MacGillivray's warblers (*Oporornis tolmiei*; Berger et al., 2001), has been attributed to reduced availability of sites for nesting and foraging. In particular, diminished bird abundance has been associated with reductions in understory vegetation density through browsing by hyper-abundant white-tailed (*Odocoileus virginianus*; DeCalesta, 1994; McShea & Rappole, 2000) and black-tailed deer (*Odocoileus hemionus*; Allombert et al., 2005; Martin et al., 2011; Chollet & Martin 2013).

With the exception of Cardinal et al. (2012) who studied the impact of white-tailed deer in a boreal setting, most studies have assessed browse-related changes to temperate forest songbird communities (Alverson & Waller, 1997; McShea & Rappole, 2000; Allombert et al., 2005). Here we present a study examining the impact of moose (*Alces alces*) which were introduced to the island of Newfoundland, Canada approximately 100 years ago and have since proliferated to occupy most suitable habitat on the island (Bergerud & Manuel, 1968; Gosse et al., 2011). We focused on the hyper-abundant moose population of Gros Morne National Park (GMNP) in western Newfoundland; an extensive area containing a mosaic of forest types exhibiting a range of moose-induced habitat change. We took a natural experiment approach that incorporated the variable impact of moose browsing; however, given the absence of hunting in this national park, moose impacts are pervasive and there was no unbrowsed control. Overall, our study contributes to a broader assessment of the ecological consequences of high ungulate populations and to a better understanding of the role and potential cascading impacts of large carnivores, and/or hunting, on biodiversity in northern forests. Specifically, we investigated the influence of moose browsing on forest bird occurrence at multiple spatial scales. In particular we assessed the occurrence of birds: (1) at the level of species and communities in the context of varying extents of impaired forest regeneration associated with intense moose browsing, and (2) as a function of habitat degradation levels associated with moose browsing at multiple spatial scales. To understand current and potential future impacts, we developed and evaluated

habitat models containing variables that represent both healthy and impaired regenerating habitats.

3.3. Materials and Methods

3.3.1. Study area

GMNP (49°29'00"N, 57°40'00"W; Fig. 3-1) is characterized by forest covering 44% of the total area and found primarily in the two ecoregions (of three found in the park) to which our sampling was restricted: the Northern Peninsula and Western Newfoundland Forest ecoregions (Damman, 1983). The Northern Peninsula ecoregion occupies the coastal plain west of the Long Range Mountains. Habitat is naturally patchy in this ecoregion and forest stands are interspersed with bog, softwood scrub, and lakes. Annual precipitation ranges from 900 to 1150 mm (Bajzak and Roberts, 1996). The Western Newfoundland Forest ecoregion is more productive, supports greater tree growth and a greater proportion of mixed conifer-deciduous forest and mean precipitation ranges from 1200 to 1300 mm (Banfield, 1983). Sampled stands were dominated by balsam fir (*Abies balsamea*) with varying amounts of white birch (*Betula papyrifera*), white spruce (*Picea glauca*) and black spruce (*Picea mariana*) comprising <50% of canopy trees. The primary natural disturbance agent is infestation by hemlock looper (*Lambdina fiscellaria*) and spruce budworm (*Choristoneura fumiferana*).

Intense and selective browsing by moose across Newfoundland has altered vegetation community composition, successional trajectory, and soil characteristics of the island's balsam fir-dominated forests (McLaren et al., 2004). In GMNP, the density of

preferred woody browse species such as Canada yew (*Taxus canadensis*), white birch saplings, and mountain maple (*Acer spicatum*) have all been severely reduced (Connor et al., 2000). Loss of these species dramatically increased the browsing pressure on less-palatable but more available balsam fir (Connor et al., 2000). In mature balsam fir-dominated stands, browsing by moose on most understory woody plants, in combination with the advanced regeneration of fir saplings, translates to reduced density and diversity of understory vegetation (Whitaker & Gallant, Parks Canada, unpublished data). Where mature forest stands are lost by natural disturbance or senescence, regenerating stands in areas with hyper-abundant moose are characterized by heavily damaged balsam fir saplings that display growth stunted to less than 0.6 m height by repeated browsing of the leader; this browsing eventually leads to the death of saplings and greatly reduced sapling density (Bergerud & Manuel, 1968; Gosse et al., 2011). With sapling regeneration impaired, suppressed sun-loving shrub and herb species become the dominant cover type. This leads to the creation of open “moose meadows”, characterized by grasses, ferns, non-palatable woody shrubs and a low density canopy of less palatable spruce and mature white birch (Gosse et al., 2011).

Analysis of SPOT5 satellite imagery for GMNP from 2006 indicated low regeneration rates following insect outbreaks in recent decades; only 44% or 42.4 km² of mapped forest disturbances exhibit normal regeneration patterns (Taylor & Sharma, Parks Canada, unpublished data). Insect-disturbed patches range in size from 0.5 to 60.4 ha (mean 0.64 ha; Taylor and Sharma, Parks Canada, unpublished data), with failed regeneration at these sites primarily attributed to browsing by moose. Moose populations

increased dramatically when GMNP was established in 1973 and hunting was prohibited; contemporary densities are ~3 moose/km² overall but often exceed 10 moose/km² in high-quality forest habitat (Parks Canada, unpublished data; McLaren et al., 2000). The cumulative effect has been the creation of large areas of severely impaired balsam fir regeneration similar to that observed on Isle Royale in Lake Superior (Pastor et al., 1988; McLaren et al., 2004). In the two national parks on the island of Newfoundland, the failure of up to 12% of forest stands to regenerate to typical tree composition following disturbance has been associated with the browsing activities of hyper-abundant moose (Gosse et al., 2011).

Sampled sites were chosen from a set of 3485 points randomly distributed across the study area using ArcGIS 9.2 (ESRI, 2008) and based on the following initial criteria: greater than 20 m from edge of the stand, situated within a stand of at least 1 ha, >300 m from the nearest neighboring point. In total, 590 sites from the complete set of random points were sampled (Fig. 3-1). Sites were also selected based on accessibility by foot as determined by topography and proximity to trails or roads. Where the initial point was less than 50 m from the stand edge, observers relocated the point further into the target stand at the time of sampling to meet the point count criteria described below. Each site was classified by forest type using Forest Resource Inventory (FRI) for GMNP, and an effort was made to visit a roughly even number of mature, regenerating, and disturbed forest sites.

3.3.2. Bird surveys

From 3 June to 8 July 2010, four trained observers conducted fixed-radius point counts of forest birds (Ralph et al., 1995). Only birds detected within 50 m of the point were included to ensure they were associated with the target habitat (Petit et al., 1995). Points were visited once during the season and counts took place between 0.5 h before sunrise and 10:30 h NST. Surveys were not conducted during periods of rain or high wind. Each count consisted of an 8-minute silent listening period followed by an 8-minute broadcast of black-capped chickadee (*Poecile atricapillus*; hereafter, scientific names of birds are given in Table 3-2) predator mobbing calls. Broadcasting chickadee mobbing calls has been shown to elicit responses from a variety of forest birds and is presumed to increase detection rates (Hurd, 1996; Gunn et al., 2000; Betts et al., 2007). Counts of all birds detected either through auditory or visual means were recorded for each 8-minute interval. Preliminary comparisons between silent and playback periods showed greater detections of species with the use of playbacks. All species were grouped according to habitat assemblage following Whitaker & Montevercchi (1997) to aid in summary and comparison of responses across species.

3.3.3. Habitat sampling

While Betts et al. (2006) suggest that remotely-sensed habitat data provide sufficient information to accurately predict the occurrence of most forest bird species, we supplemented the GMNP FRI data by conducting ground plot surveys at each site. Of particular interest with respect to the impact of browsing is the height and density of vegetation cover below the forest canopy (DeCalesta, 1994; McShea & Rappole, 2000;

Allombert et al., 2005), which cannot be estimated using remote-sensing techniques. We assessed habitat characteristics, defined by their spatial extent and resolution of measurement, for three spatial scales: local, neighborhood, and landscape. Local scale habitat represented fine resolution data collected through ground plots sampled within 20 m of each point count. Coarse resolution information was determined at two broader spatial extents: within 115 m of a point count center or 4.2 ha, a neighborhood area comparable to songbird territory sizes in the region; and within 1250 m of a point count center or 490.9 ha, a landscape comparable to songbird home range sizes in the region (Leonard et al., 2008).

3.3.4. Local scale habitat

We characterized local stand structure through the number of stems within a 2 m-wide plot, beginning at the point count center and extending 20 m to the north. Stems were categorized (and referred to in models) as >5 cm Diameter at Breast Height (dbh, i.e., at 1.3 m; ‘trees’), or <5 cm dbh (‘saplings’), and density (stems/ha) for each stem category was calculated. To assess whether site-level browse intensity directly influenced forest bird occurrence, we calculated the proportion of all saplings that had been browsed (‘browse’ in models; Table 3-1). This measure did not capture local habitat structure directly, but reflected the intensity of recent browse pressure across sites. To characterize vertical habitat structure we estimated the extent of woody vegetation cover types (shrub, deciduous and coniferous trees) for understory levels (height classes 0 to 0.5 m, 0.5 to 1 m, and 1 to 2 m from the ground) and canopy levels (2 to 5 m, and >5 m) within three 2x2 m plots located at the beginning, middle, and end of the 20 m plot described above.

We assigned a score (0: 0%, 1: 1-25%, 2: 26-50%, 3: 51-75%, 4: 76-100%) to each cover type for all height classes reflecting the extent of cover attributed to each vegetation type. To indicate overall understory and canopy cover for use in models we summed cover scores across plots and cover type for both general categories ('under' and 'canopy'; Table 3-1). Lastly, we classified site habitat as 'forest' or 'impaired' based on vegetation within 50 m of the point count. This categorical variable was not used in models but allowed us to make comparisons between sites having any forest cover and those having severely impaired regeneration of forest.

3.3.5. Neighborhood and landscape scale habitat

Coarse-scale measures of habitat were obtained from the Parks Canada's FRI database updated to include information on regeneration of disturbed sites derived from 2006 SPOT5 satellite imagery. A K-mean unsupervised classification categorized stages of regeneration with 85% accuracy (Taylor & Sharma, unpublished report). General classification of land was based on forest attributes including land cover type (e.g. forest, bog, water, etc.), forest stand height, age class (0-39, 40-59, 60-79 and >80 years), dominant tree species, and dominant tree type (e.g. hardwood or softwood). For model development, we extracted the amount of cover for the following forest types: mature softwood forest, mature mixedwood forest, immature forest, and failed regenerating forest ('SW', 'MW', 'immature', and 'failed' in models, respectively). Mature softwood forest included balsam fir, black spruce, and white spruce dominated stands in age classes >40 years. Mature mixedwood cover was comprised of stands dominated by white birch or trembling aspen (*Populus tremuloides*) or those stands containing a mixture of

hardwood and softwood. Immature forest included all forest types in the <40 years age classes. Failed regenerating forest included stands where cover was classified as forest or regenerating forest during the 1995 forest inventory, then registered as open grassland on SPOT5 satellite imagery in 2006, presumably due to insect disturbance followed by poor regeneration. We excluded 35 sites located within 1250 m of the park border because SPOT5 data were not available for lands outside the park boundary.

3.3.6. Data analysis

We examined all habitat variable pairings for collinearity using graphical methods and Spearman correlation coefficients. Where collinearity was present ($r > 0.5$; Dormann et al., 2013) we eliminated from analyses the variable which was less effective in providing a biological explanation for patterns determined (Booth et al., 1994). Coarse resolution habitat information at the neighborhood extent is by definition nested within the landscape extent, therefore high correlation was expected and observed; we did not include these variables in the same models.

We limited species-focused analyses to those species observed at more than 25% of points. Data from both silent and playback intervals were used; however, since mean abundance of individuals per species per site was low (< 2), we converted counts to presence/absence. The data were analyzed using generalized linear models with a binomial error structure and logit link (i.e., logistic regression; Vernier et al., 2002). To model species richness, the total number of species at each site regardless of overall prevalence, we used a general linear model (i.e., linear regression). Residual plots were

evaluated to ensure that regression model residuals met the assumptions of normality, independence and homogeneity. We used R version 2.13.0 for all analyses (R Development Core Team, 2004).

We took an information theoretic approach to model building which allowed us to select those variables that were more important at a given single scale (i.e., local, neighborhood, or landscape) than a randomly generated variable, for further consideration in multiscale analyses (Whittingham et al., 2005; Dallimer et al., 2012). Specifically, we took a two-step approach to assessing habitat associations. First, we compared all possible combinations of variables for each scale separately. Models in each set were ranked according to Akaike's Information Criterion corrected for small sample sizes (AIC_c). AIC_c measures model fit but penalizes for complexity (i.e. more variables); smaller values indicate a more parsimonious model (Burnham & Anderson, 2002). We then compared models using Akaike weights (ω_i). For each variable, we determined relative importance by summing ω_i across models containing the variable (Burnham & Anderson, 2002). Since relative importance values are not expected to be zero even for poor predictors, we repeatedly ran each model set with the addition of a new variable that was randomly generated from a uniform distribution (Whittingham et al., 2005). The upper 80% confidence limit on the random variable from 1000 repetitions was used as a threshold beyond which variables were retained for use in cross-scale models. To determine the relative contributions of important habitat information at different scales, cross-scale models were built using those variables from single-scale models that had a higher relative importance than the upper confidence limit of the randomly generated

variable. A null model was included as a reference in the cross-scale model set. If no variables from a single-scale model were more important than the randomly generated variable, this scale was excluded from cross-scale analysis. Therefore, the maximum number of models entering the cross-scale stage was six (local; neighborhood; landscape; local + neighborhood; local + landscape; null). From this cross-scale model set, we determined 95% confidence sets (i.e. the smallest subset of models where ω_i sums to 0.95).

3.4. Results

Across the 590 points sampled we detected 65 species, of which 17 were present at more than 25% of sites (Table 3-2). Mean incidence per point of these common species ranged from 0.11 to 0.76 for forested sites (n=367 sites) and 0.07 to 0.86 for impaired sites (n=203), while total species richness values ranged from 3 to 17 species for forested sites and 4 to 19 for impaired sites (Table 3-2) when all species encountered were included. Of the 17 species found at more than 25% of sites, only black-capped chickadee and boreal chickadee were year-round residents of the region; the remainder were short or long-distance migrants. These 17 species represented five habitat associations: forest generalist, forest interior, early successional forest, riparian and ubiquitous (Table 3-2).

Prior to model-building, pair-wise comparisons of 13 habitat variables revealed that tree density and canopy cover were correlated ($r=0.72$); tree density was retained for the analyses because density units are more easily interpreted than coded vegetation cover values. Therefore, four habitat variables were used for each scale (see Table 3-3).

3.4.1. Individual species occurrence

For all 17 species, there was at least one variable at the neighborhood scale that was more important than the randomly generated variable in logistic regression models examined at the single-scale modeling stage for species occurrence (Table 3-3). A similar pattern emerged for landscape scale habitat measures, with the exception of black-capped chickadees for which no variable at this scale was important. Among the four variables examined at both of these broader scales, the extent of mature mixedwood forest cover at the neighborhood scale and the extent of failed regenerating forest at the landscape scale were most prominent, particularly for forest generalist and interior assemblages. At the local scale, four species (American robin, black-and-white warbler, black-capped chickadee, yellow-bellied flycatcher; Table 3-3) displayed no influence by local scale variables, nor were any of the variables assessed at this scale prominent across species within a given habitat assemblage.

Cross-scale models for each species reflected similar patterns of influence by variables at the three spatial scales (Table 3-4). Between one and four (of a maximum six) models were included in 95% confidence sets of cross-scale models, and all three scales occurred in models for many species (local: 13 species; neighborhood: 10; landscape: 15). For five species (blackpoll warbler, boreal chickadee, golden-crowned kinglet, hermit thrush, ruby-crowned kinglet), habitat information from all three scales appeared to be important. Within these cross-scale logistic regression models, local scale influences of understory cover were varied: probability of occurrence for three species (fox sparrow, hermit thrush, magnolia warbler) increased with increasing understory

cover, but decreased for three other species (black-throated green warbler, golden-crowned kinglet, yellow-rumped warbler). The proportion of saplings with browsed leaders was an important predictor for the probability of occurrence for only three species, of which the relationship was positive for one (northern waterthrush) and negative for two (black-throated green warbler, golden-crowned kinglet). The amount of severely impaired regeneration at the neighborhood scale (115.failed) was included in the best cross-scale model set for five species (blackpoll warbler, boreal chickadee, golden-crowned kinglet, yellow-rumped warbler, ruby-crowned kinglet). The direction of effect for this variable was always negative, indicating that as the amount of impaired regeneration increased occurrence rates for these species decreased. Amount of severely impaired regeneration at the landscape scale (1250.failed) was included in the top model set for nine species. However, at this scale, the amount of impaired regeneration showed a positive relationship with occurrence for five species (black-and-white warbler, fox sparrow, hermit thrush, mourning warbler, white-throated sparrow) but a negative relationship for the other four (boreal chickadee, black-throated green warbler, golden-crowned kinglet, ruby-crowned kinglet).

3.4.2. Species richness

Among single-scale models there were no important stand-level predictors for species richness, however, forest cover measured at the neighborhood (115.MW) and landscape (1250.MW and 1250.SW) scales were important (Table 3-3). Cross-scale models revealed that species richness patterns were mostly driven by habitat at the landscape scale. Specifically, species richness was negatively associated with the amount of

mixedwood forest (1250.MW), and positively associated with the amount of softwood forest (1250.SW; Table 3-4).

3.5. Discussion

3.5.1. Individual species occurrence

Habitat changes resulting from browsing by hyper-abundant moose influenced the distribution of birds at local, neighborhood, and landscape scales. The nature of the association between habitat change and occurrence rate, as reflected in altered vegetation structure and landscape composition, varied across species. Likewise, the spatial scale at which species responded to habitat change ranged from one to all three scales. However, some general trends within bird-habitat associations were apparent (Fig. 3-2). Not surprisingly, the probability of occurrence for five of nine species in the forest generalist and interior forest assemblages, including boreal chickadee and black-throated green warbler, increased with increasing amounts of mature softwood or mixedwood forest cover at either the neighborhood or landscape scale. Similarly, occurrence for two of three species linked to early successional forest habitat increased with the amount of severely impaired regeneration cover at the landscape scale. In contrast, occurrence rates for species from all other assemblages were more often negatively associated with the amount of severely impaired regeneration at the neighborhood spatial extent.

Responses to habitat change brought about by intensive moose browse were consistent with expectations based on general habitat associations of the birds assessed. Particularly notable was the relationship between occurrence and the importance of

understory vegetation cover to provide nest concealment and foraging substrate. Previous studies reporting the impacts of deer browsing on songbirds have shown sensitivity to fine-scale changes in stand structure (McShea & Rappole, 2000; Allombert et al., 2005; Cardinal et al., 2012). Results from these studies support the hypothesis that species with a strong dependence on understory vegetation are negatively affected by browsing. Along these lines, we found a negative relationship between understory cover and the occurrence of species that nest relatively low to, or on the ground and have strong dependence on thick, low vegetation cover or dense, young conifer stands for nest concealment (fox sparrow, hermit thrush, magnolia warbler; Poole, 2005).

3.5.2. Species richness

Though changes in vegetative cover associated with browse damage had an influence on the presence of several species, there was no net effect of browse-related habitat change at any scale on site-level species richness (i.e. alpha diversity). Comparing across browsed and deer-free islands in British Columbia, Canada, Allombert et al. (2005) found that each island type supported the same number of species, but also that islands with and without deer had differing songbird community compositions. We lacked a true control area with complete exclusion of browsing activity and could not make the same comparisons between browsed and unaffected forest stands, nor did we find the same dramatic differences in bird abundance and species composition that others observed (see Chollet & Martin, 2013 for overview). However, the lack of relationship between species richness and moose-browsed habitat in our study is consistent with the pattern seen elsewhere and likely reflects the creation and persistence of early successional habitat

patches, within otherwise continuous forested areas, that increased habitat heterogeneity in the landscape. Such habitat modification may promote regional bird diversity, as has been seen previously with forest harvest disturbance (Drapeau et al., 2000). However, this apparent increase in diversity may come at a cost to the forest specialist species present, which decrease due to declines in both total forested area and continuity of forested habitat (Morgan & Freedman, 1986). DeCalesta (1994) found reduced species richness for birds nesting in the intermediate canopy (<7.5m) of temperate forests with a high deer density. Likewise, forest specialists such as yellow-bellied flycatcher have been shown to decline when habitat within 2000 m (i.e., at a landscape scale) declines below a threshold of 28.7% cover (Betts et al., 2010).

Higher avian species richness in temperate forests is typically associated with more diverse stands (Forsman et al., 2010) and, within homogenous stands, hardwood forest often supports a greater bird diversity than softwood forest (James & Wamer, 1982; although see Willson & Comet, 1996; Donald et al., 1998 for contrary results). Among boreal forest softwood types in Canada, balsam fir stands are reported to support the highest number of breeding bird species (Erskine, 1977). In GMNP, bird species richness was positively associated with softwood forest cover and negatively associated with mixedwood cover, both at the landscape scale. This may reflect the tendency for the majority of the most common species that prefer boreal softwood to also be found in areas with higher levels of deciduous cover (e.g. yellow-rumped warbler and black-throated green warbler, Hunt & Flaspohler, 1998; Morse & Poole, 2005). In contrast, few of the most common species in our study prefer areas with deciduous or mixedwood

forests over softwood-dominated stands (e.g. black-capped chickadee and Swainson's thrush, Mack & Yong, 2000; Foote et al., 2010). Consequently for our region, the greatest diversity could be expected to occur in areas with high softwood cover.

3.5.3. Local and broad-scale influence of browsing

We used habitat associations to assess the response of forest birds to habitat degradation linked to moose browsing. However, expected habitat associations are not always an ideal representation of habitat quality because other processes could also influence a population (Van Horne, 1983; Lindenmayer & Fischer, 2006). Furthermore, habitat degradation is often confounded with habitat fragmentation and isolation (Schmiegelow & Mönkkönen, 2002; Fahrig, 2003; Ewers & Didham, 2006). These latter processes further influence bird populations indirectly through loss of connectivity between patches due to isolation (e.g. Dorp & Opdam, 1987; Andrén, 1994; Uezu et al., 2005), and increased edge effects within remnant intact habitat patches (e.g. Wilcove, 1985; Murcia, 1995; Flaspohler et al., 2001). However, others have found that landscape composition is a better predictor of bird occurrence than habitat configuration (McGarigal & McComb, 1995; Drapeau et al., 2000). It has also been suggested that only when suitable habitat is decreased to <30% cover will patch size and isolation become important factors in species distribution (Andrén, 1994). Therefore, while we did not control directly for effects beyond changes in habitat structure and landscape composition, we believe that our measures of response were appropriate in terms of anticipated changes to bird communities in GMNP over the coming decades.

We used the same set of predictor variables for each species. However, habitat is a species-specific concept, and different variables and scales may not have the same influence on all species. A species-centered approach, where species distribution models are developed to reflect biologically-meaningful habitat relationships to control for differences in species perception (Betts et al., 2014), may have increased the accuracy and precision of this study enough to identify more general effects of moose-browsed habitat on songbirds.

While studies relating bird assemblages to the amount of habitat degraded by herbivores across multiple spatial scales are uncommon, our approach to assessing the impacts of moose browsing on birds was similar to that used when examining the influence of other disturbance types – both natural (fire; Hobson & Schieck, 1999) and anthropogenic (forest harvest; Drapeau et al., 2000; Taylor & Krawchuk, 2005; Bayne et al., 2010). Whatever the disturbance type, breeding birds select territories in these environments that meet their requirements for feeding (Marshall & Cooper, 2004) and nesting (Matsuoka et al., 1997). However, throughout the breeding season, individuals are also known to use habitat beyond their territory boundaries for activities such as foraging, extra-pair copulation, and rearing fledglings (Whitaker & Warkentin, 2010). Our study demonstrates the importance of evaluating the impacts of habitat degradation at broader spatial extents on bird occurrence. Using the same spatial extents as our study, Taylor & Krawchuk (2005) found that hermit thrush, northern waterthrush, and yellow-bellied flycatcher in western Newfoundland did not respond to habitat characteristics within 150 m radius of point counts (analogous to, but slightly greater than, our

neighborhood scale), but did respond to habitat features at broader spatial scales. In contrast, we identified important links to habitat characteristics for these three species at both the neighborhood and landscape scales. While this discrepancy could be attributed to regional or temporal variation in habitat types or habitat selection (e.g. Whitaker et al., 2006), it may simply reflect differences in the how habitat structure was measured at varying spatial scales.

The long-term dynamics of songbird assemblages in our study area depend largely upon the management of hyper-abundant moose. Zhu et al. (2010) examined potential future forest cover conditions in GMNP under different moose browse scenarios. They predicted that continued intense browsing by moose over the next 160 years would cause balsam fir cover to decline by 47-50%, and that many failed balsam fir regeneration sites would convert to open stands of white spruce (Zhu et al., 2010). Given our knowledge of songbird habitat requirements, we predict that populations of birds associated with open habitats or low density forest cover such as mourning warbler, black-and-white warbler, fox sparrow, and white-throated sparrow will increase with continued high intensity moose browsing. However, populations of mature forest specialists such as boreal chickadee, golden-crowned kinglet, black-throated green warbler, and yellow-rumped warbler will all likely decline in the park, as will species associated with high stem density habitats such as blackpoll warbler, northern waterthrush, and magnolia warbler. To maintain regional boreal bird assemblages in GMNP, management actions are required to alleviate the intense browsing pressure and enhance the recovery of palatable vegetation types. A pilot moose harvest to reduce

populations was conducted in GMNP during the 2011 and 2012 hunting seasons. However, even if browsing pressure is reduced through continued moose hunting, severely impaired regenerating areas may require additional active management to restore the native forest ecosystem (Humber, 2009; McLaren et al., 2009; Tanentzap et al., 2011). Under similar circumstances, ecosystem recovery was achieved following the reduction of hyper-abundant herbivores through culling in southern New Zealand (Tanentzap et al., 2009) and the reintroduction of predators to Yellowstone National Park, U.S.A. (Beschta & Ripple, 2008).

The broader ecological consequences of browse damage by expanding large mammal populations in forested ecosystems are twofold. First, as we have shown, the influence of intense browsing activity on stand structure and composition is expressed across a range of spatial scales that differs by species; thus this influence may not be localized but could extend beyond the area of immediate impact and into the surrounding landscape. Second, the influence of these browsing activities is expressed not only through changes to occurrence rates, but also through the impact that these changes have on the composition of avian assemblages in the wider landscape. However, our ability to understand the potential for these impacts to extend further into the community is limited by our lack of detailed knowledge about the ecosystem services provided by avian members in the communities involved (Sekercioglu 2006).

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Table 3-1: Description and mean (range) values of habitat predictor variables from three spatial scales used in logistic regression analyses

Variable	Description	Mean (range)
<i>Local</i>		
Trees	Density of trees (>5 cm dbh) per ha	2400 (0-14500)
saplings	Density of saplings (<5 cm dbh) per ha	5600 (0-51800)
Browse	Proportion of total saplings that have browsed leaders	0.45 (0-1.0)
under_cover	Sum of cover score for trees and shrubs between 0.5 and 2 m	12.0 (0-29)
<i>Neighborhood</i>		
115.immature	Area (ha) of SW, MW and regenerating forest <40 years within 115m radius	1.11 (0-4.15)
115.failed	Area (ha) of failed regeneration within a 115m radius	0.39 (0-4.07)
115.mwmature	Area (ha) of MW >40 years within a 115 m radius	0.75 (0-4.15)
115.swmature	Area (ha) of SW >40 years within a 115 m radius	1.12 (0-4.15)
<i>Landscape</i>		
1250.immature	Area (ha) of SW and MW <40 years within a 1250 m radius	100.13 (2.09-258.12)
1250.failed	Area (ha) of failed regeneration within a 1250 m radius	21.05 (0-163.57)
1250.mwmature	Area (ha) of MW >40 years within a 1250 m radius	66.24 (0-318.87)
1250.swmature	Area (ha) of SW >40 years within a 1250 m radius	96.85 (3.46-312.47)

MW = mixedwood (white birch dominated, or softwood-white birch mix)

SW= softwood (balsam fir or spruce dominated stands)

Table 3-2: Common and scientific species names and mean incidence (SD) per point across forested (n=367) and impaired (n=203) habitats in Gros Morne National Park, Newfoundland during the 2010 breeding season. * indicates species for which browsed habitat was revealed to influence species occurrence in occupancy models.

Common name	Scientific name	Code	Incidence	
			Forested	Impaired
<i>Forest Generalist</i>				
Black-and-white Warbler*	<i>Mniotilta varia</i>	BAWW	0.76 (0.49)	0.86 (0.44)
Black-capped Chickadee	<i>Poecile atricapillus</i>	BCCH	0.43 (0.50)	0.39 (0.49)
Boreal Chickadee*	<i>Poecile hudsonicus</i>	BOCH	0.30 (0.46)	0.20 (0.40)
Golden-crowned Kinglet*	<i>Regulus satrapa</i>	GCKI	0.43 (0.43)	0.07 (0.25)
Ruby-crowned Kinglet*	<i>Regulus calendula</i>	RCKI	0.56 (0.50)	0.36 (0.48)
<i>Interior</i>				
Black-throated Green Warbler*	<i>Setophaga virens</i>	BTNW	0.41 (0.49)	0.28 (0.45)
Hermit Thrush*	<i>Catharus guttatus</i>	HETH	0.16 (0.37)	0.20 (0.40)
Swainson's Thrush	<i>Catharus ustulatus</i>	SWTH	0.44 (0.50)	0.30 (0.46)
Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	YBFL	0.52 (0.50)	0.46 (0.50)
<i>Early successional forest</i>				
Magnolia Warbler	<i>Setophaga magnolia</i>	MAWA	0.60 (0.49)	0.56 (0.50)
Mourning Warbler*	<i>Geothlypis philadelphia</i>	MOWA	0.11 (0.31)	0.41 (0.49)
White-throated Sparrow*	<i>Zonotrichia albicollis</i>	WTSP	0.47 (0.50)	0.80 (0.40)
<i>Riparian</i>				
Northern Waterthrush	<i>Parkesia noveboracensis</i>	NOWA	0.37 (0.48)	0.31 (0.46)
<i>Ubiquitous</i>				
American Robin	<i>Turdus migratorius</i>	AMRO	0.52 (0.50)	0.50 (0.50)
Blackpoll Warbler*	<i>Setophaga striata</i>	BLPW	0.31 (0.46)	0.32 (0.47)
Fox Sparrow*	<i>Passerella iliaca</i>	FOSP	0.17 (0.37)	0.18 (0.39)
Yellow-rumped Warbler*	<i>Setophaga coronata</i>	MYWA	0.43 (0.50)	0.42 (0.49)
<i>Species richness</i>				
Total			10.5 (2.5)	11.0 (2.6)

Table 3-3: Relative importance of habitat variables from single-scale occupancy models for birds in Gros Morne National Park during the 2010 breeding season. Relative importance values for each variable were obtained by ranking, according to AIC_c, a model set containing all combinations of variables for each scale, then summing the Akaike weights (ω_i) of models containing the variable. Threshold values are the upper 80% confidence limit of a randomly generated variable that was included in each single-scale model over 1000 repetitions. Variables with a relative importance value exceeding the threshold were deemed more important than random and on that basis were included in cross-scale models. Bold indicates relative importance values that exceeded the threshold.

	Local scale					Neighborhood scale (115 m)					Landscape scale (1250 m)				
	trees	browse	under_cover	saplings	Threshold	failed	MW	immature	SW	Threshold	failed	MW	immature	SW	Threshold
<i>Forest Generalist</i>															
BAWW	0.228	0.305	0.602	0.314	0.617	0.446	1.000	0.909	1.000	0.605	0.834	1.000	0.231	1.000	0.596
BCCH	0.350	0.271	0.312	0.214	0.583	0.243	1.000	0.287	0.372	0.593	0.354	0.566	0.245	0.277	0.655
BOCH	1.000	0.217	0.213	0.319	0.596	1.000	1.000	0.298	0.483	0.589	0.884	1.000	0.790	1.000	0.621
GCKI	1.000	1.000	0.911	0.352	0.602	1.000	0.441	0.317	0.731	0.619	1.000	0.360	0.222	0.226	0.576
RCKI	0.616	0.374	0.279	0.414	0.556	1.000	0.451	0.768	0.346	0.567	1.000	0.409	0.237	0.393	0.613
<i>Interior</i>															
BTNW	0.279	1.000	0.778	0.549	0.598	0.274	1.000	1.000	1.000	0.596	0.807	1.000	1.000	1.000	0.587
HETH	0.565	0.238	0.651	0.260	0.589	0.263	1.000	0.449	0.270	0.606	0.663	0.961	0.443	0.277	0.601
SWTH	1.000	0.282	0.464	0.333	0.580	0.335	1.000	1.000	1.000	0.587	1.000	0.397	0.961	0.817	0.613
YBFL	0.308	0.245	0.404	0.263	0.590	0.274	0.299	0.972	0.328	0.586	0.193	0.384	1.000	0.284	0.571
<i>Early successional forest</i>															
MAWA	0.215	0.383	0.786	1.000	0.575	0.478	1.000	0.375	0.916	0.615	0.528	1.000	1.000	1.000	0.570
MOWA	1.000	0.447	0.402	0.252	0.575	1.000	1.000	0.581	0.333	0.607	1.000	1.000	0.749	0.592	0.605
WTSP	1.000	0.547	0.197	0.288	0.562	1.000	0.226	0.423	0.576	0.579	1.000	0.310	1.000	0.198	0.580
<i>Riparian</i>															
NOWA	0.389	0.633	0.436	1.000	0.592	0.683	0.593	0.324	0.441	0.606	0.460	0.964	0.314	0.897	0.585
<i>Ubiquitous</i>															
AMRO	0.238	0.367	0.302	0.358	0.603	0.381	0.860	1.000	1.000	0.574	0.222	0.208	1.000	1.000	0.585
BLPW	0.216	0.226	0.403	1.000	0.583	1.000	1.000	1.000	1.000	0.581	0.203	1.000	0.258	1.000	0.576
FOSP	0.294	0.570	0.951	0.307	0.611	0.274	0.617	0.303	0.600	0.577	0.601	1.000	1.000	0.807	0.549

MYWA	0.600	0.238	1.000	0.374	0.582	0.811	0.758	0.943	0.626	0.572	1.000	0.773	0.264	0.390	0.610
<i>Species richness</i>															
Total	0.223	0.291	0.266	0.268	0.588	0.271	0.854	0.269	0.369	0.575	0.352	1.000	0.286	0.934	0.600

Table 3-4: Summary of 95% confidence sets of cross-scale habitat models for birds in Gros Morne National Park during the 2010 breeding season.

Species	Model	K	logLik	AIC _c	ΔAIC _c	ω _i
<i>Forest Generalist</i>						
BAWW	1250.failed (+) 1250.MW (-)	3	-325.3	656.70	0.00	1.00
BCCH	115.MW (+)	2	-371.9	747.80	0.00	0.96
BOCH	trees (+) 1250.failed (-) 1250.immature (-) 1250.MW (-) 1250.SW (+)	6	-297.7	607.50	0.00	0.85
	trees (+) 115.failed (-) 115.MW (-)	4	-301.6	611.30	3.82	0.13
GCKI	browse (-) trees (+) undercover (-) 1250.failed (-)	5	-236.2	482.60	0.00	0.63
	browse (-) trees (+) undercover (-) 115.failed (-) 115.SW (+)	6	-235.7	483.70	1.08	0.37
RCKI	115.failed (-) 115.immature (-)	3	-369.3	744.60	0.00	0.60
	trees (+) 115.failed (-) 115.immature (-)	4	-369.1	746.30	1.72	0.25
	1250.failed (-)	2	-372.1	748.30	3.67	0.10
<i>Interior specialist</i>						
BTNW	browse (-) undercover (-) 1250.failed (-) 1250.immature (+) 1250.MW (+) 1250.SW (+)	7	-267.8	549.80	0.00	0.91
	1250.failed (-) 1250.immature (+) 1250.MW (+) 1250.SW (+)	5	-272.1	554.30	4.54	0.09
HETH	undercover (+) 1250.failed (+) 1250.MW (-)	4	-252.0	512.00	0.00	0.30
	1250.failed (+) 1250.MW (-)	3	-253.0	512.10	0.09	0.29
	115.MW (-)	2	-254.3	512.60	0.66	0.22
	undercover (+) 115.MW (-)	3	-253.5	513.10	1.08	0.18
SWTH	trees (+) 115.immature (+) 115.MW (+) 115.SW (+)	6	-336.4	682.90	0.00	0.93
	115.immature (+) 115.MW (+) 115.SW (+)	4	-340.0	688.00	5.04	0.07
YBFL	1250.immature (-)	2	-377.7	759.50	0.00	0.94
	115.immature (-)	2	-380.6	765.20	5.72	0.05
<i>Early successional forest</i>						
MAWA	saplings (+) undercover (+) 1250.immature (+) 1250.MW (-) 1250.SW (-)	6	-340.4	693.00	0.00	1.00
MOWA	trees (-) 1250.failed (+) 1250.immature (-) 1250.MW (+)	5	-256.1	522.40	0.00	1.00
WTSP	trees (-) 1250.failed (+) 1250.immature (-)	4	-327.3	662.80	0.00	1.00
<i>Riparian</i>						
NOWA	browse (+) saplings (+) 1250.MW (-) 1250.SW (-)	5	-346.2	702.50	0.00	0.91
	browse (+) saplings (+)	3	-351.5	709.10	6.56	0.03
	1250.MW (-) 1250.SW (-)	3	-351.7	709.50	6.98	0.03
<i>Ubiquitous</i>						
AMRO	1250.immature (+) 1250.SW (+)	3	-373.6	753.20	0.00	0.71
	115.immature (+) 115.MW (+) 115.SW (+)	4	-373.5	755.10	1.81	0.29

BLPW	saplings (+) 115.failed (-) 115.immature (-) 115.MW (-) 115.SW (-)	6	-315.9	644.00	0.00	0.88
	saplings (+) 1250.MW (-) 1250.SW (-)	6	-320.0	648.10	4.06	0.12
FOSP	undercover (+) 1250.failed (+) 1250.immature (+) 1250.MW (-) 1250.SW (-)	6	-235.7	483.50	0.00	0.57
	1250.failed (+) 1250.immature (+) 1250.MW (-) 1250.SW (-)	5	-237.0	484.10	0.58	0.43
MYWA	undercover (-) 115.failed (-) 115.immature (+) 115.MW (+) 115.SW (+)	6	-357.1	726.40	0.00	0.99
<i>Richness</i>	1250.MW (-) 1250.SW (+)	4	-1289.0	2586.00	0.00	1.00

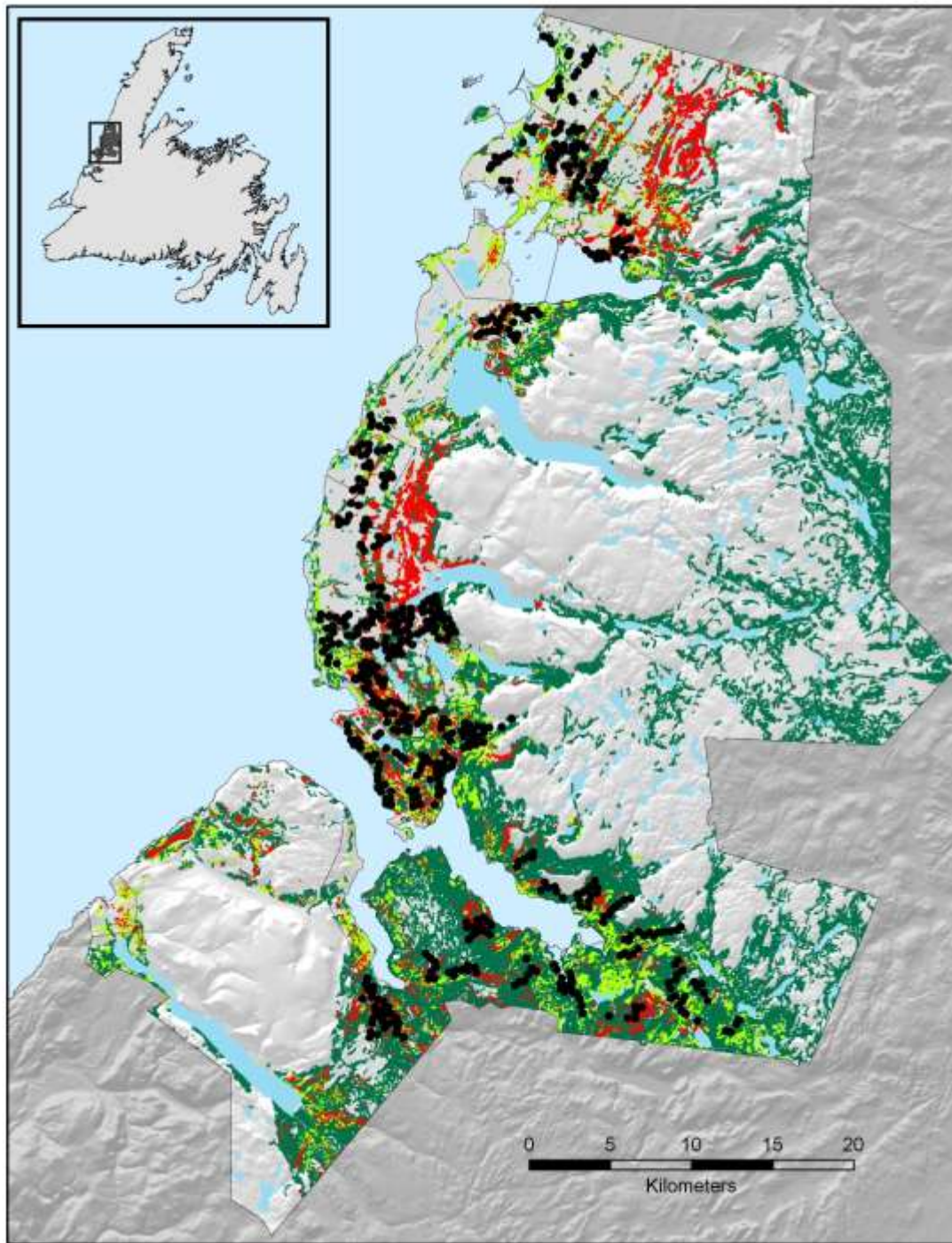


Figure 3-1: Map of 2010 bird point count locations and habitat within Gros Morne National Park (light green = regenerating forest, dark green = mature forest, red = severely impaired forest regeneration). Inset shows the location of Gros Morne National Park on the island of Newfoundland, Canada.

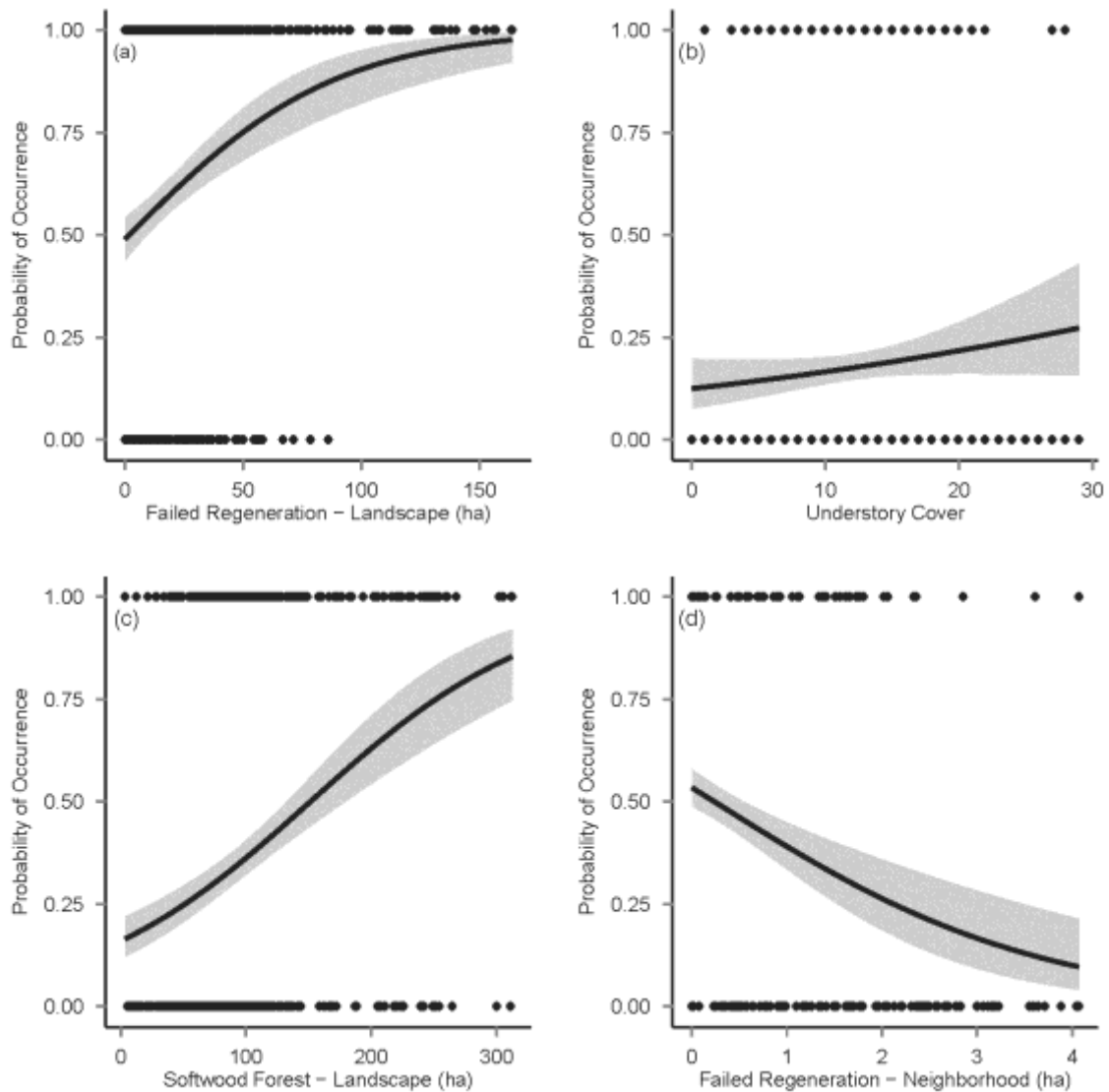


Figure 3-2: Relationships between early successional ((a) white-throated sparrow), interior forest specialist ((b) hermit thrush and (c) black-throated green warbler), and forest generalist ((d) ruby-crowned kinglet) species occurrence and habitat measures at multiple scales representative of the trends observed in Gros Morne National Park during the 2010 breeding season. Dots represent presence/absence (probability of occurrence) data used as the response variable in single-predictor habitat models which produced the logistic regression curve shown; gray shading indicates the standard error. Note change in scale of x-axis depending on the variable examined.

4. Summary

4.1. Using playback to enhance detectability

Measuring the impacts of browse-related habitat degradation on forest birds requires a reliable survey method. Gunn et al. (2000) proposed that exploiting the interspecific response of forest songbirds to black-capped chickadee (*Poecile atricapillus*) mobbing calls would improve the point count survey method by increasing detection probabilities. Higher detection probabilities would allow for less biased estimates of relative abundance and therefore more reliable comparisons could be made across healthy and disturbed habitats. In my assessment of the effectiveness of black-capped chickadee mobbing calls at increasing bird detection probabilities in Chapter 2, I found that results were variable across the suite of boreal bird species encountered during my surveys. Detection probability during the silent period was higher than the playback portion for ten species (American robin, blackpoll warbler, black-throated green warbler, fox sparrow, hermit thrush, northern waterthrush, ruby-crowned kinglet, Swainson's thrush, white-throated sparrow and yellow-bellied flycatcher; see Table 2-1 for scientific names) and lower during the silent period compared with the playback for four species (black-and-white warbler, black-capped chickadee, boreal chickadee and yellow-rumped warbler). These findings are comparable with a similar study carried out in a temperate forest (Mitchell and Donovan 2008).

Although I only built models for two resident species, a comparison of mean detections across silent and playback intervals suggested that detection probabilities of

less abundant, year-round resident species may increase if chickadee playback is used. While I could not test this directly, my data support the suggestion of Turcotte and Desrochers (2002) that chickadee playbacks are an efficient method of increasing detection probabilities for resident species outside of the breeding season. I also found that the behavioural response to playbacks allowed for increased visual detections for the majority of species in this study, again in agreement with the findings of others (Gunn et al. 2000, Doran et al. 2005). Therefore, while the addition of mobbing call playbacks for surveys of common boreal forest birds may not improve the outcome for multispecies surveys during the breeding season, the technique is effective for some species. Where researchers aim to increase visual detections or detections of species with predictably low detection rates, then a playback-based survey should be considered. For example, through the use of playback in this study my field crew and I were more likely to observe individuals that were present in the point count area for four species (the two warblers and two chickadees listed above). Additionally, the minor differences in detection probabilities between habitat types for the majority of species in both silent and playback intervals confirms that comparing apparent abundance across habitats would not be biased by differences in detection probability within different habitat types.

4.2. The impacts of a hyper-abundant herbivore

Moose in Newfoundland have altered forest succession by limiting advanced regeneration of balsam fir saplings, resulting in the development of large expanses of failed regenerating forest following insect disturbance (Connor et al. 2000, McLaren et al. 2004, Gosse et al. 2011). Such changes to forest structure impact breeding songbirds,

which have specific habitat requirements for carrying out breeding and foraging activities. I measured habitat structure and composition using ground plots and remotely sensed forest resource inventory (FRI) data to reflect these features at three spatial scales across which changes may have influenced forest bird abundance: local (fine resolution measure of habitat within 20 m of the point count), neighbourhood (coarse resolution measure of habitat within 115 m of the point count) and landscape (coarse resolution measure of habitat within 1250 m of the point count). I determined responses, through species-specific occurrence and species richness, to the extent of failed regenerating habitat in Gros Morne National Park (GMNP) by building habitat association models. As reported in Chapter 3, I found that habitat assemblages provided a guideline for predicting species response to moose-induced habitat change, though there was some variation within assemblages. In general, early-successional species responded positively to severely impaired regenerating habitat at the landscape scale. In contrast, forest interior birds responded negatively to severely impaired regenerating habitat at the neighborhood scale. I also found that species that rely on understory vegetation to provide habitat requirements for nesting or foraging, responded to habitat change measured at a fine scale (e.g. understory cover), as is well documented for areas where intense deer browsing alters forest structure (McShea & Rappole 2000, Allombert et al. 2005, Cardinal et al. 2012).

Species richness was only associated with mixedwood (negatively) and softwood (positively) cover at the landscape scale; there was no effect of severely impaired regenerating habitat on alpha diversity, a finding consistent with a comparison of species

richness across islands with and without deer browsing (Allombert et al. 2005).

Therefore, while an effect of browsing on species richness was not apparent at this stage in the development of modified forests in GMNP, future losses of balsam fir and white birch (*Betula papyrifera*) forest attributable to continued overbrowsing by hyper-abundant moose over the next 160 years, as modeled by Zhu et al. (2010), could cause declines in forest bird diversity across the region (Drapeau et al. 2000). As a specific example, I found that species such as Swainson's thrush did not respond negatively to severely impaired regeneration but were strongly associated with healthy forest attributes such as high density of trees or saplings. This type of habitat association indicates that if forest cover continues to decline as predicted by Zhu et al. (2010), more species than what my study has indicated are likely to experience a decline in population.

Hardwood species like white birch and trembling aspen (*Populus tremuloides*) are highly palatable to moose, and since their density is naturally low in GMNP, the persistence of hardwood dominated and mixedwood stands would be uncertain if overbrowsing by moose continues. However, it is difficult to predict what the impacts on regional bird species richness might be if the expected changes to forest cover did occur, since at least some of this habitat would become more suitable for certain early successional species at the expense of others, and many failed regenerating sites may eventually be replaced by stands dominated by white spruce (Zhu et al., 2010). However, ongoing loss of the two dominant forest types would likely negatively influence typical boreal breeding birds in the region. Specifically, I would predict species that are known to be associated with immature forests like magnolia warbler (Poole 2013), would

experience declines almost immediately. In the longer term, as remaining forests matured and senesced without new regeneration, declines in species that rely on intact forests, like black-throated green warbler and Swainson's thrush, would be expected. In contrast, early-successional species that I regularly found in open, severely impaired regenerating forest habitat, like white-throated sparrow and mourning warbler, would be expected to increase based on known habitat associations.

To maintain bird assemblages characteristic of the region, I recommend that park managers continue to allow controlled harvest of moose in GMNP to reduce population densities such that changes to forest vegetation species composition and structure are no longer observed. Given the duration of intense browsing pressure on GMNP forests, existing severely impaired regenerating areas may also require active management in order to restore native forest ecosystem (Humber 2009, McLaren et al. 2009, Tanentzap et al. 2011). Continuous monitoring of forest health and wildlife responses to declining moose populations will be essential to the success of the program and our broader understanding of how large herbivores influence forest ecosystems.

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