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Spruce Grouse Habitat Ecology in Maine's Commercially Managed Acadian Forest

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SPRUCE GROUSE HABITAT ECOLOGY IN MAINE'S COMMERCIALLY

MANAGED ACADIAN FOREST

By

Stephen W. Dunham

B.S. University of Maine, 2011

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SPRUCE GROUSE HABITAT ECOLOGY IN MAINE'S COMMERCIALLY

MANAGED ACADIAN FOREST

By Stephen W. Dunham

Thesis Advisor: Dr. Daniel J. Harrison

An Abstract of the Thesis Presented
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Spruce grouse (*Falcipennis canadensis*) inhabiting the mixed coniferous-deciduous forests of the northeastern United States are at the southern extent of their range. These mixed forests are known collectively as the Acadian forest and represent the transitional zone between the boreal forest to the north and the deciduous northern hardwoods forests to the south. Often assumed to be associated with mature, unharvested forest in this region, few studies have assessed habitat relationships of the species within areas dominated by commercial forest management. We investigated the influence of stand maturity, vertical and horizontal cover, and patchiness on the occupancy and abundance of male spruce grouse during the breeding season (Chapter 1); as well as within stand-scale habitat selection of spruce grouse hens during the brood-rearing season (Chapter 2) in the commercial forests of northcentral Maine. Our study was comprised of six townships that covered 612 km^2 within the largest contiguous undeveloped forest in the U.S.

Patterns of occupancy and abundance by male spruce grouse were examined by surveying 30 stands during each breeding season (May-June) in 2012-2014. Areas

surveyed represented four forest harvest histories including regenerating clearcut (n = 10), pre-commercially thinned (n = 10), selection harvest (n = 4), and mature unharvested conifer (n = 6) stands. We constructed single season occupancy and abundance models with years and stand types considered as groups, while accounting for nuisance variables that could affect survey outcomes (e.g., weather, density of woody vegetation). Probability of detection given occupancy was 0.61, and the probability of occupancy varied by successional stage from 37.4 to 76.8. Across our study area, individual male grouse had a probability of detection of 0.24 and the abundance of male grouse also varied by successional stage from 0.67 to 2.75. Based upon the covariates included in the models, both occurrence and abundance of breeding male spruce grouse were highest in mid-successional, moderately dense, conifer dominated stands that have experienced intensive forestry practices such as clearcutting, herbicide application, and pre-commercial thinning to promote coniferous regeneration.

We investigated within stand-scale (i.e., 4th-order selection) habitat selection by female spruce grouse during the brood rearing season (June-October) in 2012-2014 by tracking 30 hens captured in 12 stands, which we equipped with VHF transmitters. We used general linear mixed models to construct resource selection functions to compare use to availability for each hen. Female spruce grouse selected for abundant low vegetation structure (<0.5m), lowest tree branches 3-9 m above ground, and for tree densities <1000 /ha. We also developed home range estimates based on 80% fixed kernel utilization distributions to determine appropriate scales for managing brood season habitat. We estimated fixed kernel home ranges for 27 hens, and observed an average home range area of 37.7 ha (SE = 23.9 ha).

Spruce-fir forests in the region have declined in recent years and are predicted to decline further under all future climate scenarios. Thus, forms of harvesting and post-harvest treatments that promote moderately dense conifer-dominated regeneration are recommended to maintain spruce grouse presence in commercially managed forests within the Acadian region. Currently, these conditions selected for by spruce grouse occur predominantly in stands with a past history of clearcutting, followed by post-harvest herbicide application and/or pre-commercial thinning. Changing markets, regulations, and other factors have caused the majority of forest harvests to shift towards partial harvest methods in Maine. Given that the extent and size of residual conifer forest patches has declined substantially over the past three decades, opportunities to manage for spruce grouse and other conifer-dominant species in Maine's commercially managed forests will require future attention and monitoring.

TABLE OF CONTENTS

LIST OF FIGURES

.

CHAPTER 1

BREEDING SEASON PATCH OCCUPANCY AND ABUNDANCE OF SPRUCE GROUSE IN MANAGED CONIFEROUS FORESTS

ABSTRACT

Spruce grouse (*Falcipennis canadensis*) populations are rare or declining along their southern range boundary, especially within the northeastern U.S. The species has special status designations in New York, Vermont, and New Hampshire. In Maine, spruce grouse are protected from hunting and the Maine Department of Inland Fisheries and Wildlife's Wildlife Action Plan lists spruce grouse among the species of greatest conservation need. Spruce grouse are known to be dependent on short-needle conifer forests and, in this region, are most often associated with stands with mid-late successional characteristics. Thus, forest harvesting may influence both the composition and structural attributes affecting habitat quality for this species. Commercially managed forests represent > 6 million hectares in Maine and recent harvesting activities have reduced the extent of mature conifer forests, while decreasing average patch size and increasing the number of small patches; these changes present uncertain outcomes for spruce grouse. To address knowledge gaps regarding effects of forestry practices on spruce grouse, we studied occupancy of displaying males across 4 different forest harvest treatments during 3 breeding seasons (May-June) in northern Maine, 2012-2014. We broadcasted female calls to elicit male display behaviors and detect male spruce grouse within 30 sites representing mature conifer, regenerating clearcut, pre-commercially thinned, and selection harvest stands. We repeated these surveys three times each year, and used

repeated detections or presence as well as counts of responding grouse to construct occupancy and abundance models, respectively. We constructed single season occupancy and abundance models with year and stand type considered as group effects, while accounting for nuisance variables that could affect survey outcomes (e.g., weather, density of woody vegetation). At the scale of a stand, probability of detection was 0.61 and the probability of occupancy was 0.768four our early-mid successional stands and 0.374 for our mid-late successional stands. Across our study area the probability of detecting an individual male grouse during a single survey was 0.19, and the mean abundance of displaying male grouse in occupied stands across our harvest types ranged from 0.67 – 2.75. Based on the covariates in the models, both occurrence and abundance of breeding male spruce grouse were highest in mid-successional, moderately dense, conifer dominated stands that experienced intensive forestry practices such as clearcutting, herbicide application, and pre-commercial thinning. Because the amount of spruce-fir forest on the landscape is predicted to decline under all future climate scenarios, forms of harvesting and post-harvest treatments that promote moderately dense conifer-dominated regeneration (e.g., clearcutting followed by herbicide application and/or pre-commercial thinning) may be beneficial in maintaining spruce grouse occupancy in managed landscapes.

INTRODUCTION

The spruce grouse (*Falcipennis canadensis*) is a small species of forest grouse that is found in conifer-dominated forests that occur across North America between the tundra in the north and deciduous forests in the south (Boag and Schroeder 1992). Spruce grouse use a variety of conifer forest stand types across this range, but are most common in mid-

successional stands that contain at least one type of short-needled conifer (Boag and Schroeder 1992). The southeastern extent of the geographic range of spruce grouse coincides with the Acadian Forests of Maine, northern New Hampshire, northern Vermont, the Adirondacks region of New York State, and the eastern maritime provinces of Canada. This region, referred to as the Acadian Forest, is the ecological transition zone between the boreal forests to the north and the temperate deciduous forests to the south (Seymour and Hunter 1992). In this portion of their range, spruce grouse are thought to be associated with mid- late successional coniferous forests, especially coniferous forested wetlands (Ouellet 1974, Williamson et al. 2008, Ross and Johnson 2011). Although abundant throughout most of their range, a recent range-wide assessment concluded that populations near the southeastern extent of their range, especially in the Northeastern U.S., are rare or declining (Williamson et al. 2008). Within this region, spruce grouse are found in four states where they are protected from hunting and have some form of official conservation status. These include designations of "state endangered" (New York, Vermont), "species of conservation concern-near threatened" (New Hampshire), and "species of greatest conservation need-moderate priority" (Maine).

Changes in forest structure and composition may affect the quality of spruce grouse habitat. In the Acadian forest, extensive forest harvesting and historical land clearing for agriculture have had the greatest effect on the composition of current forests (Thompson et al. 2013). Today, forest harvesting continues throughout the region and those activities can have varying effects on spruce grouse. For example, clearcutting reduces the survival and reproductive success of spruce grouse in Canada in the short

3

term by forcing them to move into adjacent uncut areas (Turcotte et al. 2000, Potvin and

Courtois 2006). Additionally, male spruce grouse in Quebec were less likely to occur in

commercially thinned versus un-thinned stands (Lycke et al. 2011). In contrast,

occupancy of spruce grouse in the protected portions of the Adirondack Forest Preserve,

New York, was reported to have declined coincident with forest maturation (Bouta and

Chambers 1990, Ross et al. 2016). Notably, spruce grouse occur in pine plantations

(Szuba and Bendell 1983) in Ontario and have been observed in pre-commercially

thinned (PCT) stands in northern Maine (Homyack 2003), suggesting that some forms of

forest management may provide conditions suitable for habitat occupancy.

In this mixed forest zone at the edge of their range, the type, quality, and

distribution of suitable conifer patches are important determinants of spruce grouse

occupancy, and dispersal through unfavorable habitat is important to maintain presence

within occupancy of small patches (Whitcomb et al. 1996). Forests in the northeastern

US are dominated by private ownership. In Maine, 97% of the 7.08 million hectares of

forest land are privately owned and harvested commercially (McCaskill 2015).

Additionally, in the spruce-fir forests of the region, periodic salvage harvest operations

occur following cyclical outbreaks of the eastern spruce budworm (*Choristoneura

fumiferana*), which cause widespread defoliation and mortality of spruce (*Picea* spp.) and

balsam fir (*Abies balsamea*) (Seymour 1992). The last outbreak in Maine occurred in

1972-1988 and was followed by large-scale clearcutting that exceeded long-term

allowable harvest levels (Irland et al. 1988). These harvests were followed by public

concern over the harvesting of the forests and the Maine state legislature subsequently

enacted the Forest Practices Act (MFPA) (12 MRSA 8867-A to 8888 & Maine Forest

Service Rules Chapter 20), which defined and regulated clearcut harvests. This regulation, additional public referendums to eliminate clearcutting, and changing market demands contributed to a dramatic shift in harvest methods from clearcut systems to selection harvest, shelterwood harvest, and overstory removal systems, which have resulted in a near doubling of the annual harvest footprint to achieve similar statewide harvest volumes (Ducey et al. 2013). This resulted in a 31% decline in, and an increasing fragmentation of, mature conifer forest between 1975 and 2007 (Simons 2009, Legaard et al. 2015). Additionally, there has been a 9.2% decline in spruce-fir forest between 1995 and 2008 and a subsequent 8.4% increase in northern hardwoods (McCaskill et al. 2011). Given that Maine contains the largest contiguous block of undeveloped forest land in the United States (Legaard et al. 2015) and thus, contains the greatest extent of potential spruce grouse habitat in the northeastern U.S., it is important to understand how these land-use patterns affect spruce grouse populations.

Our goal was to understand how commonly used harvest regimes influenced spruce grouse breeding habitat in commercially managed forests. Specifically, we investigated how the maturity, structure, and composition of forest stands affected patterns of occupancy and abundance of breeding male spruce grouse. Male spruce grouse, like most grouse species, perform a conspicuous courtship display during the breeding season and should have a sex ratio of nearly 1 to 1 (Potapov and Sale 2013). Thus, we assumed that presence of displaying males would identify stands occupied by reproductive females. To include a representative sample of available forest conditions, we performed auditory surveys for male spruce grouse over three years in stands representing four common harvest histories. We then modeled both the occupancy and

abundance of grouse within those stands in relation to a suite of habitat covariates.

Finally, to facilitate interpretation, we used principle components analysis to visualize

relationships among our stands along component axes defined by our structural and

vegetation variables.

STUDY AREA

Our study area consisted of 30 forest stands with a minimum surveyed area of 16.8 ha

that were distributed across six townships (T6R13, T5R11, T4R12, T4R11, T3R12, and

Trout Brook TWP) within an area of 613 km^2 in northern Piscataquis County Maine

(Figure 1.1). The area consisted of lands privately owned and managed by Katahdin

Forest Management LLC for a variety of forest products, and state owned lands within

the Scientific Forest Management Area of Baxter State Park (Trout Brook TWP) that are

managed for multiple uses including sustainable timber harvest. From 2012-2014 this

region had an annual mean temperature of 4.6°C, with a mean July temperature of 18.6°C

and a mean January temperature of -13.0°C. Mean annual precipitation was 62.5 cm with

a mean annual snowfall of 122.3 cm (National Oceanic and Atmospheric Administration,

2012-2014). The majority of the study area consisted of the "Spruce-Fir Wet Flat"

community type with generally level terrain, moderately to poorly drained soils, and was

dominated by stands comprised of balsam fir (*Abies balsamea*), red spruce (*Picea*

rubens), black spruce (*P. mariana*), red-black spruce hybrids, eastern larch (*Larix*

laricina), and northern white cedar (*Thuja occidentalis*) (Maine Natural Areas Program

2010). On low ridges and on better-drained soils, mixed stands comprised of red and

white spruce (*P. glauca*), white pine (*Pinus strobus*), white birch (*Betula papyrifera*),
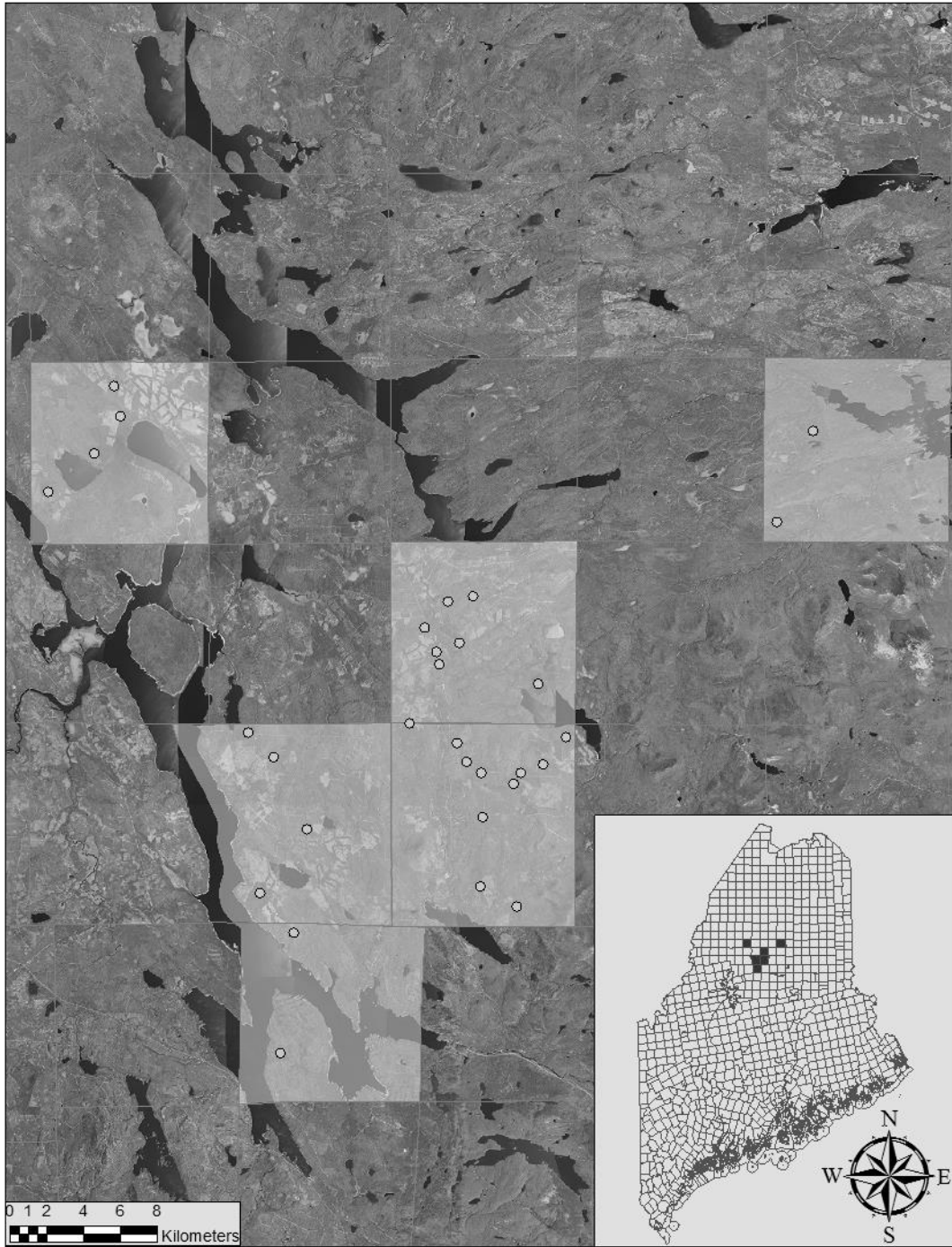
Figure 1.1. Locations of the 30 stands surveyed for male spruce grouse during the breeding season (May-June) across six townships (T6R13, T5R11, T4R12, T4R11, T3R12, and Trout Brook TWP) within our 613 km^2 study area in Piscataquis County, Maine, 2012-2014.

yellow birch (*B. alleghaniensis*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), and American beech (*Fagus grandifolia*) were common.

We surveyed for male spruce grouse within 30 stands that represented four dominant forest management approaches, including: regenerating conifer clearcuts, selection harvests, pre-commercially thinned (PCT) stands, and residual mature, late successional conifer stands (Table 1.1). Regenerating conifer clearcuts (n = 10) resulted from clearcutting techniques common during and immediately following the spruce budworm outbreak of the 1970s. These stands were clearcut an average 30.3 years prior to 2012 (range 18-40), then aerially treated with herbicide (e.g. Glyphosphate at ≈ 1.68 kg/ha acid equivalent) to reduce deciduous regeneration an average of 8.7 years post-harvest (range 5-13). These stands were densely stocked with balsam fir and red and black spruce, with some residual intrusion of deciduous species such as paper birch, red maple, and quaking aspen *(Populus tremuloides)*. Pre-commercially thinned stands were similarly clearcut an average of 33.4 years prior to 2012 (range 29-38), treated with herbicide an average of 6.6 years post-harvest (range 3-14), and were then subsequently thinned by crews using brush saws an average of 18.3 years post-harvest (range 13-23). Pre-commercial thinning became increasingly common in the 1990s and early 2000s as forest managers attempted to accelerate growth in densely stocked stands resulting from the large-scale clearcuts of the 1970-1990 era. These stands (n = 10) contained approximately 20% fewer conifer trees/ha than comparably aged unthinned stands (n = 10), but also contained about 50% fewer deciduous stems and average tree diameter was about 15% greater (measurements taken in 2012). Partial harvest stands were selectively harvested by hand crews or single-grip mechanized harvesters using a method designed

Table 1.1. Location, stand treatment, and treatment history of the 30 stands surveyed for spruce grouse occupancy during the breeding season (May-June) in northcentral Maine, 2012-2014. NA = no treatment. UNK = unknown.

Stand Name	Township	Stand Treatment	Harvest Treatment	Herbicide Treatment	Thinning Treatment	Years Surveyed
1-1-T	T4R11	PCT	1982	1988	1999	3
1-2-T	T4R12	PCT	1980	1983	1999	3
1-3-T	T4R11	PCT	1977	1983	1999	3
1-4-T	T4R11	PCT	1982	1988	1999	3
1-5-T	T4R12	PCT	1976	1983	1999	3
15Y1	T5R11	PCT	1974	1988	1995	3
15Y2	T5R11	PCT	UNK	1983	1995	3
15Y3	T6R13	PCT	1983	UNK	1994	3
6-4-T	T5R11	PCT	1974	1982	1994	3
6-6-T	T5R11	PCT	1979	1982	1994	2
JH01	T4R11	Clearcut	1978	1988	NA	3
JH02	T4R11	Clearcut	1978	1983	NA	2
JH03	T4R11	Clearcut	1981	1984	NA	3
JH04	T5R11	Clearcut	1983	1988	NA	3
JH05	T4R11	Clearcut	1975	1985	NA	2
JH54	T5R11	Clearcut	1972	1982	NA	2
JH56	T4R11	Clearcut	1978	1988	NA	2
TLRG1	T4R12	Clearcut	1994	NA	NA	2
TLRG2	T3R12	Clearcut	1991	1999	NA	2
TLRG3	T3R12	Clearcut	1992	2005	NA	2
AF1	T5R11	Selection	1994+1995	NA	NA	2
AF2	T5R11	Selection	1994+1995	NA	NA	2
AF5	T4R11	Selection	1992+1995	NA	NA	2
AF7	T4R11	Selection	1994	NA	NA	2
MSW3	T5R12	Mature	1970	NA	NA	3
MSW9	T4R12	Mature	1970	NA	NA	2
MSW10	T6R13	Mature	1970	NA	NA	3
MSW11	T6R13	Mature	1970	NA	NA	3
MSW12	SFMA	Mature	1970	NA	NA	1
MSW13	SFMA	Mature	1970	NA	NA	1

to leave one overstory tree every 4.5 m, which resulted in a reduction in basal area of 52-59% greater (measurements taken in 2012). Partial harvest stands were selectively harvested by hand crews or single-grip mechanized harvesters using a method designed to leave one overstory tree every 4.5 m, which resulted in a reduction in basal area of 52-

59% compared to pre-harvest conditions (Fuller and Harrison 2005). Selection harvests were common in northern hardwoods-dominated and mixed forest stands prior to the spruce budworm outbreak (Seymour 1995) and became common again after the passage of the MFPA. These harvests resulted in deciduous-dominated mixed-forest stands with an average of 23.7 m^2/ha of basal area (range 20.5 – 29.1 m^2/ha) by 2012, and an average age of 17.3 years post-harvest (range 17 – 18). Mature conifer stands were residual second-growth stands that had no history of harvest during the prior 42 years (reliable record keeping began in 1970). Previous work in the region estimated the average age of mature conifer patches to be to be >80 years old (Simons-Legaard et al. 2013). These stands were typified by tall trees (13 – 19 m), closed canopies (62 – 90%), and relatively little understory (BA of saplings: 3.7 – 9.8 m^2/ha; measurements taken in 2012).

METHODS

Field Methods

From 7 – 28 May 2012, 4 May – 6 June 2013, and 8 – 30 May 2014 we conducted auditory surveys for male spruce grouse using a broadcasted female call to elicit male responses. Surveys were conducted at pre-established broadcast locations along standardized transects in forested stands. Each stand contained eight broadcast locations separated by ≥ 120 m that were ≥ 70 m from the edge of the stand. Twenty-nine of 30 stands contained two transects with four survey points each (Figure 1.2), and one stand had an altered configuration because of irregular stand boundaries to ensure that our spacing and edge separation criteria were maintained. The survey window extended from 30 minutes before sunrise until noon (Lycke et al. 2011). At each broadcast location a recording of a female aggressive call (cantus) was played using a FOXPRO®
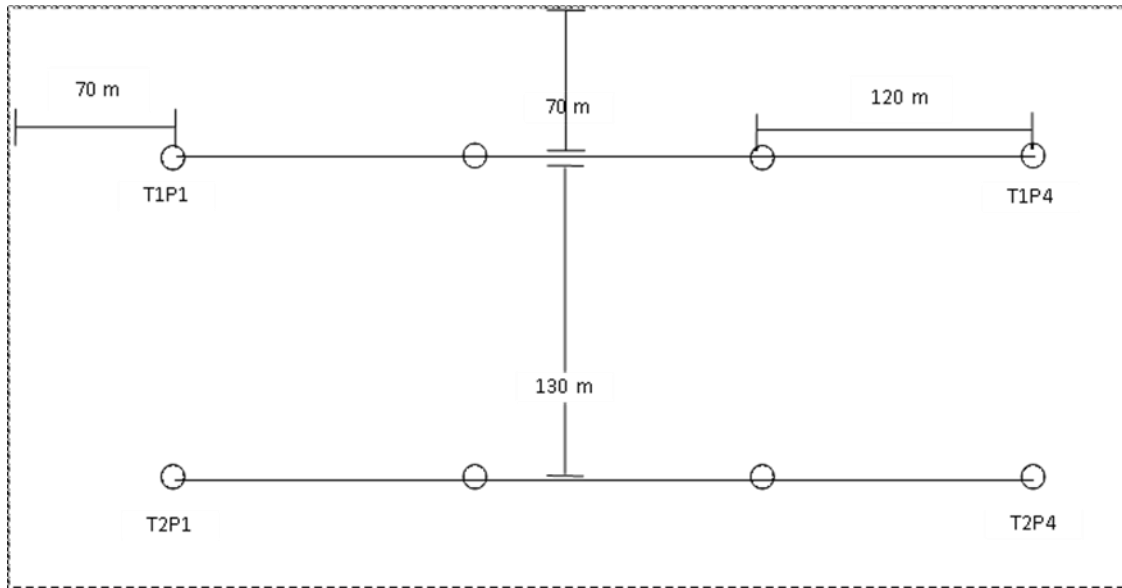
Figure 1.2. Generic survey map depicting the spacing and location of broadcast locations used in the 30 forest stands surveyed during the breeding season (May-June) in northcentral Maine, 2012-2014.

(Lewistown, PA) NX3 game caller over a period of six minutes. We allowed one minute of settling time followed by the following pattern of one minute sections: broadcast, listen, broadcast, listen, listen (adapted from Worland et al. 2009). Males typically responded to calls by performing a flutter-flight display, which is characterized by repeated flights up and down from low branches or from the ground. All responses were noted, and we attempted to capture the responding grouse using a 20' telescoping fiberglass fishing rod (Shakespeare WonderPole®, Columbia, SC) fitted with a sliding noose made of 80-lb test fishing line (Zwickel and Bendell 1967). Captured grouse were individually marked with a numbered aluminum butt-end leg band and a unique pattern of 1-3 plastic colored leg bands (Schroeder and Boag 1989, Keppie 1992). Survey start and end times, temperature, cloud cover, date, and observer were recorded for each survey. We restricted our inferences to only actively displaying males, and excluded

females and non-displaying males; thus our inferences are specific to habitat associations of territorial male spruce grouse during the breeding season. Survey, capture and marking protocols were reviewed and approved by the University of Maine's Institutional Animal Care and Use Committee.

During each season, field technicians were trained and observed to ensure proficiency at capturing grouse. Among surveys of each stand we alternated observers and among sampling events in each year we reversed the order in which each stand was visited. To ensure favorable survey conditions, we did not conduct surveys during steady rain or during periods with winds that exceeded a value of 3 on the Beaufort scale (Martin et al. 1997).

We collected vegetation data at 20 randomly-established points within each surveyed stand to characterize stand structure and composition (Table 1.2). Basal area was measured with a 2-factor prism (BA m^2/ha) for saplings and trees from the center of the plot. Saplings were defined as woody stems <7.6 cm diameter, > 1.5 m tall, and trees as woody stems >7.6 cm diameter at breast height. Stem cover units are an alternative method to quantify live stems [calculated as # deciduous stems + 3*(# conifer stems)] where extra consideration is given to the horizontal cover provided by conifer stems (Litvaitis et al. 1985). Stem cover units and total sapling density were measured by counting all stems within a 10 m^2 circular plot centered on sampling points. Canopy cover was assessed using the average of four spherical densitometer readings taken at the center of the plot in each of the cardinal directions. The patchiness of canopy cover was determined by calculating the coefficient of variation from the four measurements at each plot. Tree data were measured using the point-centered quarter method (Cottam and

Table 1.2. Eleven independent vegetation variables measured in each of the 30 stands surveyed during the breeding season (May-June) in Piscataquis County, Maine, 2012-2014.

Variable	Description	Units	Measurement Method
TBA[a]	Total basal area	m^2/ha	$2m^2$/ha wedge prism
SCU[a]	Stem cover unit	#/ha	Number of saplings in $10m^2$ plot
CC[b]	Canopy closure	% closed	Densitometer at 1m high
CCV	Canopy closure variation	% variation	Coefficient of Variation of CC
BAT	Basal area of trees	m^2/ha	$2m^2$/ha wedge prism
TH[c]	Total tree height	height in m	Hypsometer
LL[c]	Lowest limb > 1cm thick	height in m	Meter Tape or Hypsometer
TSD	Total sapling density	stems/ha	Number of saplings in $10m^2$ plot
CTD[c]	Conifer tree density	trees/ha	Point-quarter method
DTD[c]	Deciduous tree density	trees/ha	Point-quarter method
DBH[c]	Diameter at breast height	cm	Diameter tape at 1.4m

[a] Variables used as measure of vegetation density in detection models only.
[b] Measured in 4 cardinal directions from center and averaged at each point
[c] Measurements taken on the nearest tree in each of four quarters around each survey point. Based on the point-quarter method (Cottam and Curtis 1956)

Curtis 1956), where we used the cardinal directions to define four quadrants, selected the

nearest tree in each, and measured diameter at breast height (DBH), total height, lowest

live limb height, and distance to center point. We defined stand treatment type prior to

beginning surveys using a combination of site visits, harvest maps, a 20-year satellite

time series (Simons-Legaard et al. 2016), and based on information provided by

landowners.

Statistical Analysis

We modeled spruce grouse occupancy using single-season occupancy models (MacKenzie et al. 2006) implemented in Program MARK (White and Burnham 1999). Occupancy models use detections (1) or lack of detections (0) to compute a probability of occupancy (Ψ) and a probability of detecting occupancy (p). Additionally, we modeled spruce grouse abundance within stands using the single-season abundance model (Royle 2004) also implemented in program MARK (White and Burnham 1999). Abundance models rely on repeated counts of uniquely identifiable individuals to derive an abundance estimate (λ) that is presumed to reflect true abundance, given the probability of detecting an individual (r). Both occupancy and abundance models assess histories of detections across temporally replicated surveys (*n*= 3 in our case) at a particular site to account for imperfect detection within any given survey (Mackenzie et al. 2006).

Our unit of replication was the survey stand; therefore, occupancy and abundance detection histories were combined from all survey points within a stand (*n* = 8). Each stand was visited 3 times annually. In 2012 we visited 19 stands and then added 9 for a total of 19 in 2013. We subsequently added 2 more stands in 2014, while skipping 4 stands during that year that had been unoccupied in the previous 2 years. Across the three years, 30 unique stands were surveyed.

We initially considered a multi-season occupancy model (MacKenzie et al. 2003) to incorporate annual dynamics in occupancy (immigration and extinction). Occupancy across our stands did not vary enough to support those models; therefore, we used year-specific detection histories for each stand to incorporate the multiple-season nature of our data (three visits each year for three years). This approach increased our sample size to   *n*

= 73 stand/year combinations with 19 stands visited in 2012, 28 in 2013, and 26 in 2014 (Fogg et al. 2014). Testing for differences among years was still possible, and this approach was preferable given that sites that were occupied across multiple years were likely of higher habitat quality than those that were only occupied once. Stands occupied across multiple years may have higher influence on the occupancy-habitat relationship (Fogg et al. 2014).

Our occupancy and abundance models were evaluated using a two-step approach where we first modeled the effects of conditions that may have affected our ability to detect birds (i.e., nuisance variables), and then evaluated the relevant state variable once we documented the best approximating structure for detection. For the occupancy models we evaluated effects of sampling (temporally varying) and site covariates (spatially varying) on detection while retaining a fully parameterized structure for the state variable [e.g., p(start time)Ψ(group*time)]. Sampling covariates included ordinal date, start time (decimal hours after the survey window began that a survey was started), % cloud cover, the presence of precipitation within the past 24 hours (0,1), presence of precipitation during the survey (0,1), and number of observers (0=1 and 1= >1 observer). Site covariates included total basal area and stem cover units that were selected to quantify density of vegetation. We inferred that dense vegetation might reduce our ability to hear displaying males. We calculated a cumulative probability of detection (p*) for occupancy using the formula: $(p_{cumulative}=1-(1-p_{survey})^{n(surveys)})$.

For abundance models, detection (r) reflected the probability of detecting an individual, rather than the probability of detecting species presence (≥ 1 individual) during a survey. An assumption of this model is that detection is constant across time, which

precludes the use of sampling covariates that varied through time. Thus, we included only the site covariates of total basal area and stem cover units. The detection models that we evaluated (Appendix A) included both univariate and multivariate models and included tests for differences among year and stand type. All covariates were standardized to Z-scores $[z = (x - \mu)/\sigma]$ and all models were ranked using Akaike's information criterion corrected for small sample size (AIC$_c$) and Akaike weights (w_i) (Hurvich and Tsai 1989). Under an AIC$_c$ framework, it has been previously recommended to use 85% confidence intervals to evaluate support for parameter coefficients (β; Arnold 2010); therefore, we retained the best performing (lowest ΔAIC$_c$ and highest w_i) model where all variables had significant beta values (85% C.I. of β does not include 0) for inclusion in the second step of model building.

In the second step we modeled occupancy and abundance as a function of habitat covariates (Table 1.2) that we hypothesized *a priori* may affect the habitat use by breeding male spruce grouse. We Z-standardized all covariates, and also considered quadratic effects of all covariates to allow for possible non-linear relationships. Finally, we tested for differences among years and stand types. We included a successional stage model where we combined our younger successional stands (regeneration and PCT) into one group and our older successional stands (mature and selection harvest). Both occupancy and abundance models were restricted to univariate comparisons (Appendix A) because of the high degree of correlation among many of our habitat covariates (Figure 1.3), and because our focus was on evaluating how each of our selected covariates related to occupancy and abundance rather than to create a single "best" predictive model. All models included the parameterization on the detection term from
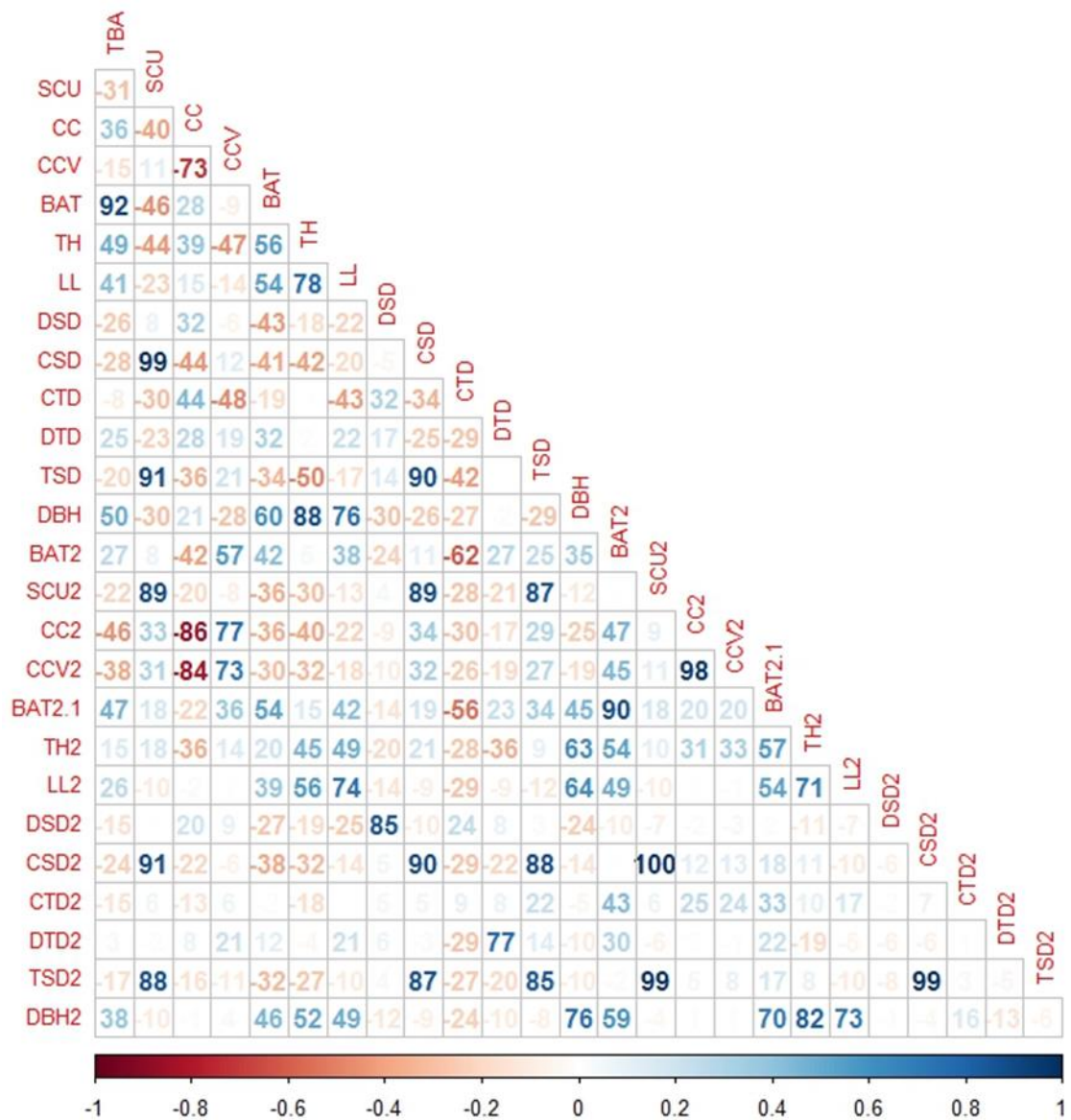
Figure 1.3. Correlation plot depicting the Pearson correlation values for all habitat variables included in our analysis of spruce grouse occupancy and abundance during the breeding season (May-June) in northcentral Maine, 2012-2014. Variables followed by 2 represent quadratic forms of the variable.

the first step in model building [e.g., p(best model)Ψ(canopy closure)]. Models were

evaluated using a combination of information-theoretic model selection (Burnham and

Anderson 2002) and evaluation of the variance around parameter coefficients (β), as we

described above. If the quadratic form of a variable outperformed the linear term, we report only the model containing the quadratic form in the final model set.

Principle Components Analysis

To reduce dimensionality and to enhance interpretability of our habitat data, all variables included in the final set of occupancy and abundance models were included in a principle components analysis (PCA) to ordinate among our 4 stand treatments. This approach allowed us to evaluate the combinations of variables that accounted for most variation between occupied and unoccupied stands (naïve occupancy). All variables were transformed using the Yeo-Johnson (Box-Cox correction for data with zeroes) family of corrections to closer approximate a normal distribution (Yeo and Jonhson 2000). These variables were then standardized and centered. After computing the principle components, we used a scree-plot and relative variance to determine how many components to retain (Zuur et al. 2007:199). We then used varimax rotation to group the loadings and components into biologically relevant descriptions for interpretation. Variables with loadings (after rotation) of > 0.30 or < -0.30 were considered to have strong effects on that component. Ordination diagrams using the first three components were constructed with Gaussian confidence ellipses around occupied and unoccupied clusters, while a fourth diagram using the first two components was constructed with Gaussian confidence ellipses around the stand types. This analysis was conducted in program R using the package "caret" and the figures were created using the package "ggbiplot".

RESULTS

Occupancy

We detected responding male spruce grouse, at least once, in 19 of our 30 surveyed stands, giving us a naïve occupancy estimate of 63%. However, we detected responding males during all three years in only seven stands. Additionally, there were six instances when we observed only females or non-displaying males during a survey, which were counted as unoccupied. Five of these non-included detections were the only detections that occurred in a year, and one of those was the only detection ever observed in a stand (Appendix A).

Of 25 detection models that we created to test the effects of nuisance variables (Appendix A), four outperformed the null, or constant model (Table 1.3), and all contained the start time variable. Although all four models were competitive (< 2.0 ΔAIC_c) we chose the top model to include in the future analyses, which contained a quadratic form of survey start time (start time $\beta = -0.77$, 85% CI: -1.11 to -0.44; start time^2 $\beta = -0.56$, 85% CI: -0.95 to -0.16) that was additive with the total basal area of each stand (total basal area $\beta = -0.52$, 85% CI: -0.96 to -0.09). Both of these influential variables had a negative influence on probability of detection. The quadratic effect on start time indicated that the probability of detection actually increased slightly until about sunrise, when it then began to decrease until surveys were completed at noon. Detection also decreased as the basal area of trees and saplings within a stand increased.

Of the 24 competing models (Appendix A) created to test the effects of habitat covariates on the occupancy of spruce grouse, seven outperformed the null, or constant model (Table 1.4) and had supported coefficients (β). These models included the

Table 1.3. Best performing, detection only, single-season occupancy models for male spruce grouse during the breeding season (May-June) in northcentral Maine, 2012-2014.

Model	AIC$_c$	Δ AIC$_c$	ω_i	No. Parameters
p(Start time^2+TBA)	240.297	0	0.342	13
p(Start time^2)	240.337	0.040	0.335	12
p(Start time+TBA)	241.684	1.388	0.171	12
p(Start time)	241.946	1.649	0.150	11
p(.)	253.713	15.162	0	2

The occupancy structure of all models was $\Phi(g*t)$

Table 1.4. Best performing single-season occupancy models for male spruce grouse during the breeding season (May-June) in northcentral Maine, 2012-2014.

Model	AIC$_c$	Δ AIC$_c$	ω_i	No. Parameters
Φ(DTD^2)	214.812	0	0.792	7
Φ(DBH)	219.255	4.443	0.086	6
Φ(TH)	219.724	4.912	0.068	6
Φ(CCV)	222.758	7.946	0.015	6
Φ(LL)	222.914	8.102	0.014	6
Φ(2 Groups)	224.001	9.194	0.008	6
Φ(TSD^2)	224.141	9.329	0.007	7
Φ(.)	226.193	11.381	0.003	5

The detection structure of all models was p(Start time^2+TBA)

successional stage term and six covariates including deciduous tree density (quadratic), diameter at breast height, tree height, canopy cover variation, lowest dead limb height and total sapling density (quadratic). The first four covariates were plotted against the probability of occupancy to aid interpretation (Figure 1.4). Deciduous tree density had a
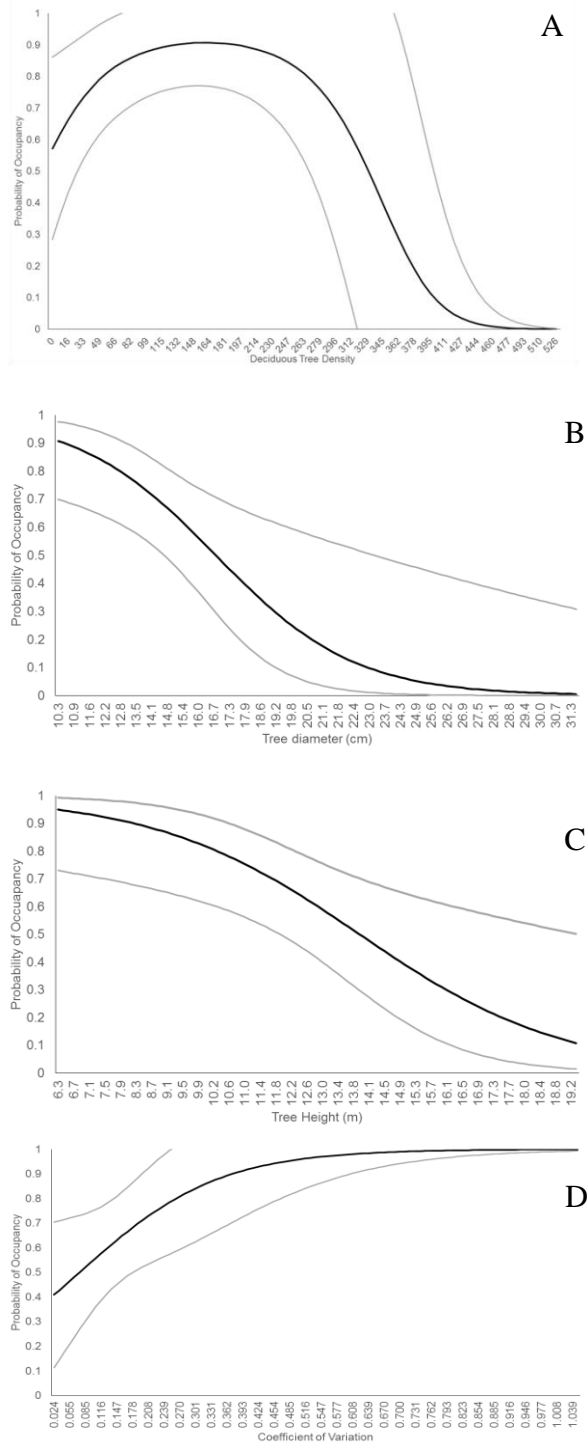
Figure 1.4. Covariate plots depicting the estimated probability of occupancy and 95% CI for male spruce grouse within the top four occupancy models based on AIC scores during the breeding season (May-June) in northcentral Maine, 2012-2014. Variables depicted include those with 85% CI on the habitat covariate that did not include zero. Deciduous tree density (A), tree diameter (B), tree height (C), and canopy cover variation (C) were included.

quadratic effect on occupancy (quadratic form; DTD β = -2.02, 85% CI: -4.14 to 0.11;

DTD^2 β = -4.01, 85% CI: -6.73 to -1.30) indicating that the highest probability of

occupancy was expected in stands with 156 deciduous trees per hectare and declined both

above and below that number. A quadratic effect of total sapling density was also

supported (TSD β = 1.34, 85% CI: 0.20 to 2.47; TSD^2 β = -0.60, 85% CI: -1.06 to -0.14),

with the highest probability of occupancy estimated to occur in stands with

approximately 12,000 saplings per hectare. Canopy cover variation (β = 1.40, 85% CI:

0.19 to 2.61) was the only other term to have a significant positive relationship with

occupancy. Diameter at breast height (β = -1.45, 85% CI: -2.24 to -0.66), tree height (β =

-1.09, 85% CI: -1.69 to -0.49), and lowest dead limb height (β = -0.91, 85% CI: -1.50 to -

0.32) were all negatively associated with occupancy. Finally, our successional stage

model showed occupancy was positively associated with early to mid-successional stands

(β = 1.20, 85% CI: 0.57 to 1.82) and negatively associated with later-successional stands

(β = -1.71, 85% CI: -2.84 to -0.59).

Our detection probability was ~61% for a given survey within a year (p = 0.603, 95%

CI: 0.457 to 0.733 for survey 1; p = 0.612, 95% CI: 0.461 to 0.736 for survey 2; and p =

0.584, 95% CI: 0.466 to 0.740 for survey 3) and this was consistent across years and

groups. The cumulative detection per season was 94.1%. Occupancy of early-mid

successional stands was 76.8% (Φ = 0.768, 95% CI:) while mid-late successional stands

had a probability of occupancy of 37.4% (Φ = 0.374, 95% CI: 0.137 to 0.691). The

probability of occupancy for selection stands (n=4) was fixed to 0 for all models because

no grouse were ever detected in those stands.

Abundance

The number of individual male grouse responding to call surveys ranged from 0-5 grouse per stand (Appendix A). Because of the assumption that detection does not vary across surveys, we could only include a limited number of models for the detection parameter. Of the 11 detection models tested, three outperformed the null, or constant, model (Table 1.5). The top performing model was an additive model that included both the total basal area of trees (β = -0.74, 85% CI: -1.11 to -0.37) and stem cover units (β = -0.48, 85% CI: -0.81 to -0.16). All beta values were negative, which indicated detection was highest in stands that had SCU values of 725 units/ha and a total basal area of 9.4 m^2/ha; detection decreased as these values increased.

Of the 24 competing models tested to evaluate influences of habitat covariates on abundance of displaying males, seven out-performed the null model (Table 1.6) and had supported coefficients (β). These models included the successional stage term and six covariates including deciduous tree density (quadratic), diameter at breast height (quadratic), tree height, lowest dead limb height, basal area of trees (quadratic), and conifer tree density (quadratic) (Table 1.6, Figure 1.5). Deciduous tree density had a quadratic effect on abundance (DTD β = -1.90, 85% CI: -3.00 to -0.80; DTD^2 β = -2.81, 85% CI: -4.00 to -1.62); highest abundance was expected in stands with 140 deciduous trees per hectare and declined both above and below that number. The effect of diameter at breast height was also quadratic (DBH β = -1.03, 85% CI: -1.50 to -0.56; DBH^2 β = -0.76, 85% CI: -1.41 to -0.11); highest abundance was expected in stands with an average DBH of 12.2 cm. Tree height (β = -0.80, 85% CI: -1.10 to -0.50) and lowest dead limb height (β = -0.60, 85% CI: -0.91 to -0.28) were negatively associated with abundance,

Table 1.5. Best performing, detection only, single-season repeated count abundance models for male spruce grouse during the breeding season (May-June) in northcentral Maine, 2012-2014.

Model	AIC$_c$	Δ AIC$_c$	ω_i	No. Parameters
r(TBA+SCU)	419.441	0.000	0.821	12
r(TBA)	422.934	3.493	0.143	12
r(SCU)	426.366	6.924	0.026	11
r(.)	429.137	9.695	0.006	11

The abundance structure of all models was $\lambda(g*t)$.

Table 1.6. Best performing single-season repeated count abundance models for male spruce grouse during the breeding season (May-June) in northcentral Maine, 2012-2014.

Model	AIC$_c$	Δ AIC$_c$	ω_i	No. Parameters
$\lambda(DTD^2)$	6054.749	0.000	0.970	6
$\lambda(DBH^2)$	6062.818	8.069	0.017	6
$\lambda(TH)$	6063.445	8.696	0.013	5
$\lambda(2\ Group)$	6071.194	16.445	0.00	5
$\lambda(LL)$	6072.077	17.328	0.000	5
$\lambda(BAT^2)$	6076.255	21.507	0.000	6
$\lambda(CTD^2)$	6079.449	24.701	0.000	6
$\lambda(.)$	6079.844	25.095	0.000	4

The detection structure on all models was r(TAB+SCU)
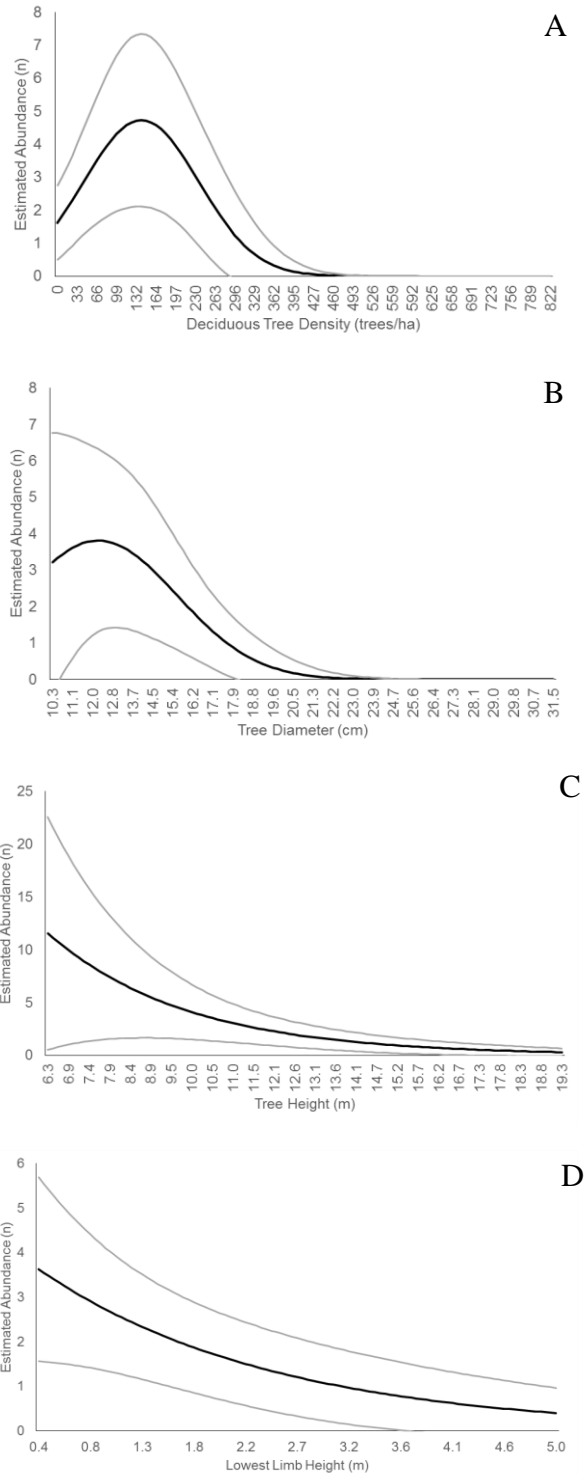
Figure 1.5. Covariate plots depicting the estimated abundance and 95% CI for male spruce grouse within the top four abundance models based on AIC scores during the breeding season (May-June) in northcentral Maine, 2012-2014. Variables depicted include those with 85% CI on the habitat covariate that did not include zero. (A), tree diameter (B), tree height (C), and lowest live limb height (D) were included.

25

indicating that stands with shorter trees and with lower lowest limb heights were expected to contain more displaying males. Basal area of trees had a quadratic effect on abundance (BAT β = -0.99, 85% CI: -1.56 to -0.41; BAT^2 β = -0.62, 85% CI: -1.24 to -0.01); we would expect to find the highest abundance of displaying males in stands with 12 m^2 per hectare of basal area. The quadratic form of conifer tree density (CTD: β = -0.04, 85% CI: -0.32 to 0.24; CTD^2: β = 0.18, 85% CI: 0.03 to 0.33) indicated that males were most abundant in stands with either low or high conifer tree densities. Finally, the successional stage model that allowed for differences in abundance between early to mid-successional stands (PCT and regenerating stands) and mid-late successional stands (selection and mature stands) showed abundance was positively associated with the former (β = 1.01, 85% CI: 0.67 to 1.35) and negatively associated with the latter (β = -1.40, 85% CI: -2.15 to -0.65). The detection probability of an individual male was 23.5% (r = 0.235, 95% CI: 0.139 to 0.369), which was consistent across years and groups. The estimated abundance (λ) early-mid successional stands was 2.75 (95% CI: 1.462 to 4.030) individuals per stand, while mid-late successional stands were estimated to contain 0.67 (95% CI: 0.072 to 0.983) individuals. The abundance estimates for selection stands were fixed to 0 for all models because no grouse were ever detected in those stands.

Principle Components Analysis

Three principle components described 86.1% of the variability of the vegetation data across our stands (Table 1.7). Principle component one (45.9% variance explained) described the degree of stand maturity and contained four positively loaded variables (rotated loadings in parentheses) that included tree height (0.4890), basal area of trees (0.4169), lowest limb height (0.3250) and tree diameter (0.4348). Negatively loaded

Table 1.7. Loadings of habitat variables that separated non-occupied and occupied stands (n=30) into three principle components after Varimax rotation. Habitat values were measured in June-August 2011-2014, except canopy cover, which was measured during Jan-May 2011-2014, northcentral Maine.

Habitat Value	Principle Components		
	PC1- Maturity	PC2- Conifer Structure	PC3- Stem Density
Canopy Cover Variation	-0.3493	-0.2750	0.1299
Basal Area Trees	0.4169	0.3124	0.2358
Tree Height	0.4890	-0.1861	-0.0053
Lowest Limb Height	0.3250	-0.4719	-0.0508
Conifer Trees	0.1679	0.5715	0.3539
Deciduous Trees	0.0488	-0.3272	0.8622
Total Saplings	-0.3739	-0.1967	0.1723
DBH	0.4348	-0.3117	-0.1631
%Variance Explained	45.9	28.2	12.0

variables included canopy cover variation (-0.3493) and total sapling density (-0.3739).

Principle component two (28.2% variance explained) represented the degree of conifer

structure and contained two positively loaded variables that described the basal area of

trees (0.3124) and conifer tree density (0.5715). Negatively loaded variables included

lowest limb heights (-0.4719), deciduous tree density (-0.3272), and tree diameter (-

0.3117). Finally, principal component three (12.0% variance explained) represented tree

density and contained two positive loadings for conifer tree density (0.3539) and

deciduous tree density (0.8622).

When plotted as ordination diagrams (Figure 1.6), the greatest difference between

occupied and unoccupied stands was observed in conifer structure, with most occupied
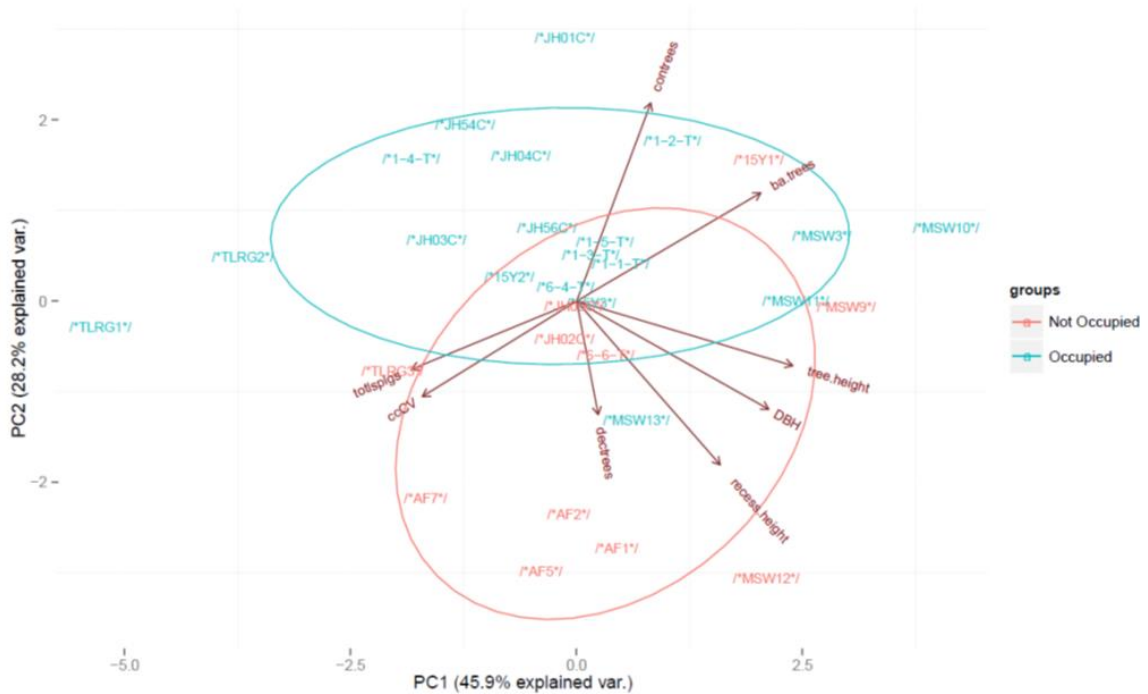
Figure 1.6. Ordination diagrams for the first two principle components (explained 86.1% of variation) describing the difference in forest structure and composition between sites where displaying male grouse were documented (n=19) and not documented (n=11) during the breeding season (May-June) in northcentral Maine, 2012-2014. Guassian confidence ellipses are shown centered around the sample means. Principle component one describes stand maturity, whereas principal component two describes conifer structure.

stands occurring towards the upper end of component two. Greater overlap was observed within component one (maturity) but the majority of occupied stands were clustered towards the center of the plot. Finally, the most overlap was observed for component three, with a nearly even spread of occupied and unoccupied stands across the observed range of tree densities.

When we ordinated stand types in relation to our top 2 principal components, differences among stand type were observed with our early and late successional stands

28

grouped on their respective ends of the maturity spectrum and our PCT stands clustered in-between (Figure 1.7). Our clearcut regeneration and PCT stands were also more tightly clumped along the conifer composition axis, while the mature stands showed the greatest variation in conifer composition. The selection harvest stands grouped in the mid-successional position on the maturity axis, however, they clustered away from all of the other stand types because of their higher deciduous composition.

DISCUSSION

Call-back surveys for territorial male spruce grouse using the female cantus call were highly effective in our study area, with an estimated detection probability per survey of nearly 61%. We believe this estimate of detection is conservative as it was generated from a data set that did not include incidental observations of females or non-displaying males that occurred during the surveys. There were only a few instances where incidental observations were the only detections in a stand within a year, and there was only one instance of a detection of a non-responding male as the sole detection in a stand across all three years. Females were detected during male surveys in seven stands (Appendix A). Females were also detected in eight additional stands that were occupied by males during subsequent brood surveys (Chapter 2). Finally, hatched nests were observed in six of the occupied stands (JH01C, JH03C, JH04C, TLRG1, TLRG2, and 1-4-T), indicating successful breeding occurred in stands where males were observed displaying..

Territorial male spruce grouse occupied the majority of our stands. Our occupancy models identified several vegetation variables associated with both forest structure and composition that increased the probability of occupancy. Probability of occupancy was inversely related to stand age (tree diameter, tree height, lowest limb
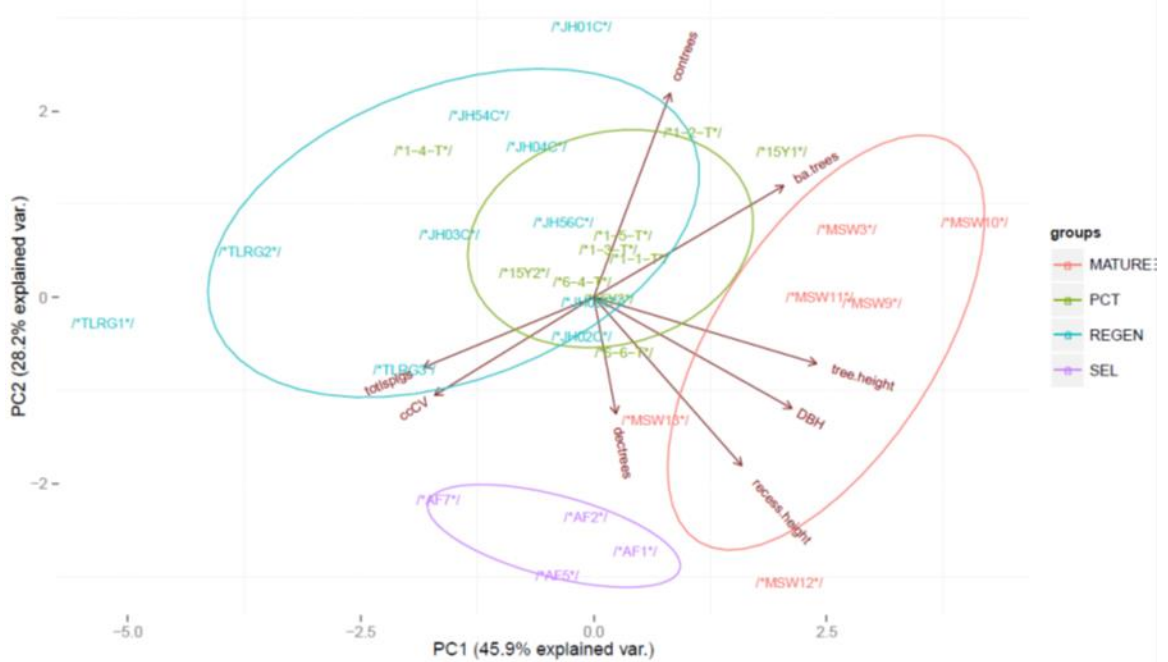
Figure 1.7. Ordination diagrams for the two principle components that best described the difference in forest structure and composition between 30 forest stands with 4 types of harvest histories: Mature (late successional), PCT (pre-commercially thinned), Regen (regenerating conifer), and Sel (selection harvest). Gaussian confidence ellipses are shown centered around the sample means. Principle component one describes stand maturity and principal component two describes conifer structure.

height) which indicated that spruce grouse occurred less-commonly in more mature stands, despite previously inferred associations of spruce grouse with late-successional conifer stands (Ouellet 1974, Williamson et al. 2008). Spruce grouse in Maine had the highest relative occupancy and abundances in early-mid successional stands.

Occupancy had a quadratic association with the probability of occupancy and although this relationship appears counter-intuitive, a small amount of deciduous trees present within a conifer stand is common where shade intolerant hardwoods are common associates of the spruce-fir forest type (Seymour 1995). Deciduous trees often occurred

where soil compaction, vegetative competition, or gaps in herbicide application prevented the establishment of coniferous regeneration. Thus, deciduous trees were associated with the breaks in coniferous tree density necessary for display locations, and the presence of shade-intolerant hardwood trees was also indicative of conifer-dominated regeneration that had advanced to a stage selected for by male spruce grouse. These results are consistent with previous work that indicated male spruce grouse in Maine use stands comprised of up to 20% deciduous trees (Allan 1985).

Occupancy was positively related to canopy closure variation. In our stands, openings in the canopy often resulted from skid roads, shallow soil, and other conditions that prevented uniform tree density. These small openings were often where we observed displaying males, and previous research has noted that displaying males prefer to use openings in the understory that provide space to perform flutter-flights (Boag and Schroeder 1992). Thus in our stands, open patches in the canopy were likely associated with potential display locations. Additionally, the number of saplings per hectare in each stand had a negative quadratic effect on occupancy, which indicated that there was a maximum density, above or below which, the probability of occupancy decreases.

Our abundance models indicated that, within occupied stands, displaying male spruce grouse were abundant with an estimated $0.67 - 2.75$ grouse in occupied stands. This translated to an estimated density of between $3.99 - 16.36$ displaying males/km^2 within our study area (95% CIs: $0.42 - 5.83$, $8.69 - 23.98$ displaying males/km^2). Given that the sex ratio for spruce grouse, like most grouse, is likely close to 1:1 (Boag and Schroeder 1992), we would expect the total density of grouse to be $7.98 - 32.72$ birds/km^2. These numbers were high when compared to other areas at the southern

boundary of spruce grouse range including Michigan (5-9 birds/km^2) and New York (1 –

10 birds/km^2), and were comparable to densities reported for Ontario (10-22 birds/km^2;

max = > 50 birds/km^2) (Potapov and Sale 2013). We are confident that spruce grouse are

common across our study area because we used conservative counts (did not include

females or non-responding males), and the stand types we surveyed, especially

regenerating conifer, are prevalent across the landscape (Legaard et al. 2015).

The abundance models were insightful because they utilized patterns of variation

in abundance, rather than being restricted to presence and absence. Thus, we could

differentiate between abundantly occupied stands (3-5 males) and those that are only

minimally occupied (1-2). Notably, our occupancy and abundance models included many

of the same influential variables such as deciduous tree diameter (quadratic), tree height,

lowest limb height, and the two group model. However, the additional sensitivity to

differences allowed abundance models to identify quadratic effects of tree diameter, basal

area of trees, and conifer tree density.

The quadratic relationship between deciduous tree density and spruce grouse

abundance indicated a similar optimum deciduous tree density of 140/hectare compared

to the occupancy model (156/hectare). The most interesting difference was the quadratic

relationship between both tree diameter and basal area of trees. Both show that maximum

abundance should be expected on sites with mid-successional characteristics associated

with moderate tree diameters (12.2 cm) and relatively low basal area of trees (12

m^2/hectare). Additionally, models for abundance and occupancy both indicated support

for negative effects of lowest limb height and total tree height. The highest estimates of

both abundance and occupancy for early-mid successional stands compared to mid-late

successional stands suggests that early-mid successional conditions following

clearcutting and herbicide application or pre-commercial thinning can be favorable for

spruce grouse in commercially managed forests. Finally, we saw the seemingly odd

quadratic relationship between abundance and conifer tree density, which shows higher

abundance at very low (124 conifer trees/ha) and very high (3034 conifer trees/ha)

conifer tree densities. Although we had originally expected a positive relationship

between abundance and conifer tree density, we observed males at sites with both

characteristics (TLRG1 = 149 conifer trees/ha; JHO1C = 3034 conifer trees/ha).

Pre-commercially thinned stands and unthinned regeneration stands (pooled) had

the highest probability of occupancy and the highest estimated abundance. In contrast,

mature stands and selection harvests (pooled) had a lower probability of occupancy and

estimated abundance. This indicates that conifer-dominated stands with a recent history

of clearcutting (18 – 40 years post-harvest) were favored by males over residual conifer

and selection harvest stands.

In combination, the occupancy and abundance models highlight three areas of

forest composition and structure important for spruce grouse: maturity, composition, and

stem density. These were the three most important principle components to explain the

variation between sites where grouse were documented versus undocumented. Occupied

stands were ordinated across the range of stand maturity and stem densities observed, but

grouse were documented only on the upper end of the conifer spectrum. When we used

the first two principle components to ordinate among the four stand types (Figure1.5),

pre-commercial thinning had our highest probability of occupancy, and was ordinated

between mature and regenerating conifer stands (Figure 1.6). Further, selection harvests,

which did not contain displaying males, were separated from the other three types by higher deciduous tree composition. This implies that the stands that experienced the most intense harvest histories, and which received post-harvest management treatments to promote conifer regeneration and growth (e.g. herbicide and PCT), provided the highest occupancy and abundance of spruce grouse.

Displaying male spruce grouse were found across the range of successional stages studied, but did not show a preference for late successional habitat as has been previously reported (Ouellet 1974, Williamson et al. 2008). Breeding male spruce grouse usually occupied, and exhibited higher abundance, in early-mid successional forests and in stands with a past history of clearcut harvesting followed by herbicide application to reduce competition from shade tolerant hardwoods. Further, stands subsequently treated with PCT appeared to support optimal conditions for displaying males.

Although still abundant across the landscapes of northern Maine, conifer dominated forests have declined since 1975. This decline was accelerated by the increased use of partial harvesting that coincided with the passage of the Forest Practices Act (Legaard et al. 2015). This trend will likely continue as all models of future forest composition under various climate and harvest scenarios indicate declines in the amount of spruce-fir forest on the landscape (Shifley and Moser 2016).

MANAGEMENT IMPLICATIONS

Given our findings of highest abundance and occupancy of spruce grouse in previously clearcut stands with post-harvest management to promote coniferous regeneration, we recommend the continued use of intensive forestry practices, such as clearcuts, herbicide application, or pre-commercial thinning to maintain patches of suitable conifer-

dominated habitat where management of spruce grouse and other conifer-dependent

species (e.g. snowshoe hares (*Lepus americanus*) and Canada lynx (Lynx canadensis);

Simons-Legaard et al. 2013) are a priority. Other methods such as shelterwood

management, commercial thinning, and overstory removal may also be targeted to

produce desired conditions of 140-148 deciduous trees/ha within conifer dominated

stands featuring moderate diameter trees (12.2 cm), and moderate basal area (12 m^2/ha).

Although clearcuts have been shown to reduce habitat quality for spruce grouse

immediately after harvest, we documented extensive use of clearcut areas by male grouse

18-40 years after harvests. Thus we recommend distributing harvests spatially and

temporally so that occupied stands are adjacent to recently harvested stands that will

regenerate into suitable habitat as the occupied stands mature and become less desirable

to displaying males.

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CHAPTER 2

HABITAT SELECTION DURING BROOD-REARING BY FEMALE SPRUCE GROUSE IN COMMERCIALLY MANAGED FORESTS

ABSTRACT

Species near geographic range boundaries are vulnerable to extirpation resulting from a variety of stressors including habitat loss and climate change. The northeastern U.S. intersects the southeastern extent of the geographic range of spruce grouse (*Falcipennis canadensis*), and within that region Maine contains the largest area of potential habitat with about 2.7 million hectares of conifer-dominant forests. Within the forests of northeastern Vermont, northern New Hampshire, and Maine, where most remaining spruce grouse persist in the northeastern U.S., the majority of lands are commercially managed for a variety of forest products. Given the low clutch sizes and high potential survival of adult spruce grouse relative to other forest galliforms, effective conservation and management of spruce grouse depends on understanding how various forms of forest harvesting affect subsequent habitat choices by females, especially during the brood rearing season. This study investigated habitat selection by female spruce grouse during brood rearing (June-October) in a commercially managed landscape where > 60% of forest stands had been harvested in the previous 40 years. During the summers of 2012, 2013, and 2014 we conducted repeated call-back surveys in 30 conifer stands that potentially contained spruce grouse, and captured 30 females in 12 stands and equipped them with VHF transmitters. Our goal was to increase understanding of within home range (i.e., 3rd-order selection) selection by grouse in a harvested forest matrix.

Therefore, we measured attributes describing maturity, cover, and patchiness of vegetation at 10 points within the focal stand associated with initial capture and geographic center of activity of females (i.e., available habitat). We compared available habitat to attributes at 15 randomly selected radio locations for each radio-equipped female (i.e. use). We used general linear mixed models to construct resource selection functions for 30 female grouse, while treating maturational, structural, and patchiness variables as fixed effects and bird identity as a random effect. Our results indicate that spruce grouse select for within-stand conditions characterized by abundant low vegetation structure (<0.5m), with lowest branches of trees 3-9 m above ground, and with tree densities <1000 /ha. Pre-commercial thinning and herbicide application to promote conifers after clearcutting can produce structural and maturational conditions, coupled with sufficient within-stand patchiness, to result in habitat conditions selected for by spruce grouse in northeastern Acadian forests. Based on 80% fixed-kernel utilization distribution home range estimates, appropriate scales for managing female spruce grouse habitat averaged 38.11 ha during the brood rearing season. Forest management promoting mid-successional and patchy conditions within conifer stands on a scale approximating the home range of spruce grouse hens should promote population persistence near the southern extent of the species' range.

INTRODUCTION

Spruce grouse (*Falcipennis canadensis*) are a species of conservation concern in the northeastern United States. This area is known as the Acadian region (Seymour and Hunter 1992) and is the ecological transition zone between the boreal forests of Canada, where spruce grouse are common, and the temperate deciduous forests of southern New

England, where the species is absent. Forests of this region are typified by a combination of species from both regions including balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), black spruce (*Picea. mariana*), red spruce (*P. rubens*), American Beech (*Fagus grandifolia*), and maple (*Acer* spp.) (Seymour et al. 2002). Although complicated somewhat by elevation and other factors, the region displays a gradient across latitude and longitude from hardwood dominated mixed forests in the southwest to conifer-dominated mixed forests in the northeast. Consequently the abundance of spruce grouse, a conifer specialist, is expected to follow a similar gradient from rare in the south to abundant in the north. Maine, which is situated in the northern portion of the Acadian region, contains a large area of historically-occupied habitat. The state contains over 7.08 million hectares of forest of which 97% are considered commercial timberland (McCaskill 2015). Approximately 2.3 million hectares are classified as spruce-fir forest (McCaskill et al. 2011), which is potentially suitable habitat for spruce grouse (Ouellet 1974, Williamson et al. 2008). Unfortunately, little is known about the current status of spruce grouse in the Acadian region, especially in the commercially managed forests of northcentral Maine where mature conifer forests have declined and become more fragmented since 1970 (Legaard et al. 2015).

Spruce grouse have high annual adult survival (22-49%) and small average clutch sizes (4-7 eggs) relative to most gallinaceous birds (Boag and Schroeder 1992). Most females will reproduce in the breeding season following their first year of life, and brood mortality of 8-48% is expected between hatching and dispersal (Boag and Schroeder 1992). In the southeastern extent of their range, spruce grouse are typically associated with mid and late successional coniferous forests, especially coniferous forested wetlands

(Ouellet 1974, Williamson et al. 2008, Ross and Johnson 2011). However, late successional conifer forests declined by 31% in Maine between 1975 and 2007 (Simons 2009), and annual harvesting footprint remains > 160,000 ha/year, with most (93%) harvests in 2014 being classified as partial or shelterwood harvests (Maine Forest Service 2015). Approximately 78% of the remaining spruce-fir stands are considered to be small-medium diameter (2.54 cm – 27.7; McCaskill 2015). Spruce grouse in the Adirondacks of New York were shown to occupy mid-successional stands rather than mature stands (Ross et al. 2016). Displaying males occupy a range of conifer stands, not just late successional stands (Chapter 1), which contrary to previous assessments (Williamson et al. 2008), suggests that spruce grouse may not be exclusively selecting older forests. Occupancy by males does not necessarily imply habitat selection or greater reproductive success in mid-successional forests; therefore, we studied within-home range scale (i.e., 3rd order *sensu* Johnson 1980) habitat selection by female spruce grouse in the commercial forests of Maine to evaluate vegetational and structural attributes associated with brood rearing activities.

Our goal was to understand how commercial forest management in the region had influenced spruce grouse brood rearing habitat. Specifically, we investigated how female habitat selection was influenced by within-stand variables associated with degree of maturity, vegetative cover, and patchiness. Maturity was selected because it is often assumed in this region that spruce grouse select for mature or late-successional conifer forest (Williamson et al. 2008). However, recent work in the region has challenged this assumption (Chapter 1, Ross et al. 2016) and we hypothesized that female spruce grouse would select for structural features and food resources found more commonly in early-

mid successional forest. Vegetative cover included the features within a stand that provided both overhead and lateral cover, given that female spruce grouse with broods needed to select sites that balanced their brood's need for cover with their need for food. We hypothesized that females would select sites with less canopy cover and greater abundance of vegetation at ground level relative to what was available within their focal stand (Anich et al. 2013). Patchiness, as measured by the variation of canopy cover within a stand, was also predicted to provide the mixed requirements of broods because areas with tree cover adjacent to open areas with more dense understories would presumably provide juxtaposition of cover, food, and escape structures (i.e. dense understory for chicks and trees for fledglings and hens). Finally, we investigated the home range size of female spruce grouse to determine an appropriate scale at which to manage for habitat conditions selected for by an individual female during the brood rearing season.

STUDY AREA

Our study was centered on the home ranges of radio-equipped female spruce grouse that were captured within 12 forest stands surveyed during the early brood-rearing season (11 June – 17 July) in 2012, 2013, and 2014 (Table 2.1). Home ranges were distributed across five townships (T6R13, T5R11, T4R12, T4R11, T3R12) in northern Piscataquis County, Maine (Figure 2.1) and encompassed an area of 511 km^2. This area was owned by Katahdin Forest Management LLC and managed for pulpwood and timber. Most of the study area consisted of the "Spruce-Fir Wet Flat" community type with generally level terrain, somewhat poorly drained soils, and dominated by balsam fir, red spruce, black spruce, red-black spruce hybrids, eastern larch (*Larix laricina*), and northern white

Table 2.1. Location, stand treatment, and treatment history of the 12 stands where spruce grouse hens were captured in northcentral Maine, during 12 June – 13 July of 2012-2014.

Stand Name	Township	Stand Treatment	Harvest Treatment	Herbicide Treatment	Thinning Treatment	Years Surveyed
1-1-T	T4R11	PCT	1982	1988	1999	3
1-4-T	T4R11	PCT	1982	1988	1999	3
1-5-T	T4R12	PCT	1976	1983	1999	3
15Y3	T6R13	PCT	1983	UNK	1994	3
6-4-T	T5R11	PCT	1974	1982	1994	3
JH01	T4R11	Clearcut	1978	1988	NA	3
JH03	T4R11	Clearcut	1981	1984	NA	3
JH04	T5R11	Clearcut	1983	1988	NA	3
JH54	T5R11	Clearcut	1972	1982	NA	2
TLRG1	T4R12	Clearcut	1994	NA	NA	2
TLRG2	T3R12	Clearcut	1991	1999	NA	2
MSW11	T6R13	Mature	1970	NA	NA	3
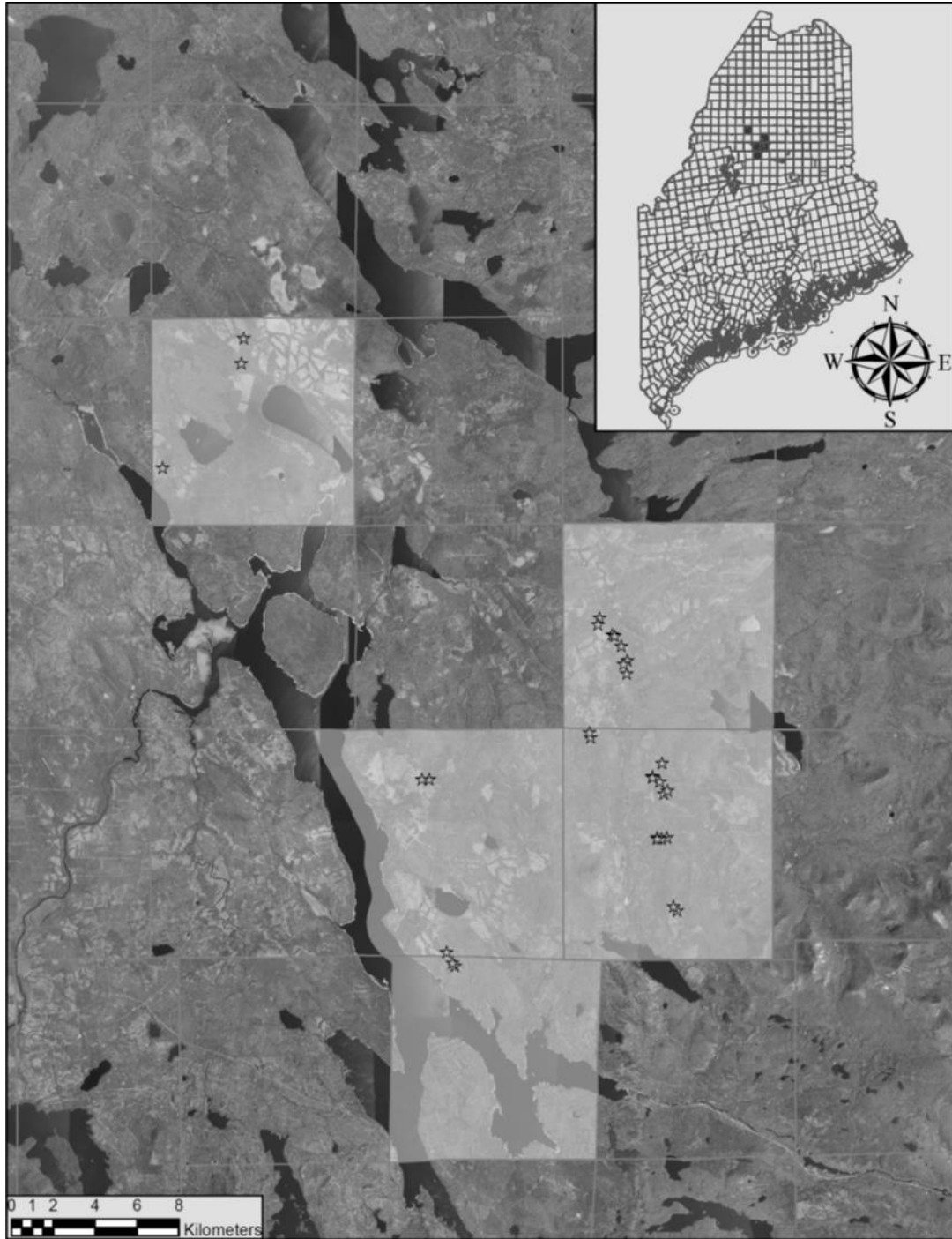
Figure 2.1. Geometric centers of activity for the 30 spruce grouse home ranges used to examine female spruce grouse habitat selection across 5 townships (T6R13, T5R11, T4R12, T4R11, and T3R12) in Piscataquis County, Maine during June-September of 2012-2014.

cedar (*Thuja occidentalis*) (Maine Natural Areas Program 2010). Other common species included white spruce (*P. glauca*), white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), white birch, yellow birch (*B. alleghaniensis*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), and American Beech.

We surveyed for female spruce grouse in 30 forested stands used in a concurrent study of male spruce grouse occupancy during the breeding season (Chapter 1). This study focuses on habitat selection within the home ranges of females caught within 12 stands. Of these stands, six were classified as regenerating conifer clearcuts, five were pre-commercially thinned (PCT) stands that were thinned at least 15 years prior to our study, and one was a mature conifer stand. The regenerating conifer clearcuts represented forest stands resulting from techniques common during and immediately following the spruce budworm (*Choristoneura fumiferana)* outbreak of the 1970s-1980s. These stands were clearcut an average of 28.8 years prior to 2012 (range 18-40), then aerially treated an average of 7.2 years post-harvest (range 3-10) with herbicide (e.g. Glyphosphate at ≈ 1.68 kg/ha acid equivalent) to reduce deciduous regeneration. Stands were densely stocked with balsam fir and red and black spruce with an interspersion of other common associates such as eastern larch, northern white cedar, eastern hemlock, paper birch, red maple, and quaking aspen (*Populus tremuloides*). PCT stands were similarly clearcut an average of 32.6 years prior to 2012 (range 29-38), were treated with herbicide an average of 6.8 years post-harvest (range 6-8), and were then subsequently thinned by crews using brush saws an average of 17.6 years post-harvest (range 11-23). This thinning, a common post-harvest management practice during the 1990s and early 2000s, resulted in stands with approximately 20% fewer conifer trees/ha, about 50% fewer deciduous stems, and

average tree diameters 15% greater than unthinned stands with a previous history of clearcut harvesting (measurements from chapter 1). The mature conifer stands that we surveyed were second-growth stands that had no history of harvest in the prior 42 years (reliable record keeping began in 1970). Previous work in the region estimated the average age of mature conifer patches to be to be >80 years old (Simons-Legaard et al. 2013). The mature stand where two radioed hens centered their activities had a tall, closed canopy with relatively little understory, but included an area characterized by poorly drained soils bordering a stream with a dominance by shrubs and patchy canopy cover of conifer trees.

METHODS

Field Methods

From 11 June – 9 July 2012, 18 June – 17 July 2013, and 19 June – 15 July 2014 we conducted call-back surveys for female spruce grouse across our 30 stands. We established four transects spaced 65 m apart with seven survey locations spaced 60 m apart along each transect for a total of 28 survey points within a stand. At each survey point we broadcasted chick distress calls from a FOXPRO® NX3 game caller over a period of 3 minutes: one minute of listening followed by one minute of chick distress calling followed by another minute of listening. All responses were recorded and we attempted to capture the responding grouse with a 20' telescoping fiberglass fishing rod (Shakespeare WonderPole®) fitted with a sliding noose made of 80-lb test monofilament fishing line (Zwickel and Bendell 1967). Captured female grouse were weighed and individually marked with a numbered aluminum butt-end leg band and a unique pattern of 1-3 plastic colored leg bands (Schroeder and Boag 1989, Keppie 1992). If larger than

400g, individuals were fitted with an Advaced Telemetry Systems (Isanti, MN) A3950 necklace mounted VHF radio transmitter (~12 grams). Survey, capture and marking protocols were reviewed and approved by the University of Maine's Institutional Animal Care and Use Committee.

During each season, field technicians were trained and observed to ensure proficiency at capturing grouse. Subsequently, we switched among observers in each stand across successive surveys to minimize detection bias. Additionally, we reversed the order of surveys across our three visits to reduce potential effects of survey timing. To ensure favorable survey conditions we did not conduct surveys during steady rain or steady winds above a 3 on the Beaufort scale (Martin et al. 1997).

To document habitat selection and home range area we used homing to visually locate each radio-equipped female at least twice per week from capture date until 31 August, while maintaining a minimum of six hours between successive locations. All relocations were diurnal and were divided evenly for each bird into four time blocks starting 30 minutes before sunrise and ending 30 minutes after sunset (Dawn-0800, 0801-1200, 1201-1600, 1601-Dusk). From 1 September to 1 October we located females once per week using a Telonics (Mesa, AR) TR-2 or Communications Specialist (Orange, CA) R-1000 receiver and a directional "H" antenna (Telonics RA-14K, Mesa, AR). We recorded geographic coordinates with a Garmin® GPSMAP® 62s using location averaging with estimated accuracy of 5-10 m. The date, time, and position (i.e., ground vs. tree) of marked females was recorded at each location.

Given logistics and shared objectives with companion studies for male spruce grouse (Chapter 1) and snowshoe hares (Scott 2009, Olson 2015), vegetation

measurements to assess habitat availability within our surveyed stands were conducted prior to grouse being captured and monitored. We selected 16 variables that were determined *a priori* to be biologically relevant to spruce grouse hens during the brood-rearing season (Table 2.2). We measured vegetation variables at 20 randomly selected sites within each stand. Canopy cover was assessed using the average of four spherical densitometer readings taken at the center of the survey point in each of the cardinal directions. The patchiness of canopy cover was determined by calculating the coefficient of variation from the four measurements at each plot. Basal area (BA) was measured for saplings and trees with a 2-factor prism from the center of the survey point and was expressed as m^2/ha. Saplings were defined as <7.6 cm diameter and >1.5 m tall. Trees were defined as >7.6 cm diameter and >1.5 m tall. Lateral cover was estimated using a 600 cm^2 silhouette that was 19.5 cm tall, approximating the size and height of a spruce grouse, placed upright on the ground in a random orientation in the plot center. Ocular estimates of coverage from 5 m distant and 0.5 m above ground were made from each of two directions 180° from each other. To eliminate potential observer bias we painted the board fluorescent pink for contrast and limited estimates to eight categories: 0%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95%, 96-99%, or 100% obscured. The patchiness of lateral cover was estimated by taking the difference between the two measurements of lateral cover at each plot. Tree densities, diameters, and heights were measured using the point-centered quarter method (Cottam and Curtis 1956). Using the cardinal directions to define four quadrants, we selected the closest tree in each to identify the species and to measure diameter, height, lowest live limb (LLL) height, lowest dead limb (LDL) height, and distance to plot center. Quadratic mean diameter and total tree density were derived

Table 2.2. Sixteen vegetation variables measured at both use and available points for spruce grouse hens in northcentral Maine, July-August 2012-2014. Variables 1-7 are included in the stand maturity model, variables 8-14 are included in the stand structure model, and variables 15-16 are included in the stand patchiness model.

Variable	Description	Units	Measurement Method
1. QMD[a]	Quadratic mean diameter	cm	Calculated from DBH and BA
2. TTD[a]	Total tree density	trees/ha	Point-quarter method
3. BAS	Basal area of saplings	m^2/ha	$2m^2$/ha wedge prism
4. TH[a]	Total tree height	height in m	Hypsometer
5. LLL[a]	Lowest live limb	height in m	Meter Tape or Hypsometer
6. LDL[a]	Lowest dead limb	height in m	Meter Tape or Hypsometer
7 MGC	Moss ground cover	% cover	$10m^2$ point-intercept plot
8 LC1	Lateral cover (side 1)	% obstruction	Hare silhouette at 5m
9 LC2	Lateral cover (side 2)	% obstruction	Hare silhouette at 5m
10. LVC	Low vegetative cover	% cover	$10m^2$ point-intercept plot
11. MVC	Mid vegetative cover	% cover	$10m^2$ point-intercept plot
12. OC	Overhead cover	% cover	$10m^2$ point-intercept plot
13. TBA	Total basal area	m^2/ha	$2m^2$/ha wedge prism
14. CC[b]	Canopy closure	% closed	Densitometer at 1m high
15. CCV[b]	Canopy closure variation	% variation	Calculated from canopy closure
16. LCV	Lateral cover variation	% obstruction	Difference in LC between LC1 and LC2

[a] Measurements taken on the nearest tree in each of four quarters around each survey point based on the point-quarter method (Cottam and Curtis 1956).
[b] Canopy closure was measured by taking 4 readings oriented in the cardinal directions from the center of the plot with a spherical densitometer. The CCV is simply the coefficient of variation between those four measurements at each site.

from these measurements. Vegetative cover was quantified in four layers: ground to 7 cm high (ground cover), 7 cm–50 cm (LVC), 50 cm–150 cm (MVC), and overhead (OC).

This was measured using a GRS densitometer™ (point-intercept; Graphic Resource

Solutions, Arcata, CA) at 18 points/layer based on a 10 m^2 rectangular plot placed beside the survey point in a random orientation. This data was used to determine the ground cover by moss (%), low vegetation cover (%), mid vegetation cover (%), and overhead cover (%).

We developed three groupings for these variables and modeled each group independently. Maturity was modeled with terms relating to the age and structure of vegetation found at our used and unused sites. These included quadratic mean diameter (QMD), total tree density (TTD), basal area of saplings (BAS), total tree height (TH), lowest live limb (LLL), lowest dead limb (LDL), and moss ground cover (MGC). Vegetative cover was modeled with terms relating to overhead cover, lateral cover, and stand density. These included measures of lateral cover (LC1 and LC2), low vegetative cover (LVC), mid vegetative cover (MVC), overhead cover (OC), total basal area (TBA), and canopy cover (CC). Patchiness was modeled by including terms relating to the variation in canopy cover (CCV) and lateral cover (LCV) caused by small openings, as well as variation in the understory.

To quantify vegetation at sites used by spruce grouse, the same suite of variables were measured using plots centered on 15 randomly chosen radio locations (obtained from 15 June – 1 October) for each female grouse; no locations were included after a female initiated a post-brood rearing range shift (see statistical analysis). Locations were flagged, numbered, and mapped using a GPS during walk-in observations of radio-marked hens. Vegetation measurements at telemetry locations were taken during July-August in the subsequent year to avoid influencing behavior of the marked hen, while maintaining mid-summer phenology of vegetation.

Statistical Analysis

We compared use to availability for each bird in a design III resource selection function framework (RSF; Manly et al. 2002) with the intent to focus on within-home range habitat selection by females during the brood-rearing season. We chose this scale to provide the opportunity to make recommendations on maturational, structural, and within-stand patchiness to foresters managing stands for fiber production. We defined the characteristics of used habitat at the telemetry locations of observed female spruce grouse from capture (June-July) until brood break-up, which we defined as October 1. Spruce grouse are known to move between discrete summer and winter habitats with substantial variation in the timing of this shift (Herzog and Keppie 1980, Schroeder 1986); therefore, we developed a test to screen all birds for evidence of a range shift. First we calculated the geometric mean center of all locations prior to 15 August in ArcMAP (ArcGIS Version 10.0, Environmental Systems Research Institute, Redlands, CA). Next we plotted the distance of each location from the mean center sequentially. Finally, we calculated the mean distance and two standard deviations from center a bird traveled during the summer and we truncated the data when a female moved greater than two standard deviations than the mean and did not return.

Budgetary and logistical constraints prevented us from using paired random points to define availability. Thus, we defined availability as the focal conifer-dominated stand where we surveyed and captured each female spruce grouse. These stands, with a minimum size of 16.8 ha, approximated home range areas documented for females during brood rearing prior to our study (Potapov and Sale 2013) and represented forest

conditions common in the study area. Because multiple females were captured within all but one of the 12 included stands, we restricted our definition of availability to the 10 vegetation plots within the surveyed stands that were closest to the geographic mean center of a female's sample of radio locations. This approach allowed us to focus on individual availability (i.e. Type III design; Thomas and Taylor 2006) and to reduce potential for pseudo-replication.

We constructed our resource selection functions using generalized linear mixed effects models (GLMM) with a binomial distribution (Zuur et al. 2009). Although yearly differences in resource selection could potentially influence our results (Schooley 1994), there was little indication of behavioral differences among years, and thus we pooled our data across years to maximize our power to identify trends (Carpenter et al. 2010). We also included a random effect term for bird identity that accounted for differential selection across individuals, years, and brood status (some females did not have broods when captured or lost them shortly after capture).

Model comparison was completed in two steps. First, we constructed univariate models for each variable and for the quadratic form of each variable. The variables of interest were treated as fixed effects and bird identity was considered a random effect. All univariate models were compared to a null model. Models were evaluated with a combination of information-theoretic model selection and evaluation of the variance around parameter coefficients (β), where we retained all variables that had AIC_c values $\geq$ 2.0 units less than the null model and which contained coefficients whose 85% confidence intervals did not include zero (Burnham and Anderson 2002, Arnold 2010). Similarly, we considered the quadratic version of a variable to be supported when it

performed ≥ 2.0 AICc values less than the linear form and had a significant beta value

(85% C.I. of β does not include zero). Variables were then checked for multicollinearity

with a Pearson's correlation matrix and only variables with a Pearsons's $r \leq 0.70$ were

included within the same model during subsequent analysis (Figure 2.2). In cases where

influential variables were highly correlated, we retained the variable with the lowest AIC.

Secondly, we used an exploratory method to determine the most influential

covariates with which to guide forest management practices. First we grouped the

variables retained from step one into three global models based on within stand measures

of maturity, cover, and patchiness. We then tested all possible combinations of the

variables within these models to determine the most parsimonious model where each

retained variable improved model performance by ≥ 2.0 AICc, while only retaining

variables with 85% confidence intervals around β coefficients that did not include zero

(Burnham and Anderson 2002, Arnold 2010). All variables were standardized to Z-scores

$[z = (x - \mu)/\sigma]$, so that we could assess the relative effect of a variable by the magnitude

of its β coefficient. All models were constructed in program R using the packages "lme4"

and "MuMIn".

Home Range

We estimated the area of female spruce grouse home ranges during brood rearing to

provide insights into the appropriate scale for managing habitat of a female grouse during

the brood rearing season. Because each grouse was monitored for only one season, we

included all birds that had ≥ 25 locations retained after we screened for evidence of range

shifts. We then calculated brood rearing season home ranges with a fixed kernel

utilization distribution (Worton 1989) using the h_{ref} method of bandwidth selection
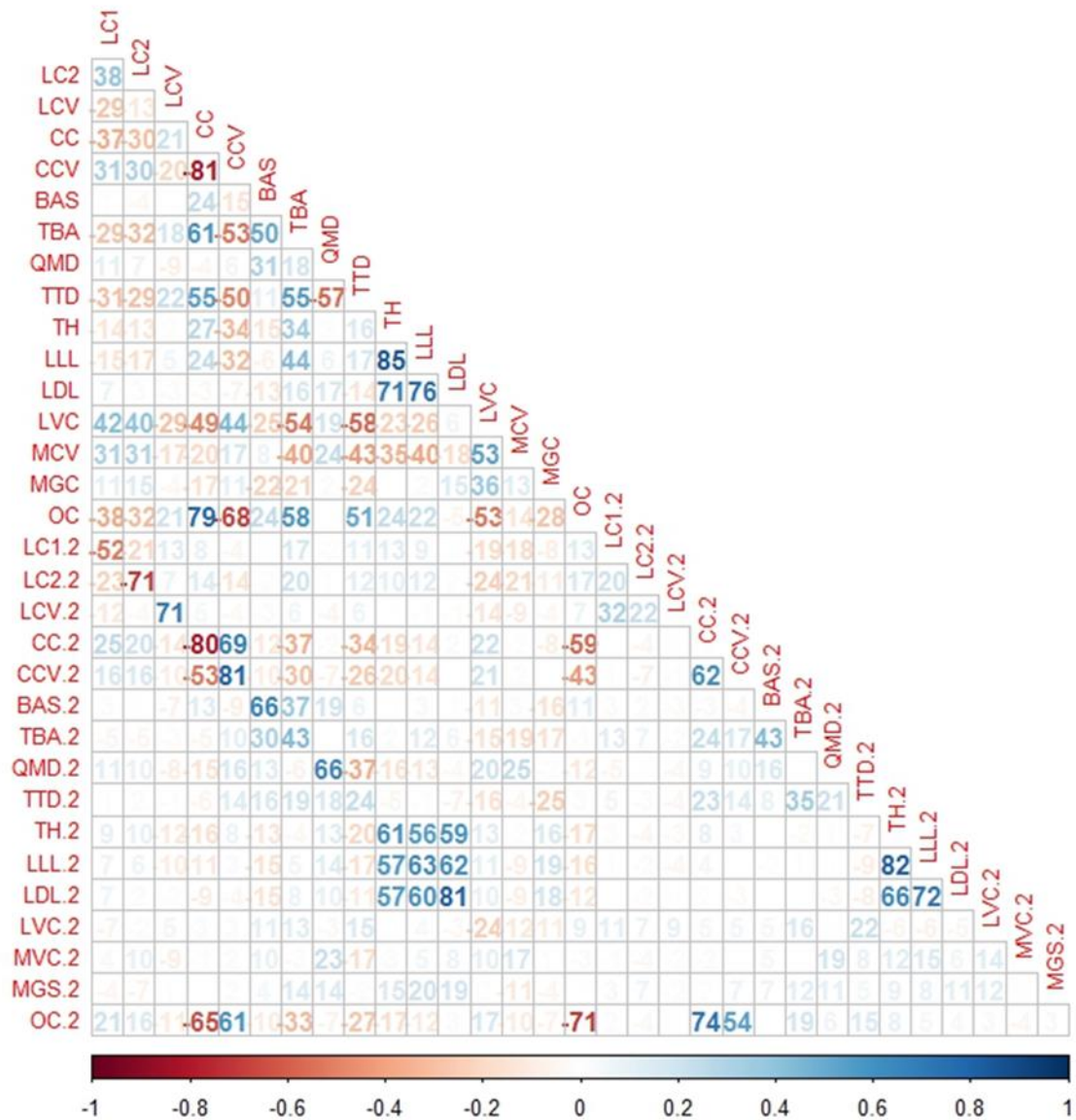
Figure 2.2. Correlation plot depicting the Pearson correlation values (x100) for all variables included in the analysis of habitat selection by female spruce grouse in northcentral Maine, July-September 2012-2014. Terms followed by .2 represent quadratic versions of the term.

(Silverman 1986). All home ranges were constructed with the package "adehabitatHR" in program R. We chose the h_{ref} method over least squares cross validation (LSCV) because our small sample of radioed birds (n=27) could cause LSCV to perform poorly (Horne and Garton 2006). The isopleth size was selected by graphing all potential isopleths

between 50-100% in 5% increments and visually determining the break in slope. For our set, the break occurred after the 80% isopleth; therefore, 80% fixed kernel home ranges were created for all included hens.

RESULTS

Resource Selection

From 2012-2014 we captured 39 hens; 32 were captured during the 11 June-15 July call-back surveys; 5 were opportunistically captured within our focal stands while locating marked birds; and 2 were captured on 4 May and 12 May while we were conducting occupancy surveys for male spruce grouse as part of a companion study (Chapter 1). We obtained ≥ 19 locations on 30 of our telemetered birds and excluded the remaining birds from analyses of habitat selection because of mortality (n = 5), radio failure (n= 3), or because the hen shifted her home range prior to 15 August (n = 1). We included data for 14 hens in 2012, ten in 2013, and six in 2014. We visually documented 919 locations with an average of 30.63 locations/hen (range = 19 to 35). Overall, we measured vegetative attributes at 450 use locations and 300 random sites within 12 focal stands containing locations of 30 female spruce grouse.

Hens were detected in trees at 134, or 14.6% of all locations. Tree use increased over the brood rearing season with an average of 1.07 (range = 0 to 4) observed uses of trees per female prior to 1 August and 3.33 (range = 0 to 10) observed uses of trees per female on and after 1 August. Additionally, birds who had broods for most or all of the season (n=23) averaged 3.61 (range = 0 to 9) observed uses of trees, while females who either had no broods or lost them within the first few weeks of the season (n = 7) averaged 7.14 (range = 0 to 12) observed uses. Only two females were never detected in

trees. Larch and spruce spp. were the most commonly used trees (34.3% and 31.3%

respectively), balsam fir (17.2%), and snags (7.5%). Eleven tree observations lacked a

description of species (8.2%). We observed one hen roosted in a white pine and one hen

in a northern white cedar, and no use of live deciduous trees.

We initially considered 32 univariate models assessed in step one, and retained 14

models that performed better than the null and had meaningful β coefficients (Table 2.3).

Of those 14 models, 9 represented quadratic versions of variables that outperformed the

simpler linear term. In step two, these were divided into the three global models

representing maturity, cover, and patchiness. After running all combinations of these

variables within the three global model groups, we were left with three reduced models

(Table 2.4).

The maturity model identified three variables of importance: moss cover, total

tree density, and lowest dead limb height (Figure 2.3). The primary driver of this model

was a strong negative quadratic relationship with total tree density (TTD β = -4.10, 85%

CI: - 4.77 to-3.42, TTD^2 β = 1.04, 85% CI: 0.73 to 1.34), indicating that selection

decreases with an increase in tree density. The model predicts a 99% probability of

selection at < 200 trees/ha, about 40% probability of selection at ~1450 trees/ha, and near

zero probability of selection above 2300 trees/ha. Lowest limb height was also associated

with selection, with a positive quadratic relationship (LDL β = 1.78, 85% CI: 1.42 to

2.14, LDL^2 β = -0.32, 85% CI: -0.41 to -0.23). Selection peaked at lowest limb heights

around 4.4 m; however, probability of selection was ~40% at lowest limb heights of 0.5

m. The final component of this model was the percentage of groundcover composed of

Table 2.3. Rankings for univariate resource selection function models for female spruce grouse in northcentral Maine, June-September, 2012-2014 based on a combination of Akaike's Information Criterion (AIC) and model coefficients. Models in bold (n = 14) outperformed their counterpart or the null model and were included in subsequent analyses.

Model	Df	AIC$_c$	β	S.E.
Total Tree Density^2	**4**	**827.2309**	**0.9481**	**0.1914**
Total Tree Density	3	856.8543	-2.5793	0.2446
Low Vegetative Cover	**3**	**885.8596**	**0.9431**	**0.1269**
Low Vegetative Cover^2	4	886.4942	0.11506	0.09785
Moss Ground Cover^2	**4**	**953.8649**	**0.25375**	**0.09108**
Lowest Dead Limb^2	**4**	**957.3438**	**0.11458**	**0.08269**
Moss Ground Cover	3	959.8021	0.49395	0.07893
Lowest Dead Limb	3	971.0531	-0.51021	0.08055
Quadratic Mean Diameter	**3**	**981.1432**	**0.36024**	**0.08512**
Quadratic Mean Diameter^2	4	982.9986	-0.02074	0.05017
Total Basal Area^2	**4**	**984.7180**	**0.17323**	**0.05832**
Canopy Cover^2	**4**	**984.9058**	**-0.21950**	**0.06463**
Mid Vegetative Cover	**3**	**987.3845**	**0.28126**	**0.07694**
Lateral Cover Variation^2	**4**	**988.4752**	**0.31506**	**0.08960**
Mid Vegetative Cover^2	4	988.7231	-0.05949	0.07178
Canopy Cover Variation^2	**4**	**988.9293**	**-0.08229**	**0.03754**
Canopy Cover Variation	3	991.3964	0.25330	0.08623
Basal Area of Saplings	**3**	**992.1945**	**-0.22286**	**0.07526**
Basal Area of Saplings^2	4	992.2503	0.07060	0.05048
Total Basal Area	3	992.5517	-0.21917	0.07553
Canopy Cover	3	994.3946	-0.19992	0.07904
Overhead Cover	**3**	**994.9421**	**-0.18973**	**0.07765**
Lateral Cover (side 1)^2	**4**	**995.4203**	**0.22236**	**0.12367**
Overhead Cover^2	4	996.3245	-0.06050	0.07532
Lateral Cover (side 2)^2	**4**	**996.3440**	**0.1972**	**0.1246**
Lateral Cover (side 1)	3	996.6359	0.15779	0.07498
Lateral Cover (side 2)	3	996.8293	0.15399	0.07476
Total Tree Height^2	4	998.4633	0.03001	0.05552
null	2	999.0536	0.37386	0.07501
Lateral Cover Variation	3	999.1687	-0.10304	0.07465
Lowest Live Limb	3	999.2694	-0.09132	0.07517
Total Tree Height	3	1000.065	0.10560	0.07530
Lowest Live Limb^2	4	1001.185	-0.03153	0.04913

Table 2.4. Final reduced resource selection function models for female spruce grouse in northcentral Maine, June-September, 2012-2014.

Maturity Model	Vegetative Cover Model	Patchiness Model
% Moss Groundcover	% Low Vegetative Cover	Canopy Cover Variation
Total Tree Density^2	% Mid Vegetative Cover	Lateral Cover Variation^2
Lowest Dead Limb^2	% Overhead Cover	
	Total Basal Area^2	

Figure 2.3. Predicted probabilities of selection across the range of observed values for the variables included in the reduced maturity model for female spruce grouse during the brood rearing season (June-September) in northcentral Maine, 2012-2014. Moss ground cover (a), total stem density (b), and lowest dead limb (c) were all retained.

moss (β = 0.69, 85% CI: 0.51 to 0.87). This was a positive relationship, indicating that females were more likely to select areas with predominantly moss groundcover.

The vegetative cover model identified four influential variables (Figure 2.4). The primary driver was a positive linear effect of low vegetative cover (0 – 0.5m) (β = 1.35, 85% CI: 1.16 to 1.55). This was followed by the positive linear effect of overhead cover (β = 0.53, 85% CI: 0.37 to 0.70). Additionally, we documented a negative linear effect of mid-height vegetative cover (0.5-1.5 m) (β = -0.34, 85% CI: -0.49 to -0.18) on selection. Finally, there was a positive quadratic relationship of total basal area to selection (TBA β = -0.11, 85% CI: -0.29 to 0.07, TBA^2 β = 0.21, 85% CI: 0.12 to 0.31). These results indicate that hens had ~75% probability of selection for sites with >72% low cover (0 – 0.5 m), 100% overhead cover, an absence of mid-level cover (0.5 – 1.5 m), and total basal area either approaching 0 or above 60 m^2/hectare. This suggests that females were selecting for areas with openings for feeding and areas with increased sapling and tree density for cover from predators.

Finally, our patchiness model identified both lateral and canopy cover variation as influential (Figure 2.5). This model was driven by a negative quadratic association between lateral cover variation and selection (LCV β = -0.35, 85% CI: -0.51 to -0.19, LCV^2 β = 0.32, 85% CI: 0.20 to 0.46), as well as a positive association between canopy cover and selection (β = 0.13, 85% CI: 0.01 to 0.26). Spruce grouse seem to select for sites with either a high or low coefficient of variation in lateral cover (~62% selection at 0% variation and >75% selection at 100% variation). CCV values of about 33% result in the lowest probability of selection (50%). Thus, hens selected sites containing either
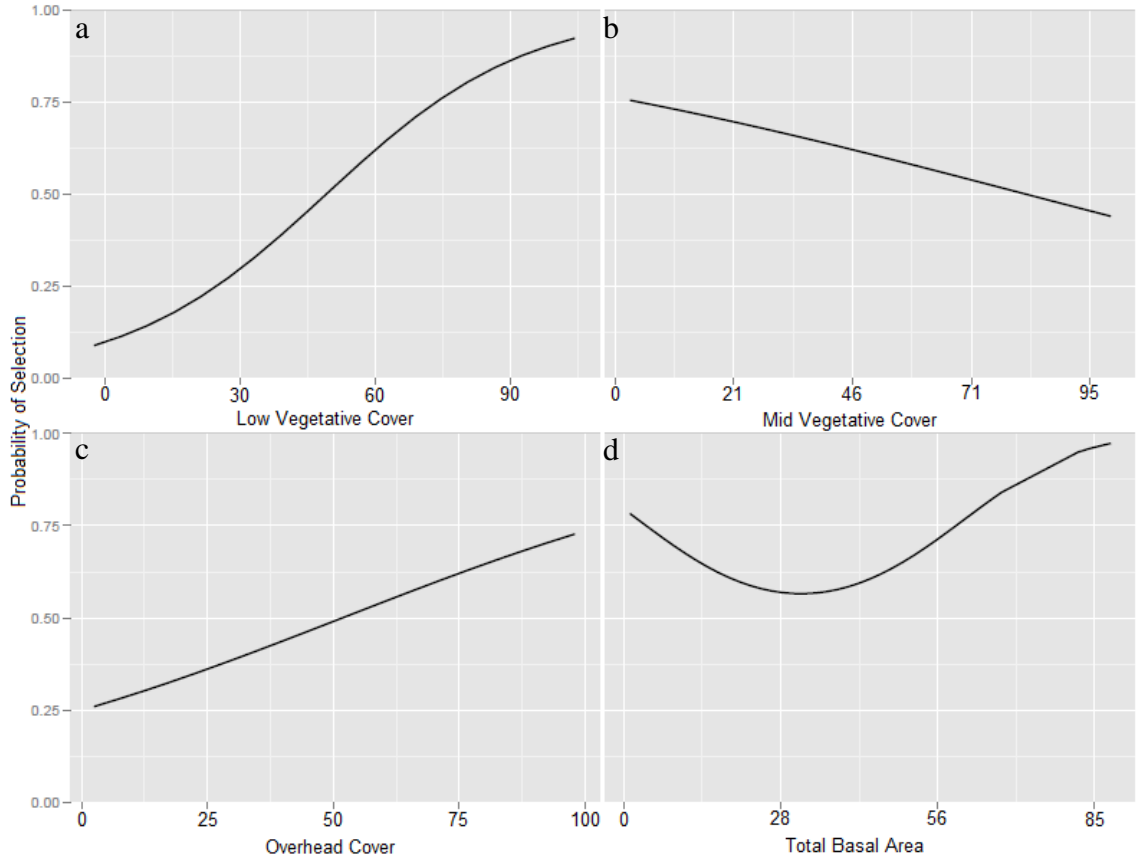
Figure 2.4. Predicted probabilities of selection across the range of observed values for the variables included in the reduced vegetative cover model for female spruce grouse during the brood rearing season (June-September) in northcentral Maine, 2012-2014. Low vegetative cover (a), mid vegetative cover (b), overhead cover (c), and total basal area (d) were retained.
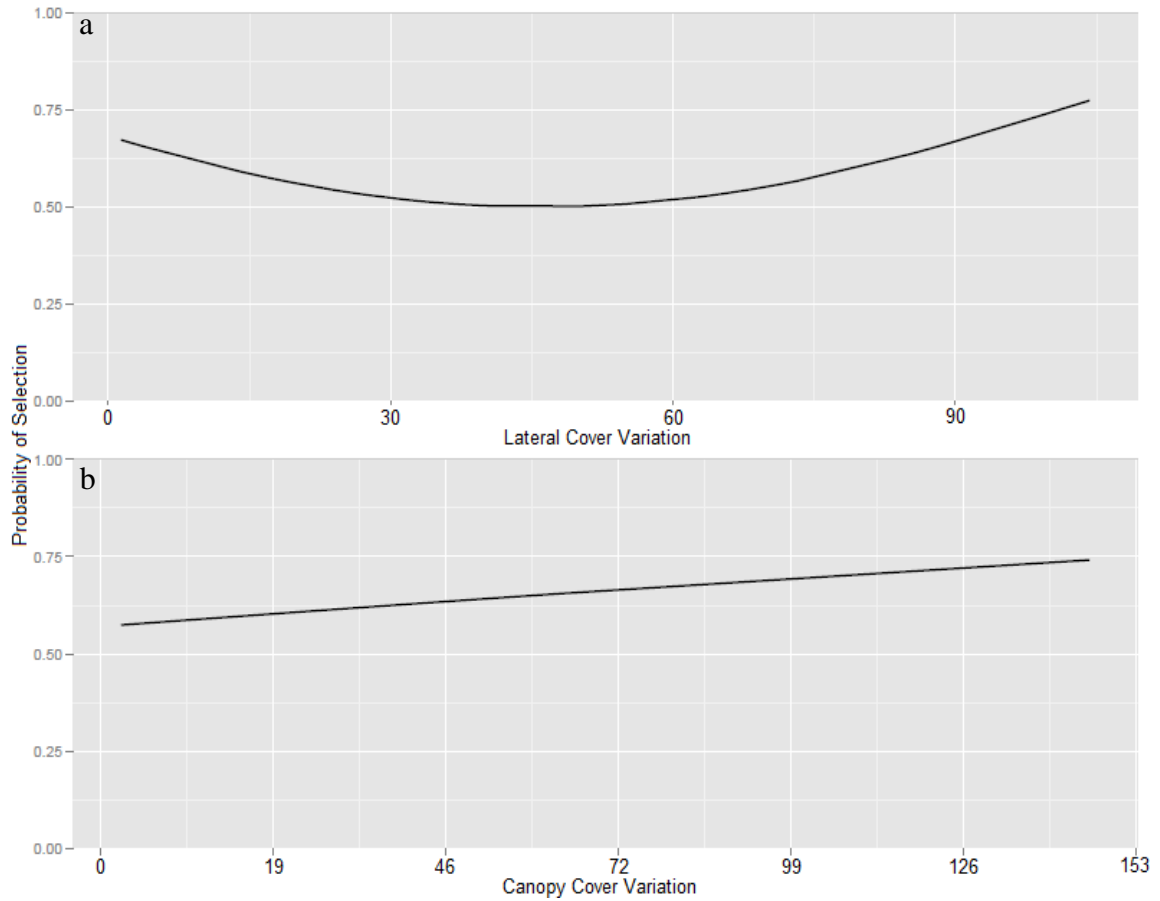
Figure 2.5. Predicted probabilities of selection across the range of observed values for the variables included in the reduced patchiness model for female spruce grouse during the brood rearing season (June-September) in northcentral Maine, 2012-2014. Lateral cover variation (a) and canopy cover variation (b) were retained.

uniform amounts of lateral cover or highly patchy sites.

Given the complexity of our results, we decided to simplify our three model system by constructing a final *post hoc* model. This model evaluated the combined effects of best performing variables from the previous three models. We defined the best performing variables as those with β values greater than one. Because our patchiness model did not contain any variables with β values greater than one, we simply took the variable with the largest β value. This model should approximate how a highly desirable

site would be categorized within a female's home range during brood rearing. This model included variation in lateral cover, total tree density, lowest limb height, and low vegetative cover variables (Figure 2.6). The strongest component of this model was the quadratic relationship between total tree density and selection (TTD β = -3.36, 85% CI: -4.03 to -2.69, TTD^2 β = 0.86, 85% CI: 0.56 to 1.17). This was followed by the quadratic relationship of lowest dead limb heights and selection (LDL β = 2.25, 85% CI: 1.84 to 2.66, LDL^2 β = -0.44, 85% CI: -0.55 to -0.34). Next was the positive association between low vegetative cover and selection (β = 1.19, 85% CI: 0.96 to 1.41). The final component driving the model was a quadratic relationship between lateral cover variation and selection (LCV β = -0.13, 85% CI: -0.36 to 0.09, LCV^2 β = 0.34, 85% CI: 0.16 to 0.52).

Home Range

We obtained $\geq$ 25 locations (mean = 30.4, range = 25-35) for 27 of the 30 hens included in our habitat selection analysis. We excluded 3 hens because of radio loss (n = 1), mortality prior to the end of the season (n = 1), and evidence of seasonal home range shift prior to 25 August (n = 1). Nine hens had at least one location removed after screening for evidence of home range shifts believed to represent seasonal migration (mean = 5 September; range = 23 August to 22 September). Seven females had no brood at time of capture or lost their brood well before brood break-up. Because presence of brood could potentially affect the size of a hen's home range, we tested for differences in home range area between birds without broods (n=7) and brooded females (n=27) and observed no significant difference (Mann-Whitney U = 70, Z = -0.51, p = 0.30). When all hens were pooled, mean 80% fixed kernel home range area was 37.7 ha (SE = 23.9 ha; range = 9.1 – 82.7 ha; n = 27) during the brood rearing season. We calculated the 75th percentile, which
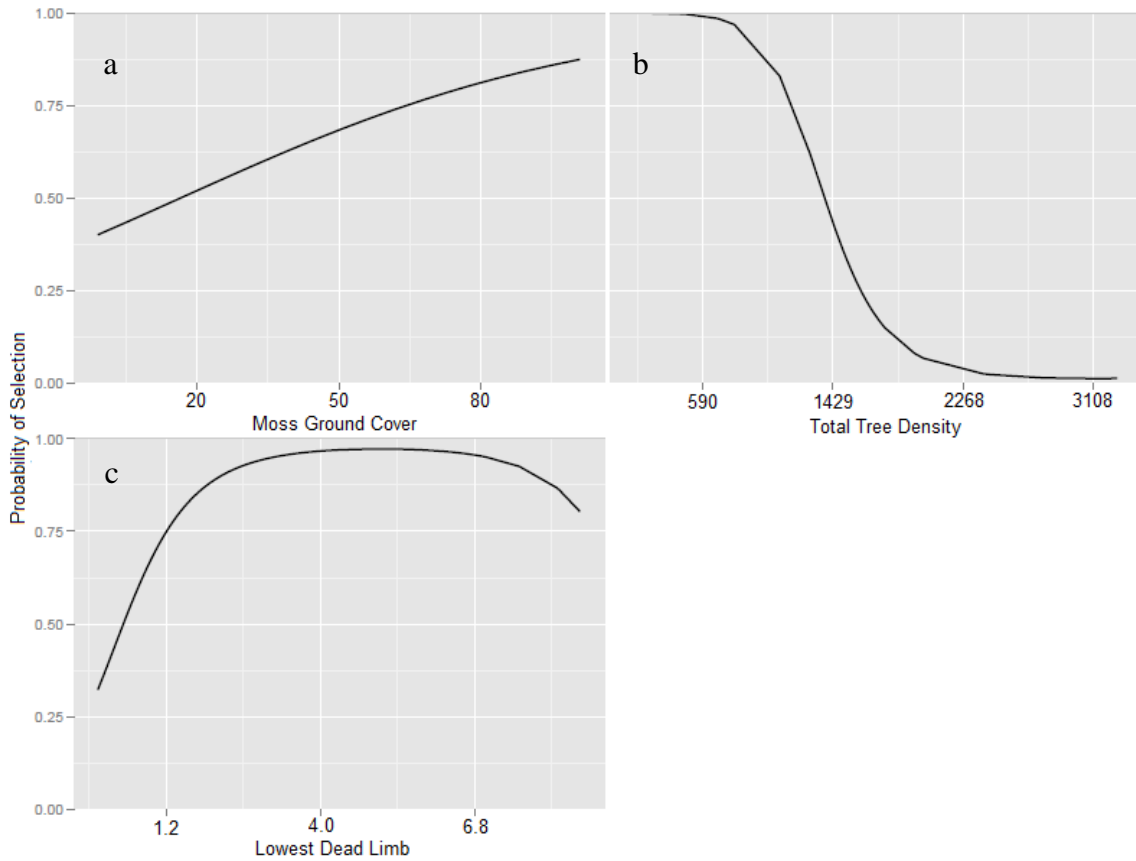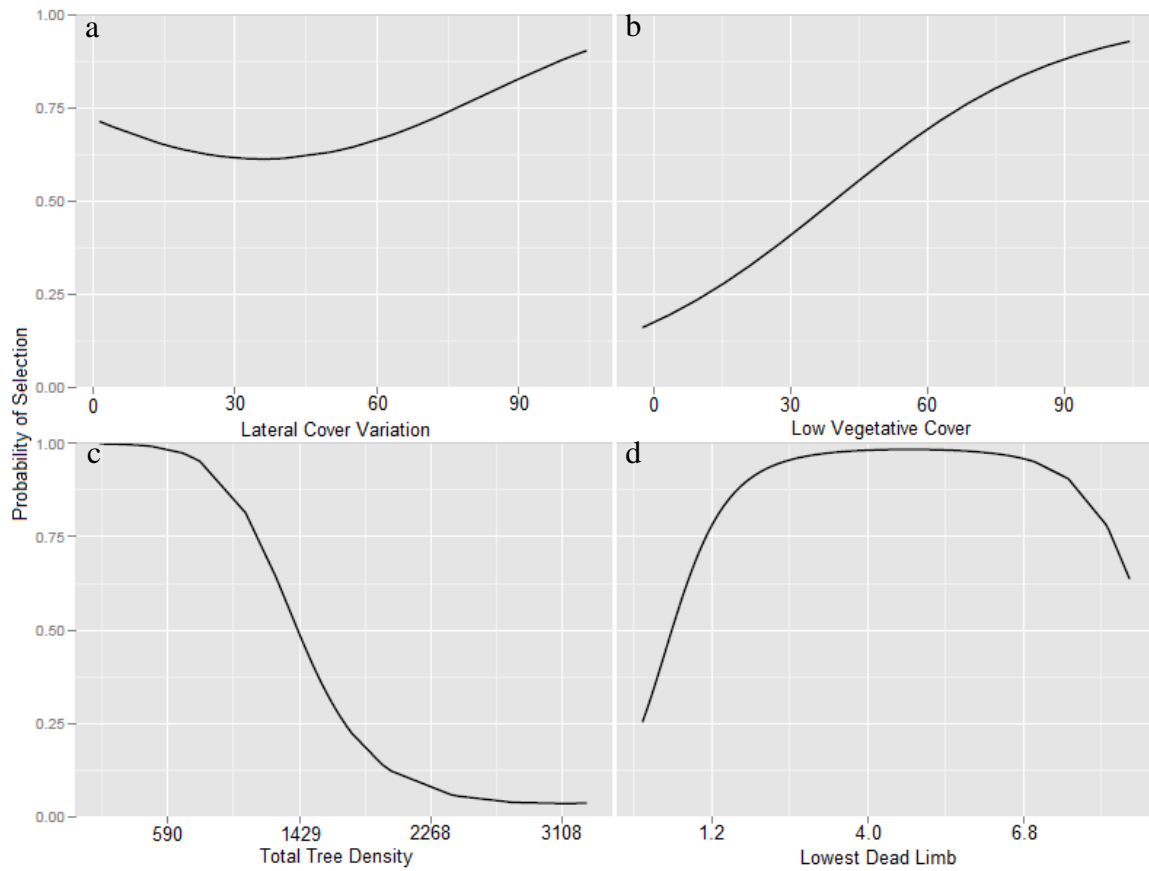
Figure 2.6. Predicted probabilities of selection across the range of observed values for the variables included in the post-hoc "top" model for female spruce grouse during the brood rearing season (June-September) in northcentral Maine, 2012-2014. Lateral cover variation (a), low vegetative cover (b), total tree density (c), and lowest dead limb height (d) were included.

was 55.1 ha, in order to provide a relevant scale of habitat management that would

encompass the majority of home range sizes observed.

DISCUSSION

Female spruce grouse selected for sites with low stem density, elevated lowest limb

heights, and abundant ground cover. Those conditions were observed in coniferous

wetlands, sites which had a history of overstory removal, sites with a history of

clearcutting, and sites with a history of clearcutting followed by pre-commercial thinning.

Some of these latter conditions, particularly the more recent clearcuts (harvested < 20 years prior) with retention of scattered trees resulted in conditions characterized by abundant regeneration but relatively few trees (> 7.6 cm DBH). Most live trees in these areas were residual white pines that were below diameter limits for harvests and were widely spaced with very tall lowest limb heights. This is likely why our maturity model and our post-hoc model predicted positive selection across such a wide range of lowest limb heights and for such low tree densities. Females are selecting for immature and open stands that can provide both food and cover for themselves and their broods.

Moss can be a food resource in the spring (spore capsules primarily; Naylor and Bendell 1989) and is also indicative of moist to wet soil conditions where conifer trees would have a competitive advantage over most deciduous trees (Westveld 1953). Collectively, female spruce grouse selected for sites with moderate to low densities of trees, relatively high lowest limb heights, and an abundance of moss groundcover relative to what was available in the conifer-dominated stands where they were captured. These conditions often occur in conifer stands with relatively low (Briggs 3- to 4+) site quality (Briggs 1994). Eight of our 12 stands had established site quality ratings in this range (Homyack et al. 2004).

It has been previously reported that breeding females choose areas where food is abundant in the low shrub and ground layers (Naylor and Bendell 1989). Vegetation at that height (7 cm-0.5 m) would be readily available to grouse and their chicks to provide both food and cover. Conversely, we were surprised that vegetation in the layer above (0.5 m – 1.5 m) was negatively associated with spruce grouse use as vegetation at that level was hypothesized to provide concealment from avian predators. However,

vegetation at that height could also reduce the amount of vegetation in the lower layer

resulting from shading or competition, and could potentially interfere with the ability of a

hen to escape via flight from terrestrial predators. The positive linear relationship

between probability of selection and overhead cover (1.5 m and above) was also not

expected as we assumed greater overhead cover would shade out low vegetative cover

essential for food an concealment. However, because this term was included in the same

model with low vegetative cover and had a lower standardized β value, we know that

female selection is more strongly related to abundant low cover. Additionally, we know

from the previous model that females selected for stands with elevated lowest limb

heights. Stands with abundant low cover and trees with branches at or above 1.5 m were

often utilized by females. Overhead cover is important to reduce predation risk from

avian predators because many raptors, including northern goshawks (*Accipiter gentilis*),

Cooper's hawks (*A. cooperii*), sharp-shinned hawks (*A. striatus*), red-tailed hawks (*Buteo

jamaicensis*), and broad-winged hawks (*B. platypterus*) prey on grouse (Hewitt et al.

2001). Females selected for areas with higher densities of saplings and trees, such as pre-

commercially thinned stands, or areas with relatively low densities of woody vegetation,

such as young regenerating clearcuts dominated by shrubs. We frequently observed

females in both regenerating clearcuts with well-developed low cover, as well as in areas

that had been pre-commercially thinned at least 15 years prior.

Spruce grouse females selected areas with greater canopy cover variation because

brood rearing females must balance the nutritional needs of their chicks with protective

cover from predators. It is important to note that although perfectly uniform lateral cover

(i.e., completely open or covered in dense vegetation) showed somewhat elevated

probability of selection (> 60%), areas of highly variable cover showed the highest

selection (~90%). Similarly, in Wisconsin, broods used habitat with both greater low

shrub cover and lower lateral cover density (Worland et al. 2009). We hypothesize that

selection for increased patchiness in low shrub cover (7 cm – 0.5 m), in our study area

and in Wisconsin result from brooded hens attempting to balance needs for food with

ease of escape, as has been documented for eastern wild turkeys during nesting (Fuller et

al. 2013). Although we expected females to select for moderate amounts of canopy cover

variation, we observed a positive and linear relationship between variation in canopy

cover and probability of selection. Lateral cover variation had a stronger effect in the

model, however, and a patchy canopy would be directly linked to patchiness in the

understory.

The results from our *post hoc* model corroborated the conclusion that probabilities

of selection exceeded 75% for immature sites. Specifically, sites with low-moderate tree

densities, high lowest limb heights, and abundant shrub and herbaceous cover. These

conditions were common in coniferous wetlands, regenerating clearcuts on poorly

drained soils, and pre-commercially thinned stands.

The home ranges of female spruce grouse during the brood rearing season were

highly variable but 75% of birds used 55 hectares or less. These results are comparable to

home ranges that varied from 22 ha for females without broods to 75 ha for brooded

females in the boreal forests of Canada (MCP; Turcotte et al. 1994) and which averaged

57.7 ha in the Adirondacks of New York (95% ADK; Ross et al. 2016). Female home

ranges during the breeding season are likely to overlap (Ellison 1973) and we often

observed unmarked females with broods within the known home range of marked

females. This indicates that forest management that creates suitable conditions at the home range scale of a female can provide habitat for multiple birds and broods. Retrospectively, the area of the focal conifer stands where grouse were captured averaged 44.6% of the average home range for a female grouse.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Current projections predict a decrease in spruce-fir forests, an increase in maple-beech forests, and a general increase in the age and size-class of all forests in the northeastern U.S under all future climate models (Shifley and Moser 2016). Although spruce grouse have historically been associated with mature conifer forests, we found evidence of females selecting for sites within regenerating clearcuts, pre-commercially thinned stands, and forested wetlands. Our models indicate that female grouse focused their home range within conifer-dominated stands and selected for sites with low to moderate stocking (< 1100 trees/ha), taller lowest limb heights (1.3 m $- 8.0$ m), and abundant low shrub and vegetation cover ($> 72\%$), which provide both food and cover. Management that promotes these conditions within areas of ~55 ha should provide sufficient habitat for female spruce grouse. In Maine timber harvests have declined by 11% since 2009 (McCaskill 2015), but there has been a recent (2013-2014) increase in herbicide use for crop-tree release and pre-commercial thinning (Maine Forest Service 2015). Because of the mixed nature of Maine's forests, harvest operations and pre- or post-harvest treatments can easily transform spruce-fir forests to northern hardwoods or vice-versa (McCaskill et al. 2011). Continued use of herbicide, pre-commercial thinning, and the promotion of coniferous regeneration prior to harvest may mitigate the predicted long-

term loss of spruce-fir forests in this region, and may benefit spruce grouse and other species dependent on conifer forests.

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APPENDICES

Survey results and models tested in Chapter 1.

Table A.1. Occupancy survey detection histories across all 30 stands resulting from acoustic surveys in northcentral Maine, May-June 2012-2014. Periods mark years without surveys.

Stand	2012	2013	2014
MSW3	110	000	000
MSW9	000	000	…
MSW10	000	100	000
MSW11	000	000	010
MSW12	…	…	000
MSW13	…	…	010
JH01	111	111	111
JH02	000	000	…
JH03	001	110	000
JH04	010	100	000
JH05	000	000	…
JH54	…	110	000
JH56	…	101	100
TLRG1	…	101	011
TLRG2	…	011	110
TLRG3	…	000	000
AF1	…	000	000
AF2	…	000	000
AF5	…	000	000
AF7	…	000	000
1-1-T	011	100	101
1-2-T	010	000	000
1-3-T	011	101	100
1-4-T	000	101	111
1-5-T	010	111	110
15Y1	000	000	111
15Y2	110	011	110
15Y3	111	111	100
6-4-T	011	001	011
6-6-T	000	000	…

Table A.2. Counts of responding male spruce grouse detected during acoustic surveys within 30 stands in northcentral Maine, May-June 2012-2014. Periods mark years without surveys.

Stand	2012 Counts	2013 Counts	2014 Counts
MSW3	01 01† 00	00 00 00	00*† 00 00
MSW9	00 00 00	00 00 00	.. .. ..
MSW10	00 00 00	01† 00 00	00 00 00
MSW11	00 00 00	00 00 00	00* 01 00
MSW12	.. .. ..	.. .. ..	00 00 00
MSW13	.. .. ..	.. .. ..	00 01 00
JH01	04 04 03	04 05 04*	03* 01 01*
JH02	00 00 00	00 00 00	.. .. ..
JH03	00† 00 01	02 02 00	00† 00 00
JH04	00 01 00	01 00† 00	00 00 00
JH05	00 00 00	00 00 00	.. .. ..
JH54	.. .. ..	01 01 00	00 00 00
JH56	.. .. ..	02 00 01	01 00 00
TLRG1	.. .. ..	01 00 01	00 01 01
TLRG2	.. .. ..	00 01 01	02 02 00
TLRG3	.. .. ..	00 00 00	00 00 00
AF1	.. .. ..	00 00 00	00 00 00
AF2	.. .. ..	00 00 00	00 00 00
AF5	.. .. ..	00 00 00	00 00 00
AF7	.. .. ..	00 00 00	00 00 00
1-1-T	00 02 03	04 00 00	01 00 01
1-2-T	00 01 00	00 00 00	00* 00 00
1-3-T	00 01 01†	03† 00 01	01* 00* 00
1-4-T	00* 00 00	03 00 02	01*† 02 02
1-5-T	00 03 00	01 01 01	02 01 00
15Y1	00 00 00	00 00* 00	00 00 00
15Y2	03 01 00	00 02 01	02 02 00
15Y3	03 01 02	02† 02 01	02 00 00*
6-4-T	00 01 02	00 00 02	00 01 01
6-6-T	00 00 00	00 00 00	.. .. ..

* Non-responsive male observed

† Female observed

80

Table A.3. Hypotheses and resulting models used to test for nuisance variable effects on the detection parameter (p) of our single-season occupancy models for male spruce grouse in northcentral Maine, May-June, 2012-2014. The occupancy parameterization was kept fully interactive (g*t) for all models.

#	Hypotheses	Models
1	Detection is constant (null)	p(.)
2	Detection varies across survey, stand type, and year.	p(g*t)
3	Detection varies across stand type and year	p(stand type+year)
4	Detection varies across stand type	p(stand type)
5	Detection varies across year	p(year)
6	Detection varies across survey	p(survey)
7	There is a linear trend across years	p(year trend)
8	There is a linear trend across surveys within a year	p(survey trend)
9	Detection decreased across day of survey	p(Julian date)
10	Detection decreased after some ideal survey day	p(Julian date^2)
11	Detection decreased with start time	p(time)
12	Detections decreased after some ideal start time	p(time^2)
13	Detection increased with temperature	p(temperature)
14	Detection increased until some ideal temperature was reached	p(temperature^2)
15	Detection decreased with cloud cover	p(% cloud cover)
16	Detection decreased after some percentage of cloud cover	p(% cloud cover^2)
17	Detection was lower if precipitation occurred in the previous 24 hours	p(precipitation in past 24 hours)
18	Detection was lower if there was precipitation during the survey	p(precipitation during survey)
19	Detection was higher when two observers completed the survey	p(>1 observer)
20	Detection decreased as stem cover units increased	p(SCU)
21	Detection decreased after a certain density of stem cover units	p(SCU^2)
22	Detection decreased as total basal area increased	p(TBA)
23	Detection decreased after a certain amount of total basal area	p(TBA^2)
24*	Detection decreases with time and total basal area	p(time+TBA)
25*	Detection decreases after some ideal start time and with total basal area	p(time^2+TBA)

* To reduce the number of models tested, we only included terms with meaningful coefficient estimates (85% CI does not include 0).

Table A.4. Hypotheses and resulting models used to test for the effects of habitat variables on occupancy within our single-season occupancy models for male spruce grouse in northcentral Maine, May-June, 2012-2014. The best performing detection parameterization p(best) was included in all models.

#	Hypotheses	Models
1	Occupancy is constant (null)	$\Psi(.)$
2	Occupancy varies by the interaction of stand type and year	$\Psi(g*t)$
3	Occupancy varies across stand type and year	$\Psi(\text{stand type+year})$
4	Occupancy varies across stand type	$\Psi(\text{stand type})$
5	Occupancy varies between successional groups*	$\Psi(\text{2 Groups})$
6	Occupancy varies across year	$\Psi(\text{year})$
7	There is a linear trend across years	$\Psi(\text{year trend})$
8	Occupancy decreases with canopy closure	$\Psi(CC)$
9	Occupancy decreases from an ideal amount of canopy closure	$\Psi(CC^2)$
10	Occupancy increases with canopy cover variation	$\Psi(CCV)$
11	Occupancy increases until it reaches an idea amount of canopy cover variation	$\Psi(CCV^2)$
12	Occupancy decreases with an increase in basal area of trees	$\Psi(BAT)$
13	Occupancy decreases after some ideal basal area of trees	$\Psi(BAT^2)$
14	Occupancy decreases with tree height	$\Psi(TH)$
15	Occupancy decreases after some ideal tree height	$\Psi(TH^2)$
16	Occupancy decreases with lowest limb height	$\Psi(LL)$
17	Occupancy decreases after some ideal lowest limb height	$\Psi(LL^2)$
18	Occupancy decreases with total sapling density	$\Psi(TSD)$
19	Occupancy decreases after some total sapling density	$\Psi(TSD^2)$
20	Occupancy increases with conifer tree density	$\Psi(CTD)$
21	Occupancy increases until some ideal conifer tree density	$\Psi(CTD^2)$
22	Occupancy decreases with deciduous tree density	$\Psi(DTD)$
23	Occupancy decreases after some dieal deciduous tree density	$\Psi(DTD^2)$
24	Occupancy decreases with tree diameter	$\Psi(DBH)$
25	Occupancy decreases after some ideal tree diameter	$\Psi(DBH^2)$

*Successional groups are defined as combinations of the stand type groups: early-mid (Regeneration+PCT) and mid-late (mature+Selection)

Table A.5. Hypotheses and resulting models used to test for nuisance variable effects on the detection parameter (r) of our single-season abundance models for male spruce grouse in northcentral Maine, May-June, 2012-2014. The abundance parameterization was kept fully interactive (g*t) for all models.

#	Hypotheses	Models
1	Detection is constant (null)	p(.)
2	Detection varies across the interaction of stand type and year.	p(g*t)
3	Detection varies across stand type and year	p(stand type+year)
4	Detection varies across stand type	p(stand type)
5	Detection varies across year	p(year)
6	There is a linear trend across years	p(year trend)
7	Detection decreased as stem cover units increased	p(SCU)
8	Detection decreased after a certain density of stem cover units	p(SCU^2)
9	Detection decreased as total basal area increased	p(TBA)
10	Detection decreased after a certain amount of total basal area	p(TBA^2)
11	Detection decreases with both stem cover units and total basal area	p(SCU+TBA)

Table A.6. Hypotheses and resulting models used to test for the effects of habitat variables on abundance within our single-season abundance models for male spruce grouse in northcentral Maine, May-June, 2012-2014. The best performing detection parameterization p(best) was used in all models.

#	Hypotheses	Models
1	Abundance is constant (null)	$\lambda(.)$
2	Abundance varies by the interaction of stand type and year	$\lambda(g*t)$
3	Abundance varies across stand type and year	$\lambda(\text{stand type}+\text{year})$
4	Abundance varies across stand type	$\lambda(\text{stand type})$
5	Occupancy varies between successional groups*	Ψ (2 Groups)
6	Abundance varies across year	$\lambda(\text{year})$
7	There is a linear trend across years	$\lambda(\text{year trend})$
8	Abundance decreases with canopy closure	$\lambda(CC)$
9	Abundance decreases from an ideal amount of canopy closure	$\lambda(CC^2)$
10	Abundance increases with canopy cover variation	$\lambda(CCV)$
11	Abundance increases until it reaches an idea amount of canopy cover variation	$\lambda(CCV^2)$
12	Abundance decreases with an increase in basal area of trees	$\lambda(BAT)$
13	Abundance decreases after some ideal basal area of trees	$\lambda(BAT^2)$
14	Abundance decreases with tree height	$\lambda(TH)$
15	Abundance decreases after some ideal tree height	$\lambda(TH^2)$
16	Abundance decreases with lowest limb height	$\lambda(LL)$
17	Abundance decreases after some ideal lowest limb height	$\lambda(LL^2)$
18	Abundance decreases with total sapling density	$\lambda(TSD)$
19	Abundance decreases after some total sapling density	$\lambda(TSD^2)$
20	Abundance increases with conifer tree density	$\lambda(CTD)$
21	Abundance increases until some ideal conifer tree density	$\lambda(CTD^2)$
22	Abundance decreases with deciduous tree density	$\lambda(DTD)$
23	Abundance decreases after some dieal deciduous tree density	$\lambda(DTD^2)$
24	Abundance decreases with tree diameter	$\lambda(DBH)$
25	Abundance decreases after some ideal tree diameter	$\lambda(DBH^2)$

*Successional groups are defined as combinations of the stand type groups: early-mid (Regeneration+PCT) and mid-late (mature+Selection)

APPENDIX B:

Dates of capture and dates of lost contact for all captured females.

Table B.1. Dates of capture and dates of last contact for all females captured during the breeding (May-June) or brood-rearing (June-September) seasons in northcentral Maine, 2012-2014. The cause of lost contact and comments are included.

Band #	Date Captured	Date of Last Contact	Days Monitored	Cause of Contact Loss	Comments
217	6/12/2012	7/9/2013	392	Radio Removed	Had ≥ 1 chick in 2013
219	6/15/2012	9/30/2012	107	Radio Failure?	Fate Unknown
221	6/16/2012	6/1/2013	350	Battery Expired	
223	6/17/2012	6/25/2013	373	Battery Expired	Had nested in 2013
225	6/17/2012	5/30/2013	347	Battery Expired	Had nested in 2013
220	6/18/2012	5/16/2013	332	Removed Collar	
222	6/19/2012	1/18/2013	214	Mortality	Predation
224	6/23/2012	8/10/2012	49	Dropped Radio	
226	6/23/2012	3/8/2013	259	Mortality	Predation
227	6/23/2012	6/24/2013	366	Mortality	Predation
228	6/29/2012	5/27/2013	333	Battery Expired	Had nested in 2013
229	7/1/2012	6/25/2013	360	Battery Expired	Had ≥ 1 chick in 2013
230	7/1/2012	6/19/2013	354	Mortality	Predation
231	7/1/2012	6/24/2013	358	Battery Expired	Had ≥ 2 chicks in 2013
232	7/6/2012	7/8/2012	2	Mortality	Predation/stress
233	7/9/2012	1/18/2013	194	Mortality	Predation
234	5/4/2013	9/6/2013	126	Mortality	Predation
249	6/18/2013	4/27/2014	313	Battery Expired	
251	6/20/2013	5/28/2014	342	Battery Expired	
253	6/23/2013	7/8/2014	380	Battery Expired	Had re-nested successfully in 2014
255	6/23/2013	5/30/2014	341	Battery Expired	
256	6/24/2013	1/13/2014	203	Mortality	Predation
257	6/25/2013	8/10/2013	47	Mortality	Predation
258	6/25/2013	6/25/2013	0	Not Radioed	Same stand as 257
259	6/25/2013	6/25/2013	0	Not Radioed	Same stand as 257
261	6/30/2013	7/9/2013	10	Mortality	Predation
263	7/9/2013	9/27/2013	81	Radio Failure?	Fate Unknown
265	7/12/2013	8/20/2013	40	Mortality	Missing Tail
267	7/12/2013	5/29/2014	322	Battery Expired	Had nested in 2014

Table B.1. Continued

Band #	Date Captured	Date of Last Contact	Days Monitored	Cause of Contact Loss	Comments
No Band	7/13/2013	7/28/2014	380	Mortality	Predation
264	5/12/2014	1/22/2015	255	Mortality	
268	6/21/2014	8/3/2014	43	Dropped Radio	Saw hen with new brood in Aug. 2015
305	6/23/2014	7/31/2015	385	Battery Expired	Lost brood in 2015
269	6/28/2014	11/10/2015	505	Mortality	
270	6/29/2014	1/22/2015	213	Mortality	
307	6/29/2014	6/29/2014	0	Dropped Radio	
272	6/29/2014	7/2/2014	4	Mortality	Predation/stress
309	7/1/2014	7/13/2014	12	Mortality	Predation
490	7/11/2014	2/2/2016	590	Mortality	

BIOGRAPHY OF THE AUTHOR

Stephen W. Dunham was born in Lynn, Massachusetts on August 10, 1988, but spent most of his childhood in New Hampshire where he developed a passion for the outdoors while playing, hiking, and camping, especially in the White Mountains National Forest. He graduated from St. Thomas Aquinas High School in Dover, New Hampshire in 2007. He attended the University of Maine in Orono, Maine where he majored in Wildlife Ecology and worked as an outdoor trip leader for the Maine Bound Adventure Center. His undergraduate summers were spent gaining wildlife experience in the field, including two summers spent working at Moosehorn National Wildlife Refuge as a biological science technician. He graduated *magnum cum laude* with honors in 2011. After a brief volunteer stint with the Maine Department of Inland Fisheries and Wildlife's Bear Monitoring Program, he became a research technician in his former department at the University of Maine in July of 2011. The project he was helping to initiate had been designed as a project for a graduate student; therefore, in October of 2011 he applied and was accepted to the Graduate School at the University of Maine. In January of 2012 he officially began work toward his Master of Science degree working with the spruce grouse project. He got married to his high school sweetheart, LeAnne, in 2012 and welcomed his son, Walden, in 2016. Stephen is a candidate for the Master of Science degree in Wildlife Ecology from the University of Maine in August 2016.