Fall 2013

Ecology and management of moose in northern New England

Haley A. Andreozzi

University of New Hampshire, Durham

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Ecology and management of moose in northern New England

Abstract
This study examined three facets of moose ecology in northern New England: impact of moose browsing on forest regeneration, physical characteristics of harvested bull moose, and winter habitat use. Forest regeneration was not considered a major problem in northern Vermont based on stocking levels of commercial tree species. Increasing dominance of softwood species coupled with suppressed growth of hardwoods suggests possible local shifts in composition. Bull moose in Maine had stable body weight and antler spread, and selective harvest of trophy bulls was not apparent over 30 years. Winter locations from aerial surveys indicated that moose preferentially used deciduous/mixed forest proximate to cuts; wetlands and conifer stands were used less. Good physical condition of harvested moose and similarities in habitat use at multiple scales indicates that commercial timber harvesting provides long-term, high quality moose habitat in northern Maine.

Keywords
Agriculture, Wildlife Conservation, Agriculture, Wildlife Management, Biology, Ecology

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ECOLOGY AND MANAGEMENT OF MOOSE IN NORTHERN NEW ENGLAND

BY

HALEY A. ANDREOZZI
B.S., University of Rhode Island 2009

THESIS

Submitted to the University of New Hampshire
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in

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July 25, 2013
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ABSTRACT

ECOLOGY AND MANAGEMENT OF MOOSE IN NORTHERN NEW ENGLAND

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University of New Hampshire, September 2013

This study examined three facets of moose ecology in northern New England: impact of moose browsing on forest regeneration, physical characteristics of harvested bull moose, and winter habitat use. Forest regeneration was not considered a major problem in northern Vermont based on stocking levels of commercial tree species. Increasing dominance of softwood species coupled with suppressed growth of hardwoods suggests possible local shifts in composition. Bull moose in Maine had stable body weight and antler spread, and selective harvest of trophy bulls was not apparent over 30 years. Winter locations from aerial surveys indicated that moose preferentially used deciduous/mixed forest proximate to cuts; wetlands and conifer stands were used less. Good physical condition of harvested moose and similarities in habitat use at multiple scales indicates that commercial timber harvesting provides long-term, high quality moose habitat in northern Maine.
INTRODUCTION

Moose (*Alces alces*) populations have experienced a regional increase in New England over the last several decades, making them an increasingly valuable wildlife resource. Their population growth has created new economic and recreational opportunities associated with tourism, as well as the establishment of regulated hunting seasons in Maine, Vermont, and New Hampshire. Management of moose is necessary to maintain an acceptable balance among sustainable population levels, recreational and economic benefits, and forest health.

Moose, specifically high density populations, have the ability to damage woody plants and alter plant communities (Renecker and Schwartz 1997). For example, repeated browsing can suppress height growth and recruitment of saplings into the canopy (Risenhoover and Maass 1987), and moose can drastically alter localized species composition, (e.g., Isle Royale, Michigan, Snyder and Janke 1976). Additionally, there is a strong relationship between moose habitat quality and abundance and commercial forest management, and moose show preference for clearcut and early-successional habitat that is typical of the managed landscape of the northeast (Westworth et al. 1989, Scarpitti et al. 2005). In New Hampshire Bergeron et al. (2011) found low regeneration in specific cutover sites adjacent to traditional moose wintering areas, and predicted that such sites could change from hardwood to softwood dominance.

Habitat use in winter is influenced by environmental conditions and declining food resources related to snow depth and foraging intensity. While relatively mobile in the conditions typical of northern New England winters, moose minimize energy expenditure and reduce home range in winter, indirect evidence of the importance of
winter habitat relative to individual and population productivity. At the fine scale, cut/regeneration habitat is used more than other habitat types during winter in New Hampshire, presumably because of high forage availability and preference (Scarpitti 2006). Areas where moose concentrate in high seasonal density are typically associated with forest damage globally (Heikkila et al. 2003); therefore, to best manage moose in a landscape dominated by commercial forests, it is critical to evaluate winter habitat use and associated impacts on forest production.

It is usually assumed that a direct relationship exists between habitat quality and physical condition of moose; measurement of physical characteristics of harvested moose provides the opportunity to assess temporal trends and relative condition of a moose population. Additionally, hunting has the ability to influence moose populations by altering age and social structure, sex-ratio, and population dynamics (Milner et al. 2006); it is important to assess if selective harvest pressure (specifically towards older, trophy bulls) has resulted in any negative effects. A recent >20 year temporal analysis (1988-2009) of physical parameters of harvested moose in New England indicated that body weight and ovulation rate of yearling cow moose in both New Hampshire and Vermont are trending downward, yet remain stable in adult cows; similarly, body weight and most antler measurements of bulls declined (Bergeron et al. 2011). In New Hampshire, parasitism by winter ticks (Dermacentor albipictus), not habitat quality, is believed to most influence survival and growth of moose calves and subsequent productivity of yearlings (Musante et al. 2010, Bergeron 2011). To date, there has been no similar analysis of bull harvest data in Maine despite a continuous data set of ~30 years. Of consequence is whether Maine adult and yearling bulls reflect a similar trend as measured
in Vermont and New Hampshire, and if selective harvest and decline of older bulls occurs in the largest and longest harvested population in the northeastern United States.

Northern New England is home to the largest regional moose population in the continental United States. Therefore, it is important to understand how habitat use, impacts on forest production, and population characteristics are linked in high-density populations within the region. Together, the three facets of this research provide insight into moose management in northern New England through analysis of impacts to forest regeneration, winter habitat use, and the physical characteristics of the population.
CHAPTER 1

IMPACT OF MOOSE BROWSING ON FOREST REGENERATION
IN NORTHEAST VERMONT

**Introduction**

Moose (*Alces alces*) populations have experienced a regional increase in northern New England over the last several decades, making them an increasingly valuable wildlife resource. They play an important role ecologically and economically in Vermont, with 78% of the state open to regulated moose hunting and 406 hunting permits issued statewide in 2011 (VTFWD 2008, 2011). With forests also covering 78% of Vermont’s landscape, the state generates over $1.5 billion annually from forest-based manufacturing and forest-related recreation and tourism (NEFA 2007). The majority of forestland, 4 million acres, is owned privately or by timber investment management organizations (TIMO); local, state, and federal government owns ~19% (919,440 acres) (NEFA 2007). Forest and wildlife management aimed at sustainable forest production is critical for the long-term stability of both Vermont’s economy and moose population.

With adult moose weighing 300-600 kg, substantial browse is required to maintain such large body size (Bubenik 1997), estimated at daily dry matter intake of 2.8 kg/moose/day in January (Pruss and Pekins 1992). Moose have the ability to substantially alter plant communities and are capable of damaging woody plants (Renecker and Schwartz 1997); repeated browsing can suppress height growth and recruitment of saplings into the canopy (Riesenhoover and Maass 1987). Moose browsing has the
capability to affect the structure and dynamics of forest ecosystems over the long-term (McInnes et al. 1992), which has important implications for the management of forests where moose populations are regulated. Moose show preference for forage in clearcut and early-successional habitat that is typical of the commercially managed forests of the northeast (Westworth et al. 1989, Scarpitti et al. 2005). For example, productive moose habitat in New Hampshire was linked directly to the early successional forage created by commercial forest harvesting and early-successional browse is a dietary component year-round (Scarpitti et al. 2005, Scarpitti 2006). Clearcuts 5-20 years old provide suitable early winter habitat, as regenerating hardwood and softwood species provide both browse and cover for moose (Thompson and Stewart 1997). While the impact of moose browsing on forest regeneration has received substantial attention elsewhere, little attention has been paid to the potential and actual effects in northern New England (Scarpitti 2006, Bergeron et al. 2011).

To manage moose and forest resources with respect to moose density and damage to regeneration, it is important to have extensive ecological knowledge of the relationships among moose, the ecosystems they inhabit, the plants they use as forage (Edenius et al. 2002), and the associated impacts on forest production such as timber quality impairment. As moose populations have increased in northern New England, land managers have implied that a relationship exists between high population density and reduced forest regeneration in clearcuts. On Isle Royale, McInnes et al. (1992) found that moose browsing affected the structure and dynamics of forest ecosystems on a long-term scale; however, in larger landscapes such impacts are usually more localized and often relate to high seasonal density. For example, in New Hampshire Bergeron et al. (2011)
found specific cutover sites with low regeneration adjacent to traditional wintering areas, and predicted that such sites could change from hardwood to softwood dominance.

By the early 2000s, there was anecdotal evidence that the moose population in northeastern Vermont, specifically wildlife management unit (WMU) E, was causing measurable damage to forest regeneration; moose densities in WMU E were thought to be well over 1.5 moose/km² (4 moose/mile²) (C. Alexander, VTFWD wildlife biologist, pers. comm.). To achieve the desired population level, hunting permit numbers were dramatically increased by the Vermont Department of Fish and Wildlife (VTFWD) from 440 to 833 permits in 2004, when it was believed moose had approached their biological carrying capacity (VTFWD 2008). The number of hunting permits rose to 1046 in 2005 and continued to increase until 2009, when 1223 permits were issued statewide in an effort to accelerate population reductions to protect forest habitat. By 2008, the population density was approaching the goal set by the 10-year moose management plan (0.7 moose/km² [1.75 moose/mile²]) and the number of permits was reduced to 765 in 2010 and 405 permits in 2011. In response, this study was designed to evaluate the impact of moose browsing on regeneration of commercial tree species in WMU E1 in northeast Vermont.

**Study Area**

The study area was located in northeast Vermont and encompassed all of VTFWD WMU E1, covering an area of 682 km² bordered by New Hampshire and Quebec (Fig. 1-1). It was delineated from the flight lines/area used in moose aerial surveys conducted in winter 2010. Elevation ranges from ~250-1,130 m, and it is dominated by maple (*Acer*
Figure 1-1. The location of the study area in Vermont used to assess the impact of moose browsing on forest regeneration, 2012. The area included all of WMU E1 in northeast Vermont.
saccharum, A. pensylvanicum, A. rubrum) and birch (Betula alleghaniensis, B. papyrifera) hardwoods, and conifer stands of balsam fir (Abies balsamea) and red spruce (Picea rubens). While heavily forested, timber harvesting is common throughout as the majority of the land is privately owned and commercially harvested (NEFA 2007). The 2011 moose density was estimated at 0.77 moose/km² (1.96 moose/mi²) based on a rolling 3-year average of moose sightings by November deer hunters, and was previously estimated in 2010 as 0.93 moose/km² (2.41 moose/mile²) based on aerial surveys (Millette et al. 2011).

Methods

Regeneration surveys (Leak 2007, Bergeron et al. 2011) were performed to measure the impact of moose browsing on forest regeneration in clear-cuts 3-20 years old. Clear-cuts were separated into 4 age classes (3-5, 6-10, 11-15 and 16-20 years old) to assess temporal changes during both the period of typical browsing (0-10 years) and at least 10 years post-browsing. In each age class, 8-10 clear-cuts were located using aerial photography; each was a minimum of 4.1 ha (10 acres) and a maximum of 16.2 ha (40 acres) in size to reflect the typical range in size of clear-cuts in the region (M. Langlais, Vermont Department of Forests, Parks & Recreation County Forester, pers. comm.). In certain cases, clear-cuts >16.2 ha were used to achieve appropriate sample sizes within an age class; a section ≤16.2 ha was surveyed.

Small plot surveys (milacre, ~2.3 m diameter circle) were evenly spaced on equidistant transects throughout each clear-cut (Fig. 1-2). In each milacre plot, the dominant stem was recorded as a commercial or non-commercial tree species. If the dominant stem was non-commercial, the plot was searched for the presence of
Figure 1-2. Example of the sampling design used to measure browse damage in clearcuts in northeast Vermont, summer 2012. Equidistant transects were established upon which 100-400, 2.3 m diameter plots were established to measure the presence of dominant commercial stems, stem quality, and relative height; modeled after Bergeron et al. 2011.
Figure 1-3. The 3 qualitative browse categories used to describe browsing damage of dominant stems in milacre sample plots (Bergeron et al. 2011).
commercial species (Appendix A); commercial species included yellow and white birch, sugar and red maple, American beech \((Fagus\ grandifolia)\), aspen \((Populus\ spp.)\), black cherry \((Prunus\ serotina)\), balsam fir, red and black spruce \((Picea\ mariana)\), and tamarack \((Larix\ laricina)\). Stem damage was assessed on a qualitative basis as fork, broom, or crook (Fig. 1-3). The height of the damage above or below breast height (approximately 1.4 m) was recorded, as well as the number of forks and crooks, and the severity of crooks based on angle. Light crooks were those \(\leq 30^\circ\), moderate crooks were those 30-60°, and severe crooks were those \(\geq 60^\circ\) from the dominant stem. The relative height of the dominant stem was estimated to the nearest foot when <3.05 m (10 ft), or as \(\geq 3.05\) m.

Broomed stems and multiple forks above breast height were considered browse defects indicative of a severely damaged tree, otherwise, damage was considered light or moderate. Trees with lesser damage are expected to recover during future growth (Switzenberg et al. 1955, Carvell 1967, Trimble 1968, Jacobs 1969). A fully stocked stand at 80 years was assumed if a minimum of 40-60% of plots (threshold) contain a commercial tree without severe damage (Leak et al. 1987). To evaluate relative height between age classes and further assess browse impact, comparisons were made of the proportion of plots containing a dominant commercial stem \(\geq 3.05\) m without severe damage, as vegetation \(\geq 3.05\) m was presumed to be above the typical height of moose browsing (Bergström and Danell 1986).

Temporal comparisons were made to assess if younger age classes with high initial browse pressure recover to fully stocked stands after 10-15 years. Analysis of variance (ANOVA) and pairwise Tukey's test were used to look for differences in
browse damage between clear-cuts and age classes. Significance for all tests was assigned a priori at $\alpha = 0.05$. Results are presented throughout as $\bar{X} \pm \text{SE}$.

**Results**

A total of 37 clearcuts were surveyed: 11, 8, 8, and 10 in the 3-5, 6-10, 11-15, and 16-20 year age classes, respectively. There were 1709, 1291, 1442, and 1585 milacre plots surveyed in the 4 age classes, respectively. Stocking rate of commercial trees was high in all age classes, and increased with age class (Table 1-1); it ranged from 74-76% in the 3-5, 6-10, and 11-15 year age classes, increasing to 86% in the 16-20 year age class. The proportion of commercial trees with severe damage was low overall, with <10% damaged severely in all age classes except in the 16-20 age class (11%, Table 1-1).

The proportion of plots containing a commercial tree without severe damage was above the defined threshold stocking level of 40-60% in all age classes (Table 1-1, Fig. 1-4), ranging from 67-68% in the 3-5, 6-10, and 11-15 year age classes, and increasing to 75% in the 16-20 year class. The proportion of dominant commercial trees $\geq$3.05 m without severe damage increased with age class with 1, 25, and 39% in the 6-10, 11-15 and 16-20 year age classes, respectively. The proportion of plots containing a commercial hardwood stem declined with age class, averaging 62, 51, 43, and 40% in the 4 age classes, respectively. Conversely, the proportion of plots containing a commercial dominant softwood stem increased with age class, averaging 12, 24, 33 and 46% in the 4 age classes, respectively (Fig. 1-5). The highest stocking rates (>80%) were restricted to softwood-dominated stands. The majority of plots with a dominant non-commercial stem also contained commercial stems (70-81% across age classes).
Table 1-1. Summary values indicating the stocking of commercial tree species, stocking of commercial trees with and without severe damage, the proportion of commercial trees ≥3.05m in height without severe damage, and the proportion of dominant commercial hardwood and softwood stems in clearcuts in northeast Vermont. Rows with the same letter within columns are not statistically different (P>0.05).

<table>
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<tr>
<th>Age Class</th>
<th>Stocking rate of dominant commercial trees (%)</th>
<th>Stocking rate of dominant commercial trees w/o severe damage (%)</th>
<th>Stocking rate of dominant commercial trees w/ severe damage (%)</th>
<th>Proportion of dominant commercial trees w/o severe damage and ≥3.05 m tall (%)</th>
<th>Proportion of dominant commercial hardwoods (%)</th>
<th>Proportion of dominant commercial softwoods (%)</th>
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Figure 1-5. Proportion (%) of plots containing either dominant commercial hardwood or softwood stems by age class.
The stocking rate of dominant commercial trees was lower ($P = 0.02$) in the 3-5 year age class than in the 16-20 year age class, although stocking rate was above the threshold stocking level in all age classes. The proportion of dominant commercial hardwoods was higher ($P = 0.014$) and the proportion of dominant commercial softwoods lower ($P = 0.015$) in the 3-5 year age class than in the 16-20 year age class. The proportion of plots beyond browse height ($\geq 3.05$ m) and without severe damage in the 6-10 year age class was lower than the 11-15 year ($P = 0.022$) and the 16-20 year age classes ($P < 0.001$).

At least 3 commercial species accounted for $\geq 50\%$ of the species composition within each age class (Appendix B). The majority of these species were classified with light to no damage, and the proportion of non-commercial species declined as age class increased (Table 1-1, Appendix B). The proportion of dominant commercial stems classified as hardwood declined with age class, averaging $83 \pm 7.6$, $69 \pm 8.5$, $58 \pm 8.5$ and $49 \pm 7.2$% in the 4 age classes, respectively; the opposite occurred with the proportion of dominant commercial stems classified as softwood that averaged $17 \pm 7.6$, $31 \pm 8.5$, $42\pm 8.5$, and $51 \pm 7.2$%.

Red maple and yellow birch accounted for 24 and 20% of total species composition in the 3-5 year age class; no other commercial species accounted for more than 6%. In the 6-10 year class, red maple, balsam fir, and yellow birch accounted for the highest proportion of species composition (14-16% each) and in the 11-15 year age class, these 3 species accounted for 11-17% each, and red spruce 11%. Red maple, balsam fir, and red spruce accounted for the greatest proportion of dominant commercial stems (21-23% each) in the 16-20 year age class; yellow birch fell to 6% (Appendix B).
**Discussion**

Overall, regeneration of commercial tree species due to impacts from moose browsing was not considered a major problem in northeast Vermont. The stocking rate of commercial trees without severe damage was acceptable in all age classes based upon the minimum threshold stocking level of 40-60%, and severe damage from browsing was low in all age classes in regards to acceptable levels, ranging from 6-11% (Table 1-1). While damage was low in all age classes, site-specific severe browsing can shift species composition (Edenius et al. 2002). Moose drastically altered localized species composition on Isle Royale, Michigan; browsed sites exhibited lower overall tree density than unbrowsed sites due to a decrease in balsam fir and mountain ash (*Sorbus americana*) and increase in white spruce (*Picea glauca*) densities (Snyder and Janke 1976).

The increasing proportion of dominant softwood stems with age indicates a possible shift to softwood-dominated stands due to selective browsing of hardwood species. The highest stocking rates (>80%) were restricted to softwood-dominated stands, and stands experiencing the highest levels of damage were stocked predominantly with hardwood species that had much higher damage relative to the softwood species (Appendix B); softwood species will likely dominate these stands as they mature. The most commercially valuable hardwood species in the study region are yellow birch and sugar maple; they were dominant species in the youngest 2 age classes, but accounted for only 6 and 5% of dominant stems in the 16-20 year class.

Conversely, the commercial softwood species, balsam fir and red spruce, were minimal in the youngest age classes, but accounted for a large proportion of the dominant
stems (21% each) in the 16-20 year class. Red maple, a less valuable commercial species, was dominant in all age classes ranging from 13-24% of dominant stems (Appendix B). A similar trend occurred in New Hampshire (Bergeron et al. 2011) where the proportion of dominant commercial hardwood stems also declined with age class (Fig. 1-6). While previous site compositions are unknown, it is possible a shift from hardwood to softwood dominated stands may be the natural successional trend for these sites; browsing pressure could potentially accelerate successional development by arresting or retarding the height development of preferred browse species in the region (McInnes et al. 1992, Davidson 1993).

The proportion of dominant commercial trees ≥3.05 m (beyond browse height) without severe damage increased with age class, peaking at 39% at 16-20 years; such stems are expected to recover during future growth without browsing. In contrast, average values in adjacent northern New Hampshire were 36, 60, and 71% in the 3 older age classes (Fig. 1-7), suggesting that growth was more suppressed in Vermont. Intense browsing in areas of high moose density can arrest or retard growth of preferred browse species (Bergerud and Manuel 1968, Angelstam et al. 2000). A study with exclosures on Isle Royale, Michigan indicated that repeated browsing by moose retarded vertical growth of palatable species such as aspen and paper birch, and prevented stems from growing beyond browsing height resulting in a more open canopy (Risenhoover and Maass 1987). Although heavy browsing of the same species in successive years can result in hedgy growth and lower height potential ( Peek et al. 1976, Peek 1997), such stems can compensate if browsing declines or if removed in successive years. For example, after release of a dominant stem in forked stems (Jacobs 1969) and the straightening of
Figure 1-6. The proportion (%) of commercial plots containing either hardwood or softwood species by age class in northeast Vermont and in the North and CT Lakes regions of New Hampshire.
Figure 1-7. Proportion (%) of dominant commercial trees without severe damage and ≥3.05m tall (beyond browse height) in Vermont and New Hampshire.
crooked stems with secondary growth over time (Switzenberg et al. 1955, Trimble 1968). A clipping study on Isle Royale indicated that the site-dependent survival and growth of balsam fir were related to suppression brought about by severe browsing in previous years (McLaren 1996). Accurate prediction of damage is complicated by this dynamic process that is likely influenced by local site conditions, and seasonal moose density and site fidelity.

In studies assessing browse damage in both southern and northern New England, time since harvest was negatively correlated with foraging intensity (Faison et al. 2010, Bergeron et al. 2011) which may allow compensatory growth by desirable hardwood species beyond the 16-20 year age class. However, an increasing dominance of softwood species coupled with suppressed growth of hardwood species indicates a possible shift in species composition in WMU E1. Several studies have indicated change in forest composition due to heavy moose browsing. In Finland, Heikkila et al. (2003) measured reduced height of preferred species resulting in the release of conifers from competition. On Isle Royale, moose prevented aspen, birch, and balsam fir from growing into the canopy, with little impact to spruce, resulting in a forest with fewer trees in the canopy, a well-developed understory of shrubs and herbs, and an increase in spruce biomass (McInnes et al. 1992). Similarly, selective pressure resulted in rapid occupation of spruce (Picea spp.) as the dominant species in study stands in Russia (Abaturov and Smirnov 2002). A similar trend is possibly occurring in northeast Vermont where coniferous species account for >50% of total species composition in the 16-20 year age class (Appendix B). A reduction in moose density, as implemented in the study area, may also reduce future browsing pressure and provide for the release of preferred hardwood
species. A population reduction in Newfoundland in the early 1960s resulted in dramatic decline in the proportion of white birch and balsam fir stems browsed in 6-11 and 12-17 year old stands (Bergerud et al. 1968).

High-density moose populations have the potential to damage preferred plant species (Peek 1997), but the negative impacts of over-browsing can be minimized if moose density is kept at low-moderate levels (Brandner et al. 1990). In Russia, a density of 0.3-0.5 moose/km² retarded growth of preferred forage species such as aspen, whereas normal stand development occurred at 0.2-0.3 moose/km² (Abaturov and Smirnov 1992). In Sweden, simulated densities of 0.8-1.5 moose/km² did not impact winter browse availability; impact was predicted at >2.0 moose/km² (Persson et al. 2005).

Both northern Vermont and New Hampshire are classified as a combination of spruce-fir, northern hardwood, and mixed forest types (DeGraaf and Yamasaki 2001), and measurable differences in forest regeneration presumably reflect different moose density. Bergeron et al. (2011) found a correlation between moose density and browse damage in 3 regions with different moose density in northern New Hampshire; the region with highest density had more damage. Densities in northeast Vermont were estimated at 1.2-1.8 moose/km² in 1999-2009 and were higher than those in his highest density region, estimated at 0.8–1.5 moose/km² in the same time period (C. Alexander, pers. comm., K. Rines, NHFG wildlife biologist, pers. comm.).

In both states significant differences were found in the stocking rate of dominant commercial trees, and the proportion of both dominant hardwood and softwood commercial tree species between the youngest and oldest age classes. However, the comparisons among age classes indicate that sites with high initial browse pressure are
often released from that pressure and recover to commercially valuable stands. In both Vermont and New Hampshire, stocking rate increased and damage declined over time with relative differences seemingly influenced by local moose density (Fig. 1-7). Compensatory growth in the region was measurable in the 16-20 year age class, but likely begins earlier when stems grow beyond browsing height. However, heavy browsing pressure on preferred tree species may result in lower stand height as measured in Vermont and a possible shift in forest composition to coniferous species. Further assessment is warranted to best evaluate the extent of compensatory tree growth in response to reduction in browsing due to forest aging and/or moose population density.
CHAPTER 2

ANALYSIS OF PHYSICAL CHARACTERISTICS OF BULL MOOSE
HARVESTED IN MAINE, 1980-2009

Introduction

Measurement of physical characteristics of harvested moose provides an opportunity to assess temporal trends and relative condition of a moose population; it is usually assumed that a direct relationship exists between habitat quality and physical condition. Age-specific body weight of male and female moose should reflect health and production (Schwartz and Hundertmark 1993), and antler measurements are used similarly because of the correlation between antler size and nutritional condition (Bubenik 1997). Adams and Pekins (1995) concluded that yearling moose are useful to estimate overall herd health because their potential growth rate reflects variance in body weight and onset of ovulation.

Antler morphology in cervids is determined by nutrition and genetics, and antler growth and size are strongly influenced by forage availability, quantity, and quality (Schmidt et al. 2007). Age also influences the size and formation of antlers as larger, older males invest less in body growth and allocate more resources toward antler growth, symmetry, and size (Stewart et al. 2000, Bowyer et al. 2001). As body size and age are strongly correlated with antler size and mating success (Clutton-Brock 1982), dominant males have the ability to limit the mating opportunities of younger males (Van Ballenberghe and Miquelle 1996).
Hunting has the ability to influence ungulate populations by altering age and 
social structure, sex-ratio, and population dynamics (Milner et al. 2006). Mortality 
patterns in harvested populations commonly deviate from those in non-harvested 
populations, often with an increase in the mortality of prime-aged males (Ginsberg and 
Milner-Gulland 1994, Milner et al. 2006). Selective harvest is often applied as a 
management technique throughout North America to protect adult cow moose and 
maximize productivity (Timmermann 1987); lower harvest of adult cows can transfer 
pressure to other portions of the population, often adult bulls. High harvest of older bull 
moose has the potential to impact normal age structure and reduce average body size and 
antler spread in a population over time (Solberg et al. 2000); younger, smaller males are 
eventually predominant in harvest (Schmidt et al. 2007).

Although hunting for older, large antlered moose can be a local economic 
stimulant and management tool (Monteith et al. 2013), an increasing focus and popularity 
of trophy hunting further concentrates harvest pressure on prime bulls (McCullough 
1982, Timmermann and Buss 1997). Selective effects of trophy hunting include genetic 
selection of smaller antlers as well as negative demographic consequences due to other 
fitness-related genetic traits of trophy males; however, few studies have explored such 
implications (Festa-Bianchet and Lee 2009).

Initially, the Maine Legislature set the moose hunting seasons and harvest levels 
based on goals developed during a 1985 planning process. The overall goals were to 
maintain the moose population at the 1985 level, increase harvest, and maintain viewing 
opportunities; permits were either sex prior to 1999. Since 2001, the Maine Department 
of Inland Fisheries and Wildlife (MDIFW) set the moose hunting seasons and harvest
levels under a Moose Management System (Morris 2002) that describes the decision process and actions necessary to meet population goals and objectives set by a public working group. Desired levels of hunting opportunity, viewing opportunity, and road safety were assessed to categorize each Wildlife Management District (WMD) into a Management Area type: Recreation Management, Road Safety, or Compromise Area. Meeting population goals in a WMD includes determining age and sex composition from moose sightings reported by deer and moose hunters, the age of harvested animals, and more recently from helicopter surveys. Among other measures, both the proportion of bulls and the percentage of mature bulls (>5 years old) in each WMD are examined annually and harvest levels are adjusted to achieve desired levels. This system reflects a significant management change because bull composition was not a prior management criteria.

A recent >20 year analysis (1988-2009) of physical parameters of harvested moose in New England indicates that body weight and ovulation rate of yearling cow moose in both New Hampshire and Vermont are trending downward, yet remain relatively stable in adult cows; conversely, harvested yearling cow moose in Maine show an increase in body weight. Body weight and most antler measurements of harvested bulls in New Hampshire and Vermont have also declined (Bergeron et al. 2013). Given declines in physical characteristics of yearling bull moose in New Hampshire and Vermont over the last 2 decades, there is reason to investigate baseline and trend data for Maine’s moose population. There is a >30 year history of modern moose hunting in Maine with harvest increasing from 636 in 1980 to 2,582 in 2011, and permit allocations continue to increase (MDIFW 2011); importantly, age, antler spread, and body weight
have been measured since 1980. This study provides a temporal assessment of these physical characteristics to identify trends in the relative growth and condition of bull moose harvested in Maine from 1980-2009. The primary objectives were to assess trends in body weight and antler spread within age class, the relative proportion per age class, and trophy bulls (spread ≥137cm), in the harvest.

**Study Area**

Harvest data were analyzed for 12 Wildlife Management Districts (WMD; 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, and 19) in a 45,793 km² area, roughly the northern half of Maine (Fig. 2-1). This area contains a high proportion of suitable moose habitat in the form of active commercial forestlands, has had relatively consistent harvest over the study period (1980-2009; L. Kantar, MDIFW wildlife biologist, pers. comm.), and these WMDs represent the core of Maine’s moose population (MDIFW 2013).

Northern Maine is located at the extreme northeast corner of the United States, above 44° 38’ N. It is bordered by Quebec and New Brunswick to the north, New Hampshire to the west, and the Atlantic Ocean to the south and east. Maine is 90% forested and commercial timber harvesting is common throughout the northern portion of the state (Hoving et al. 2004). The sub-boreal Acadian forest has a mixture of spruce (Picea spp.) and fir (Abies balsamea) stands and northern hardwood forests (Irland 1999); common species include beech (Fagus grandifolia), maple (Acer spp.), hemlock (Tsuga canadensis), birch (Betula spp.), spruce, and balsam fir (Hoving et al. 2004).

**Methods**

Biological data collected at moose check stations in 1980-2009 were used to assess temporal trends in the physical characteristics of bull moose. Data were broken
Figure 2-1. Maine Wildlife Management Districts (WMDs) used to assess data from harvested bull moose for temporal trends in physical characteristics, 1980-2009, are shaded.
into 4 time periods (1980-1987, 1988-1998, 1999-2004, and 2005-2009) to maintain similarity with recent assessments of regional harvest data (Adams and Pekins 1995, Musante et al. 2010, Bergeron 2011, Bergeron et al. 2013). Data were also analyzed by individual year; data were unavailable for 1981 (no harvest) and 1985 (data not age-specific). Specific measurements were field-dressed body weight, antler spread, and age. Field-dressed body weight was defined as the entire carcass weight minus the heart, liver, lungs, and rumen- reticulum and was measured on certified scales at registration stations. Antler spread was measured as the greatest measurement (cm) of the antlers on a plane perpendicular to the skull. Age was determined from cementum annuli counts on cross-sectioned canines (Sergeant and Pimlott 1959) performed by MDIFW biologists. Trophy bulls were defined as those with spreads ≥137cm (54 in); this is similar to minimum entry for Canada moose in Boone and Crockett Club’s trophy record-book (Boddington 2011).

Analysis of variance (ANOVA) was used to test for age-specific differences in physical parameters between years and time periods including body weight-age relationships, antler spread-age relationships, age class distribution, and relative condition of the population over time. Age classes were 1.5, 2.5, 3.5, 4.5, 5.5, and ≥6.5 years. Tukey’s test was used to make pairwise comparisons; significance for all tests was assigned a priori at α = 0.05.

**Results**

Total age class records ranged from 1169 (5.5 years) to 2860 (≥6.5 years), with continual increase in sample size across time periods; 1619 and 1625 in 1980-1987 and 1988-1998, and 3789 and 4533 in the 1999-2004 and 2005-2009 time periods, respectively. Overall, there was an upward trend in mean body weight of harvested bull
moose over the 30-year period. Between 1980-1987 and 2005-2009, a 4-10% increase in mean body weight occurred in the youngest 4 age classes (1.5-4.5 years old, \( P \leq 0.024 \)); minimal change (1-2\%, \( P > 0.05 \)) occurred in the \( \geq 5.5 \) year classes in the same periods (Appendix C). The current (2005-2009) mean body weight is higher than the 30 year mean in all age classes. There was no difference (\( P > 0.05 \)) in mean body weight among any time periods in the \( \geq 6.5 \) year age class. The maximum mean weight occurred in the 1999-2004 time period for the 2.5-5.5 year old age class; mean weights in this time period were higher than in other time periods for 2.5 (\( P \leq 0.002 \)) and 3.5 year old bulls (\( P \leq 0.005 \)) (Fig. 2-2, Appendix C). Maximum mean weight of yearlings (225 kg) occurred in the 2005-2009 time period (\( P \leq 0.02 \)).

The four youngest age classes (1.5-4.5 years) had an overall increase (4.0-8.3\%, \( P \leq 0.014 \)) in mean antler spread between 1980-1987 and 2005-2009, though some variation occurred in intermediary time periods; harvested bulls \( \geq 5.5 \) years showed little change (<3.6\%, \( P > 0.05 \)) between these time periods (Fig. 2-3, Appendix D). Yearlings were the only age class in which the current (2005-2009) mean spread (60 ± 15.9 cm, \( \bar{x} \pm SD \)) exceeded the 30 year mean; this age class had the most substantial increase in spread between 1980-1987 and 2005-2009 (8.3\%, \( P = 0.013 \)). Though no difference (\( P > 0.05 \)) existed between the 1980-1987 and 2005-2009 time periods in the \( \geq 6.5 \) year age class, antler spread declined (5\%, \( P < 0.000 \)) between 1988-1998 and 2005-2009. The maximum spread occurred in the 1999-2004 time period for 2.5-5.5 year old bulls; mean spreads in this time period were higher than in other time periods for 2.5 (\( P \leq 0.003 \)) and 3.5 year old bulls (\( P < 0.000 \)) (Fig. 2-3, Appendix D).

There were no differences (\( P > 0.05 \)) in the proportion of harvested bulls within
Figure 2-2. Mean (±SE) field-dressed body weight (kg) of harvested bull moose in Maine, 1980-2009. Within age classes, bars with a letter in common were not significantly different.
Figure 2-3. Mean (±SE) antler spread (cm) of harvested bull moose in Maine, 1980-2009. Within age classes, bars with a letter in common were not significantly different.
each age class between the 1980-1987 and 2005-2009 time periods; some variation occurred between intermediary time periods (Fig. 2-4). A significant decrease within the yearling age class occurred between 1988-1998 and 2005-2009 (64%, $P = 0.0003$); the only other significant change within any age class across that same time period was an increase within the 4.5 year age class (28.5%, $P = 0.027$).

The proportion of trophy bulls (spread ≥137 cm) declined in successive time periods from 8.8% in 1980-1987 (n = 152) to 5.9% in 2005-2009 (n = 319), approximately a 33% overall reduction ($P = 0.053$) (Fig. 2-5). Similarly, the annual proportion of trophy bulls had a negative relationship with increasing years ($r^2 = 0.14$, $P = 0.03$). The mean spread of trophy bulls in each time period declined 2% ($P = 0.003$) from 145.7 (SE = 0.56) to 143.3 (SE = 0.39) cm between 1980-1987 and 2005-2009. The mean age of trophy bulls was between 7 and 8.5 years of age for all time periods; 85-93% were ≥5 years old. Trophy bulls between 5.5 and 12.5 years old accounted for 86-92% of all trophy bulls across time periods, averaging 89% for all time periods (Fig. 2-6).

**Discussion**

There was no statistical evidence of a measurable decline in the physical parameters of bull moose harvested in northern Maine from 1980-2009. A minimal upward trend occurred in mean body weight during the 30-year time period as the 2005-2009 mean body weight exceeded the 30-year mean in all age classes (Fig. 2-2). Similarly, a slight overall increase occurred in the mean spread of the 4 youngest age classes across the 30-year time period, with some variability but no clear trend in bulls ≥5.5 years old. The lack of declining trends in adult physical characteristics is similar to that measured in nearby Vermont and New Hampshire and presumably indicates
Figure 2-4. Age structure of bull moose harvested in Maine by time periods, 1980-2009.
Figure 2-5. Proportion (%) of harvested bull moose considered trophy bulls (spread $\geq 137$ cm) by time period in Maine.
Figure 2-6. Proportion (%) of harvested trophy bulls (spread ≥137cm) within each age class in Maine, 1980-2009.
adequate habitat quality (Bergeron et al. 2013). However, unlike in Vermont and New Hampshire, where declines occurred in both body weight and productivity measures in the yearling age class, the physical characteristics of Maine yearlings increased slightly indicating some variability within the northeastern United States.

The downward trend in the proportional harvest within the yearling age class between 1988-1998 and 2005-2009 could indicate a reduction in the proportion of yearlings in the population possibly due to a lower recruitment (Fig. 2-5). However, this decline was not coupled with reduced physical parameters that are indicative of a decline in relative health and nutritional status; both body weight and spread increased in yearlings during the 30-year period.

Numerous factors can influence physical parameters of moose including habitat quality, weather, and disease and parasites. In nearby New Hampshire, parasitism by winter ticks is considered a primary influence in the decline in survival and growth of moose calves and subsequent productivity of yearlings (Musante et al. 2010, Bergeron 2011). Declining trends in the yearling body weight and antler spread in New Hampshire and Vermont bulls from 1988-2009 suggest such impact (Fig. 2-7, (Bergeron et al. 2013). Conversely, lack of measurable decline and slight increase in physical characteristics of yearling bulls in Maine from 1980-2009 suggests that parasitism by winter ticks could be less of a problem in Maine. The majority of the Maine study area lies above 44° 38’ N extending as far north as 47° 28’ N, an area further north than the entirety of New Hampshire and Vermont, both below 45° 18’ N. Because abundance of winter ticks and their annual impact are largely determined by length of winter and snow cover
Figure 2-7. Mean field-dressed body weight (kg) and mean antler spread (cm) of harvested yearling bull moose in Maine, Vermont, and New Hampshire (1988-2009; Bergeron et al. 2013).
Figure 2-8. Total annual moose harvest in Maine, 1980-2009 (MDIFW 2011).
(Samuel and Welch 1991), the core of Maine’s moose population may be less influenced by this parasite.

The lower proportion of trophy bulls and increasing total annual harvest over time may reflect the potential for harvest pressure to impact antler size in the older portion of the population (Fig. 2-5, Fig. 2-8). However, the 2% decrease in antler spread is minimal biologically and variation in antler size can be explained by annual weather influences, variation in population density, and population sex ratios (Solberg and Saether 1994). Additionally, the relatively stable proportion of bulls >5 years old in the harvest across time periods (30-44%) does not indicate excessive selective harvest pressure towards older, trophy bulls (Fig. 2-4). The majority of trophy bulls (86-92%) are between 5.5 and 12.5 years old in all time periods, with an average age between 7 and 8.5 years (Fig. 2-6).

A study of antler characteristics in Alaska showed spread reaching a maximum in prime age bulls (7-11 years) and declining as senescence appeared at around 12 years (Bowyer et al. 2001). The high proportion of trophy bulls >5 years old and the declining proportion beginning at age 12 in Maine indicates the proportions of trophy bulls in each age class are likely not influenced by harvest pressure, but occur at the same age that natural maximum growth and senescence would be expected.

Most studies with empirical evidence of the effects of trophy hunting on growth of horn-like structures occurs outside of the moose literature; for example, targeted hunting on bighorn trophy rams (Ovis canadensis) over a 30-year period resulted in smaller-horned, lighter rams, and fewer trophies (Coltman et al. 2003). Hundertmark et al. (1998) simulated selective harvest for bull moose based on antler size (>127 cm spread) and showed a significant decrease in the frequency of favorable antler alleles;
however, empirical evidence of the genetic impact of trophy hunting is rare and such changes are assumed to be undetectable for many generation lengths (Harris et al. 2002).

Because many hunters are willing to pay more to harvest larger antlered males, integration of trophy hunting into wildlife management programs can be used as an effective conservation tool (Hofer 2002). For example, the North American bighorn sheep population has more than tripled in the past 30 years, primarily due to the application of revenue raised from hunters towards conservation (Festa-Bianchet and Lee 2009). In Maine, general moose permits and the permit auction provide substantial revenue to the state, $1,487,214 in FY 2012 (L. Kantar, pers. comm.). Maine Public Law Chapter 370, LD 291 (2011), mandates that $100 from each non-resident permit be deposited into a Moose Management and Research Fund, and an additional $25,000 may also be deposited from application fees to carry out MDIFW moose research (Maine State Legislature 2011). As hunters often base harvest participation and decisions on antler size (Schmidt et al. 2007), temporal declines in the proportion of trophy bulls in the population or the associated mean spread could influence financial resources for moose conservation and research in Maine. The data reported here would not warrant elimination of the auction program or presumably cause hunter disinterest.

It is known that age distribution can shift toward younger age classes as harvest intensity increases (Jenks et al. 2002). Selective hunting that targets older, larger males can result in increased breeding by younger bulls and alter age structure of the population by reducing mean bull age and size over time (McCullough 1982). MDIFW maintains desired levels of bull composition by analyzing the age of harvested animals combined with sightings by deer and moose hunters, and more recently from aerial surveys (Kantar
and Cumberland 2013). For example, in WMDs 1-10 and 19, the goal is to maintain 17% mature (≥5 years old) bulls, whereas in WMD 11 it is to maintain 38% bulls (60 bulls : 100 cows) (Morris 2002). Harvest levels and permit types (i.e. sex-specific) are adjusted annually to maintain desired bull composition levels and limit over-harvest of prime age and mature bulls. Despite fourfold higher harvest after 30 years of moose hunting in Maine (MDIFW 2011), the northern population has maintained consistent age structure (Fig. 2-4). Specifically, there has been no measurable decline in the proportion of harvested bulls ≥6.5 years that would indicate an overall younger age structure due to selective harvest of larger, trophy males (Fig. 2-4).

Maine’s current moose population estimate is ~76,000 moose, and annual harvest has risen from 816 to >2000 moose from the 1980-1987 to 2005-2009 time periods (MDIFW 2011, 2012). Current harvest is only about 3% of the current population estimate, but will probably increase as hunting interest and moose conflicts increase. While this study indicates that to date physical characteristics of bull moose in Maine have not changed appreciably after 30 years of harvest, understanding the potential and realized influences of harvest on age structure and physical parameters of moose populations is fundamental to proper management. Similar harvest analyses have indicated recent declines in body weight, antler measurements, and reproductive rate in moose in nearby Vermont and New Hampshire (Bergeron et al. 2013). These productivity measurements have been collected in Maine since 2010 in combination with Potvin double-count aerial surveys and age-sex composition flights. Integration of these techniques with harvest data will provide the essential data necessary for managing moose under the 3 primary management goals in Maine. Continued monitoring of
physical parameters of harvested moose, especially trophy bulls and adult cows, is warranted to monitor the relative condition and best manage the largest and longest harvested moose population in the northeastern United States.
CHAPTER 3

USING AERIAL SURVEY OBSERVATIONS TO IDENTIFY WINTER HABITAT USE OF MOOSE IN NORTHERN MAINE

Introduction

Moose exhibit patterns of habitat use that indicate generalist behavior but often have seasonal preference for specific habitat variables. Peek (1997) considered moose "selective generalists" due to their ability to use habitat variables in higher proportion than available when seasonally advantageous. Habitat selection in all seasons is primarily driven by food abundance and quality (Vivas and Saether 1987) and access to adequate thermal cover (Karns 1997, Dussault and Ouellet 2004). In northern New England, commercial timber harvesting typically provides heterogeneous forests with stands of varying age that provide high quality cover and browse for moose (Miller 1989, Scarpitti et al. 2005).

Although moose are reasonably mobile in typical winter conditions in northern New England, habitat use can be influenced by snow depth, forage availability, and foraging intensity. Moose minimize energy expenditure and reduce home range in winter (Peek 1997, Renecker and Schwartz 1998), indirect evidence of the importance of winter habitat relative to individual and population productivity. At the fine scale, cut/regeneration habitat is used more than other habitat types during winter in New Hampshire, presumably because of high forage availability and preference (Scarpitti 2006). Areas where moose concentrate habitually in high seasonal density are often
associated with forest damage globally (Heikkila et al. 2003). For example, high winter densities of moose in Newfoundland are associated with heavy browsing and limited growth and regeneration of birch (Betula spp.) (Bergerud and Manuel 1968). In New Hampshire, Bergeron et al. (2011) found specific cutover sites with low regeneration adjacent to traditional wintering areas, and predicted that such sites could change from hardwood to softwood dominance. Heavy winter browsing pressure on preferred tree species in northeast Vermont resulted in reduced stand height and a possible shift in forest composition to coniferous species (see Chapter 1). Therefore, to best manage moose in a landscape dominated by commercial forests, it is important to evaluate winter habitat use.

Double-count aerial surveys were conducted by The Maine Department of Inland Fisheries and Wildlife (MDIFW) during winter 2011 and 2012 to measure moose abundance in specific northern Wildlife Management Districts (WMD) with presumed high moose density, and additional surveys were flown in 2012 to determine sex-age composition in select WMDs. GPS location data were collected when moose were observed, providing the ability to identify and assess general habitat use by moose during the survey period. While habitat use patterns are generally known for moose throughout their range, and specifically in New Hampshire (Miller 1989, Scarpitti et al. 2005, Scarpitti 2006) and Maine (Leptich and Gilbert 1989, Thompson et al. 1995), it is important to continually examine how these patterns are expressed on a local scale and respond to habitat (forest) change (Peek 1997). Identifying the seasonal habitat use of moose should provide information on the relative proximity and dispersion of forage and
cover resources (Hundertmark 1997) and provide regional insight about the relationship between forest harvest practices and moose.

This GIS analysis was conducted to measure habitat and landscape characteristics associated with locations of moose observed during aerial surveys in winter in northern Maine. The primary objectives were to identify the habitat associated with locations, determine if locations were random relative to habitat availability, and identify land cover characteristics related to locations.

**Study Area**

The study area in Maine encompassed those WMDs flown in each survey year; WMD 2, 3 and 6 were flown in winter 2010-2011 and WMD 1, 2, 3, 4, 5, 8, 11 and 19 were flown in winter 2011-2012 (Fig. 3-1). The survey area totaled ~32,950 km² and included Aroostook County and northern portions of adjacent Franklin, Hancock, Penobscot, Piscataquis, Somerset, and Washington Counties dominated by commercial forests comprised primarily of spruce (*Picea* spp.), balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*), and white pine (*Pinus strobus*), with mixed hardwoods of aspen (*Populus* spp.), birch (*Betula* spp.), beech (*Fagus grandifolia*) and maple (*Acer* spp.) (Kantar and Cumberland 2013). The forest composition in each WMD was described by 7 forest habitat variables (Maine Office of Geographic Information System 2004). Each survey block was representative of the proportional availability of the 7 habitat variables within a WMD. Most blocks were dominated by uncut (>50% combined) and cut (>20%, various treatments) forest; recent cuts and regenerating habitat were available in all survey blocks (Table 3-1, Appendix F, L. Kantar, MDIFW, pers. comm.).
Figure 3-1. Maine Wildlife Management Districts (shaded) used for double-count aerial surveys and composition count surveys, winter 2011 and winter 2012, Maine, USA.
Table 3-1. Forest composition (%) of survey blocks within Wildlife Management Districts (WMD) flown in double-count and age-sex composition aerial moose surveys, winters 2011 and 2012, northern Maine, USA.

<table>
<thead>
<tr>
<th>WMD</th>
<th>Mixed Forest (%)</th>
<th>Deciduous Forest (%)</th>
<th>Coniferous Forest (%)</th>
<th>Partial Cuts (%)</th>
<th>Recent Cuts/ Regenerating Forest/ Scrub-Shrub (%)</th>
<th>Wetland (%)</th>
<th>Crops/Grasslands (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>21.7</td>
<td>10.4</td>
<td>35.9</td>
<td>21.4</td>
<td>6.7</td>
<td>4.0</td>
<td>0.0</td>
</tr>
<tr>
<td>2</td>
<td>40.7</td>
<td>17.8</td>
<td>14.1</td>
<td>12.9</td>
<td>9.9</td>
<td>4.5</td>
<td>0.1</td>
</tr>
<tr>
<td>3</td>
<td>30.5</td>
<td>18.1</td>
<td>23.9</td>
<td>3.3</td>
<td>10.3</td>
<td>7.1</td>
<td>6.9</td>
</tr>
<tr>
<td>4*</td>
<td>17.4</td>
<td>16.3</td>
<td>21.7</td>
<td>18.0</td>
<td>17.6</td>
<td>8.9</td>
<td>0.1</td>
</tr>
<tr>
<td>4*</td>
<td>15.5</td>
<td>25.8</td>
<td>14.6</td>
<td>20.3</td>
<td>16.9</td>
<td>6.7</td>
<td>0.1</td>
</tr>
<tr>
<td>5</td>
<td>42.2</td>
<td>4.9</td>
<td>23.3</td>
<td>15.6</td>
<td>7.8</td>
<td>6.0</td>
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<td>6</td>
<td>33.0</td>
<td>12.0</td>
<td>20.0</td>
<td>4.7</td>
<td>4.0</td>
<td>10.0</td>
<td>15.6</td>
</tr>
<tr>
<td>8</td>
<td>15.2</td>
<td>21.0</td>
<td>29.7</td>
<td>20.6</td>
<td>10.9</td>
<td>2.6</td>
<td>0.1</td>
</tr>
<tr>
<td>11</td>
<td>42.8</td>
<td>7.0</td>
<td>20.0</td>
<td>15.4</td>
<td>4.1</td>
<td>9.5</td>
<td>1.2</td>
</tr>
<tr>
<td>19</td>
<td>30.4</td>
<td>6.8</td>
<td>34.0</td>
<td>11.3</td>
<td>7.6</td>
<td>9.6</td>
<td>0.4</td>
</tr>
</tbody>
</table>

*multiple survey blocks were located in WMD.
**Methods**

The WMDs with highest moose density based on hunter sighting rates and highest harvest rates and permit allocations were prioritized for the aerial surveys; WMD 11 was surveyed to evaluate the reliability of the technique at lower moose density (Kantar and Cumberland 2013). Survey blocks were 15 x 24 km rectangles selected by assessing the proportion of habitat variables within each survey block and prioritizing the block that was most representative of the overall habitat of the WMD (Kantar and Cumberland 2013). The double-count surveys required that moose mobility was unrestricted, when snow depth was <61 cm and ambient temperature was cold (<-12°C), and there was no obvious evidence of grouping (Kantar and Cumberland 2013); conditions during composition surveys also met these criteria (L. Kantar, pers. comm.). Moose locations (n = 481; ≥1 moose/location) were acquired from double-count aerial surveys in winter 2011 (28 January – 1 February) and 2012 (13 December 2011 – 8 February 2012), and composition count surveys in winter 2012 (13 December 2011 – 3 February 2012; Table 3-2). The GPS coordinates were collected at each sighting location; the number of moose at each location ranged from 1 moose (n = 215) to 16 moose (n = 1), with groups >5 restricted to composition surveys.

**Habitat Use**

All GPS locations of moose were defined as used locations and were mapped with ArcGIS (ESRI 2010) to identify habitat characteristics in a use-availability analysis. An equal number of random points were generated using the “Generate Random Points” tool (ESRI 2010) to represent available locations within each flight survey block.
Table 3-2. Survey dates and number of locations collected during aerial double-count and composition count surveys by WMD in northern Maine, winter 2011 and 2012.

<table>
<thead>
<tr>
<th>Date</th>
<th>WMD</th>
<th>Locations (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Double-Count</td>
<td></td>
<td></td>
</tr>
<tr>
<td>28-Jan-11</td>
<td>2</td>
<td>33</td>
</tr>
<tr>
<td>31-Jan-11</td>
<td>3</td>
<td>24</td>
</tr>
<tr>
<td>1-Feb-11</td>
<td>6</td>
<td>13</td>
</tr>
<tr>
<td>13-Dec-11</td>
<td>2</td>
<td>27</td>
</tr>
<tr>
<td>8-Jan-12</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>9-Jan-12</td>
<td>4</td>
<td>40</td>
</tr>
<tr>
<td>11-Jan-12</td>
<td>1</td>
<td>26</td>
</tr>
<tr>
<td>22-Jan-12</td>
<td>19</td>
<td>21</td>
</tr>
<tr>
<td>26-Jan-12</td>
<td>8</td>
<td>17</td>
</tr>
<tr>
<td>2-Feb-12</td>
<td>4</td>
<td>31</td>
</tr>
<tr>
<td>8-Feb-12</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td>Composition Count</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13-Dec-11</td>
<td>2</td>
<td>66</td>
</tr>
<tr>
<td>28-Dec-11</td>
<td>3</td>
<td>63</td>
</tr>
<tr>
<td>22-Dec-11</td>
<td>4</td>
<td>55</td>
</tr>
<tr>
<td>3-Feb-12</td>
<td>8</td>
<td>50</td>
</tr>
</tbody>
</table>
Because most moose were moving from the disturbance of the helicopter, and to evaluate a reasonable spatial scale of habitat use, a circular buffer (4.91 ha) was placed around each used and available location as a conservative estimate of diurnal habitat use (Fig. 3-2); this buffer also accounted for any GPS error in moose locations. The ~5 ha scale is representative of a circular polygon with a radius of 125 m; Becker (2008) determined 125 m as the average distance moved by moose in a 2-hour period in northwest Wyoming. Additionally, a larger buffer (706.9 ha) was applied to used and available locations that represented a circular polygon with radius of 1.5 km (Fig. 3-2), a value reflecting the daily movement and core area of moose in early winter. Specifically, the average daily winter movement by cow moose was 1.45 km in northwest Wyoming (Becker 2008), and 1.66 km for cow and bull moose in central and western Massachusetts (Wattles 2011). The core area of cow moose in early winter in New Hampshire was 3.7 km² (Scarpitti 2006), which yields an estimated radius of 1.09 km assuming a circular use area.

Land cover types were identified using the Maine Landcover Dataset 2004 (Maine Office of Geographic Information System 2004), and were identified for used and available units at all spatial scales. Cover types that were not utilized or did not occur in the study area or flight paths were not used in analysis. Relevant cover types were aggregated into 7 habitat variables previously used in the selection of survey blocks for the aerial surveys: 1) mixed forest, 2) deciduous forest, 3) coniferous forest, 4) partial cuts, 5) recent clearcuts/regenerating forest/scrub-shrub, 6) wetlands, and 7) crops/grasslands (Kantar and Cumberland 2013). Additionally, recent clearcuts, partial cuts, regenerating forest, and scrub-shrub were analyzed as a combined variable to reflect
Figure 3-2. Circular polygons created at two landscape scales surrounding winter moose locations and random points used to describe used and available habitat units in Maine.
an overall regenerating land cover class providing typical winter browse. A separate habitat variable was created combining recent clearcuts, heavy partial cuts, and light partial cuts to evaluate the proximity of used and available units to forest cuts in general. Used and available units were also analyzed for proximity to mature conifer, using the coniferous forest land cover classification from MELCD. National Elevation Data (NED) from U.S. Geological Survey was used to assess elevation, slope, and aspect.

Application of buffers at the 707 ha scale created overlap among units that resulted in continuous extents, some of which spanned the width of a survey block. This scale analysis was subsequently dropped because the commonality in coverage areas made comparisons between used and available units meaningless.

**Statistical Analysis**

General linear mixed model (GLMM) analysis was performed using JMP software (SAS Institute, Cary, NC, USA) to identify individual habitat variables that differed between used and available units at all landscape scales. These individual hypothesis tests were used to inform variable selection for use in eventual model selection under an information-theoretic approach (Anderson et al. 2001). Land cover classes, elevation, slope, aspect, proximity to cuts, and proximity to mature conifer were treated as fixed-effects for individual analyses; WMD was treated as a random effect in all analyses to remove variation due to differences in habitat variable values by WMD. Habitat variables with significant difference ($P < 0.05$) between used and available units were used as inputs for model selection.

Model selection was performed with a mixed effects logistic regression model using R statistical software (R Development Core Team 2013) using the lme4 package.
(Bates et al. 2012); this model selection analysis was used to identify those combinations of habitat variables that most influence moose presence. Significant habitat variables from the individual GLMM analyses were treated as fixed effects; WMD was treated as a random effect in all models. Model comparisons were made using the Akaike Information Criterion (AIC<sub>c</sub>) scores; top competing models were those with ΔAIC<sub>c</sub> < 2 and the best fitting model was determined by identifying the model with the lowest AIC<sub>c</sub> score and highest Akaike weight (Burnham and Anderson 2002). Model parameter coefficients were averaged for top competing models (i.e., ΔAIC<sub>c</sub> < 2) using the MuMIn package (Barton 2013) in R. Significance values were not reported for model parameter coefficients as they are considered inappropriate when using the information-theoretic approach (Anderson et al. 2001). Results are presented throughout as $\bar{X} \pm SE$.

**Results**

Habitat composition (~95%) of used units was dominated by 5 habitat variables that were similar (0-4% different) at the location and 5 ha scale. The primary composition of used units at the location scale was 35.1% mixed forest, 19.1% deciduous forest, 14.5% coniferous forest, 15.2% partial cuts, and 11.8% recent cuts/regenerating forest/scrub-shrub. Similarly, habitat composition of used units at the 5 ha scale was 31.3% mixed forest, 20.7% deciduous forest, 17.56% partial cuts, 14.5% coniferous forest, and 11.4% recent cuts/regenerating forest/scrub-shrub.

Significant differences between used and available units for locations and the 5 ha scale were found in the individual GLMM analyses of habitat variables. Used locations included more deciduous forest (7.3%, $F = 8.92$, $P = 0.003$) than was at available locations; conversely, wetlands (3.3%, $F = 5.64$, $P = 0.018$), crops/grassland (2.1%, $F =$
7.64, \( P = 0.006 \)), and coniferous forest (3.7\%, \( F = 3.11, \ P > 0.05 \)) were less common at used than available locations (Fig. 3-3). At the 5 ha scale, used areas included more deciduous forest (6.3\%, \( F = 8.18, \ P = 0.004 \)) and partial cuts (4.1\%, \( F = 4.50, \ P = 0.034 \)) than in available areas; coniferous forest (3.7\%, \( F = 4.58, \ P = 0.033 \)), wetlands (2.2\%, \( F = 4.56, \ P = 0.033 \)), and crops/grassland (1.9\%, \( F = 9.85, \ P = 0.002 \); Fig. 3-3) were used less than available. There was no detectable difference (\( P > 0.05 \)) between used and available units in the combined regenerating habitat variable (recent clearcuts, partial cuts, regenerating forest, and scrub-shrub) at either scale. Similarly, there was no detectable difference in mixed forests that represented the largest proportion of used and available units at both scales (28.8-35.1\%; Fig. 3-3).

Used locations were in closer proximity to cuts (\( \bar{X} = 299.4 \text{ m} \pm 66.8 \)) than available locations (\( \bar{X} = 410.4 \text{ m} \pm 66.8, \ P < 0.0001 \); similarly, at the 5 ha scale (\( P < 0.0001 \); Fig. 3-4) used units were closer (\( \bar{X} = 215.1 \text{ m} \pm 62.2 \)) to cuts than available units (\( \bar{X} = 319.1 \text{ m} \pm 62.2 \)). There was no detectable difference (\( P > 0.05 \)) in proximity to mature conifer between used and available units at either scale.

Elevation was higher at used (\( \bar{X} = 291.6 \text{ m} \pm 39.4 \)) than available locations (\( \bar{X} = 280.1 \text{ m} \pm 39.4, \ P = 0.012 \)), and at the 5 ha used (\( \bar{X} = 291.3 \text{ m} \pm 39.6 \)) than available areas (\( \bar{X} = 280.1 \text{ m} \pm 39.6, \ P = 0.014 \); Fig. 3-5). Directional aspect was not different \( (P > 0.05) \) at either scale, with the exception of northeast-facing slopes at locations used less than available (4.0\%, \( F = 3.86, \ P = 0.049 \)). Flat aspects accounted for <3\% of available units and had no data points at used units; this aspect class was removed from analysis. There was no detectable difference in slope (\( P > 0.05 \)) at either scale.
Figure 3-3. Proportion (%) of cover types within used and random units for locations and the 5 ha landscape scale during winter 2011 and winter 2012 in Maine. Units that are different ($P < 0.05$) within each cover type for the location and 5 ha scale are starred (*).
Figure 3-4. Mean distance (m) to cuts of used and available units for locations and the 5 ha landscape scale during winter 2011 and winter 2012 in Maine. Distance was less ($P < 0.05$) for both used; bars show standard error.
Figure 3-5. Mean elevation (m) of used and available units for locations and the 5 ha landscape scale during winter 2011 and winter 2012 in Maine. Elevation was higher ($P < 0.05$) for both used; bars show standard error.
The habitat parameters used in the logistic regression mixed effects models were deciduous forest, coniferous forest, wetlands, distance to cuts, and elevation; WMD was included as a random effect in all models. The model that best explained (lowest AICc score) moose presence included deciduous forest, distance to cut, and wetlands at both the location and 5 ha scales (Table 3-3). Specifically, moose locations were most influenced by a higher proportion of deciduous forest \( (\beta = 0.516, \text{SE} = 0.179) \), shorter distance to cuts \( (\beta = -0.269, \text{SE} = 0.072) \), and smaller proportion of wetlands \( (\beta = -0.596, \text{SE} = 0.318) \); likewise, at the 5 ha scale used areas were most influenced by deciduous forest \( (\beta = 0.180, \text{SE} = 0.066) \), distance to cuts \( (\beta = -0.197, \text{SE} = 0.054) \), and wetlands \( (\beta = -0.107, \text{SE} = 0.069) \); Table 3-3). Models with \( \Delta \text{AICc} < 2.00 \) also included smaller proportion of coniferous forest and elevation at both the location \( (\beta = -0.209, \text{SE} = 0.184 \) and \( \beta = -0.029, \text{SE} = 0.071 \), respectively) and 5 ha scales \( (\beta = -0.086, \text{SE} = 0.069 \) and \( \beta = -0.044, \text{SE} = 0.072 \), respectively; Table 3-3).

**Discussion**

This modeling exercise indicates that proximity to regenerating forests in the form of recent clearcuts, light partial cuts, and heavy partial cuts is an important predictor of the location of moose during winter in northern Maine (Table 3-3, Fig. 3-4). In previous research, 87% of winter observations in Maine were in areas that had been logged within 10-30 years (Thompson et al. 1995). Similarly, cut/regeneration habitat was used more than expected in early winter and dictated habitat use at the fine scale in New Hampshire (Scarpitti 2006), and regenerating stands were used more than available in early winter in Massachusetts (Wattles 2011). Unlike in summer when high quality forage is available in more habitat types (Scarpitti 2006), regenerating forests are preferentially used in winter
Table 3-3. The total number of parameters (K), log likelihood statistic (logLik), AICc score, delta AICc, and model weight for top competing location and 5 ha landscape scale models (i.e., delta AICc scores <2), and the estimates and standard error (SE) for the model-averaged coefficients.

<table>
<thead>
<tr>
<th>Locations</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Model Selection based on AICc</strong></td>
</tr>
<tr>
<td>Deciduous + Distance to Cut + Wetlands</td>
</tr>
<tr>
<td>Coniferous + Deciduous + Distance to Cut + Wetlands</td>
</tr>
<tr>
<td>Deciduous + Distance to Cut</td>
</tr>
<tr>
<td>Deciduous + Distance to Cut + Elevation + Wetlands</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model-averaged coefficients</th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.060</td>
<td>0.081</td>
</tr>
<tr>
<td>Deciduous</td>
<td>0.516</td>
<td>0.179</td>
</tr>
<tr>
<td>Distance to Cut</td>
<td>-0.269</td>
<td>0.072</td>
</tr>
<tr>
<td>Wetlands</td>
<td>-0.610</td>
<td>0.318</td>
</tr>
<tr>
<td>Coniferous</td>
<td>-0.209</td>
<td>0.184</td>
</tr>
<tr>
<td>Elevation</td>
<td>-0.029</td>
<td>0.071</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>5 ha Landscape Scale</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Model Selection based on AICc</strong></td>
</tr>
<tr>
<td>Deciduous + Distance to Cut + Wetlands</td>
</tr>
<tr>
<td>Deciduous + Distance to Cut</td>
</tr>
<tr>
<td>Coniferous + Deciduous + Distance to Cut + Wetlands</td>
</tr>
<tr>
<td>Coniferous + Deciduous + Distance to Cut</td>
</tr>
<tr>
<td>Deciduous + Distance to Cut + Elevation + Wetlands</td>
</tr>
<tr>
<td>Coniferous + Deciduous + Distance to Cut + Elevation + Wetlands</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model-averaged coefficients</th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.032</td>
<td>0.066</td>
</tr>
<tr>
<td>Deciduous</td>
<td>0.180</td>
<td>0.070</td>
</tr>
<tr>
<td>Distance to Cut</td>
<td>-0.197</td>
<td>0.054</td>
</tr>
<tr>
<td>Wetlands</td>
<td>-0.107</td>
<td>0.069</td>
</tr>
<tr>
<td>Coniferous</td>
<td>-0.086</td>
<td>0.069</td>
</tr>
<tr>
<td>Elevation</td>
<td>-0.044</td>
<td>0.072</td>
</tr>
</tbody>
</table>
because concentrated, abundant browse allows moose to forage efficiently (Belovsky 1981, Miller 1989, Scarpitti 2006).

While the distance to cut was shorter for used than available units at both the location and 5 ha scales (Fig. 3-4), the combination of habitat variables reflecting regenerating forest habitat (recent clearcuts, partial cuts, regenerating forest, and scrub-shrub) was used in proportion to availability at both scales. It is possible that partial cuts have a shorter distance to edge that provides both browse and cover in closer proximity, and therefore are more influential in moose use. For example, moose in Ontario showed preference for edge provided by strips (100-200 m) of uncut timber over locations within clearcuts without edge (Mastenbrook and Cumming 1989). However, caution should be taken in examining narrowly-defined habitat variables in use:availability analysis; variables don’t necessarily describe behavioral recognition or choice, and importance could reflect high/low availability and not absolute use. For example, moose may seem to be specialists under certain variables (i.e., distance to cut) and generalists under others, particularly as they are combined or made coarser (i.e., regenerating/foraging habitat). Additionally, high availability of a habitat can mask the importance of its use; for example, despite being used in proportion to its availability, mixed forest was the most used land cover type at both the location and 5 ha scales (35.1% and 31.3%, respectively; Fig. 3-3).

Winter habitat use is based primarily on food availability until snow depth becomes restrictive, and moose are commonly located where there is sufficient hardwood browse (Morris 1999). Deciduous forests were preferentially used and were important in predicting locations (Fig. 3-3, Table 3-3). Moose feed mostly on deciduous vegetation
(Renecker and Schwartz 1997) and seek out the highest biomass of dormant shrubs and palatable forage during the period of time after the rut and into winter (Peek 1997). While not included in the top competing model at either landscape scale, locations were associated with a smaller proportion of coniferous forest (Table 3-3). While forage is likely more accessible and nutritious in deciduous, mixed, and regenerating forests during early winter, cover provided by coniferous forest is probably an important habitat variable when snow depth impedes movement or as thermal cover in later winter/early spring as ambient temperature rises, conditions avoided in this study. Moose in New Brunswick showed preference for more open and deciduous forest types in early winter and preference for dense conifer stands in late winter (Telfer 1970), and radio-collared moose in central Massachusetts showed increasing selection for conifer stands as winter progressed (Wattles 2011). Abundance of food resources, not availability of cover, is likely the most important factor in predicting habitat use in early winter in Maine, but a heterogeneous forest that provides both forage and shelter probably increases in use as winter progresses.

Elevation, while not included in the best fitting model, was higher on average for used units, than available units throughout the study area (Fig. 3-5). Previous research in Maine found moose moved from lowland (<305 m) into mid-elevation areas (367-327 m) in early winter, and occurred at slightly higher elevations later in winter (Thompson et al. 1995). The slightly higher elevations (11.2-11.5m, Fig. 3-5) may reflect avoidance of wetlands in winter as locations had a smaller proportion of wetlands than available habitat (Table 3-3). Wetland habitats that occur at lower elevations may be important predictors in determining moose presence between late-spring and autumn when insects
and thermoregulation are a concern and aquatic forage is available, but do not play a role in habitat selection during winter (Peek et al. 1976, Peek 1997). Identifying those elevations with highest seasonal use could aid in prioritizing survey areas or habitat management. However, as used units were only ~11m higher than available units at both landscape scales, it is likely the difference in elevation may not be biologically significant in the survey area.

Trends in used habitat variables were similar for locations and the 5 ha scale; specifically, the majority of used units were found in mature (mixed, deciduous and coniferous) and regenerating forest (recent clearcuts, partial cuts, regenerating forest, and scrub-shrub, Table 3-4). The used proportion of these coarser habitat variables (i.e., mature and regenerating forest) were similar to those defined for each survey block, and ultimately the respective WMD (Table 3-4). Habitat in northern Maine is considered high quality with stands of varying age and size distributed throughout providing adequate forage and cover as a result of commercial timber harvesting; this heterogeneous forested habitat likely helps support high moose numbers that are ultimately limited by habitat availability (Morris 1999, Scarpitti 2006).

Moose browsing can substantially alter plant communities and affect the structure and dynamics of forest ecosystems (McInnes et al. 1992, Renecker and Schwartz 1997) and there are important implications for forest management since moose prefer forage in clearcut and early-successional habitat (Westworth et al. 1989, Scarpitti et al. 2005). Browse consumption is strongly determined by its spatial distribution (Vivas and Saether 1987) and forage availability is an important factor in moose foraging behavior, irrespective of spatial scale (Dussault et al. 2005, Månsson et al. 2007). Integrated
Table 3-4. Mean proportion (%) ±SE of coarse cover types (i.e., mature and regenerating forest) within used units for locations and the 5 ha landscape scale during winter 2011 and winter 2012 in Maine compared to the proportion within survey blocks.

<table>
<thead>
<tr>
<th>WMD</th>
<th>Location (Used)</th>
<th>5 ha (Used)</th>
<th>Survey Block</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>73.1 ± 8.9</td>
<td>70.7 ± 6.8</td>
<td>68.0</td>
</tr>
<tr>
<td>2</td>
<td>73.0 ± 4.0</td>
<td>75.8 ± 3.1</td>
<td>72.6</td>
</tr>
<tr>
<td>3</td>
<td>80.5 ± 4.3</td>
<td>77.5 ± 3.1</td>
<td>72.4</td>
</tr>
<tr>
<td>4</td>
<td>57.8 ± 5.2</td>
<td>57.8 ± 4.2</td>
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<td>19.0 ± 8.8</td>
<td>20.9 ± 6.9</td>
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*small sample size (n = 4) likely influenced proportions
management of an abundant moose population (MDIFW 2012) and commercial forestlands in northern Maine requires balancing the well-being of an economically and culturally important species (moose) that preferentially forages in and can impede regeneration in cutover and partially cut stands.

Extensive use of cutover areas by female moose in Maine is indicative of how forest harvesting practices create beneficial interspersion of food and cover (Leptich and Gilbert 1989). According to MDIFW’s Moose Assessment, the best moose habitat in Maine is associated with commercially harvested forest (Morris 1999), and >25% of the study area was classified as some form of cut habitat. However, there are economic, political, and social issues associated with forest harvest practices and mandated changes could influence the relative abundance of moose in northern Maine (Morris 1999).

Concern over the effects of heavy clearcutting in the 1970s and 1980s, particularly in response to the massive spruce budworm (*Choristoneura fumiferana*) outbreak (Griffith and Alerich 1996), resulted in the Maine Legislature passing The Maine Forest Practices Act in 1990 (Maine Forest Service 1999). This act limited the size of clearcuts (<250 acres) and led to a dramatic shift from clearcutting to partial cuts beginning in the early 1990s; for example, ~93% of the 444,339 acres harvest in Maine was defined as partial cuts in 2011 (Maine Forest Service 2011). These harvest practices will presumably result in patchily distributed, smaller clearcuts and partial cuts that provide increased availability of browse and cover in closer proximity than created by larger clearcuts. The relatively high moose density estimates in much of the study area (2.0-4.0 moose/km²; Kantar and Cumberland 2013) may reflect such habitat change. Similar analysis as performed here should identify temporal changes in moose abundance and distribution.
with forest succession.

Some limitations exist in modeling with data of this nature that provides single locations of individuals rather than continuous locations from radio-collared animals; results are not necessarily applicable at a larger scale or through time. However, measuring habitat use in this way can provide insight into how moose respond to individual habitat variables and can allow for the testing of predictions of moose habitat-use (Peek 1997), especially if surveys are repeated and cover a reasonable time period. The number \( n = 481 \) of locations and 5 ha areas analyzed in this study over a ~2 month time period is reasonable when compared to traditional studies. Thompson et al. (1995) assessed winter habitat use of cow \( (n = 10) \) and bull \( (n = 4) \) moose in Maine with a seasonal mean of 5.8 and 5.4 observations, respectively. In New Hampshire, Scarpitti (2006) evaluated seasonal habitat use of cow moose using 42 and 54 core areas (2.6-3.7 km\(^2\)) in early and late winter, respectively.

The collection of accurate moose locations during aerial surveys in Maine resulted in a robust dataset that, while time-specific, was efficient, relatively cheap compared to radio-collaring efforts, and repeatable. This preliminary analysis provided habitat use information that was analogous with other regional studies. Expansion of such analyses should prove useful in examining the spatial distribution of moose across the landscape, the concentration of moose in cut areas that may result in forest regenerations problems, and temporal relationships between moose population responses and timber harvesting practices in northern Maine.
CONCLUSIONS

Chapter 1: Impact of moose browsing on forest regeneration in northeast Vermont

1. Regeneration was not considered a problem based on stocking rates of commercial trees in northeast Vermont. Stocking rate without severe damage increased from 67-68% in the youngest 3 age classes (3-5, 6-10, and 11-15 year) to 75% in the 16-20 year class. Severe damage from browsing was low (6-11%) in all age classes. Temporal comparisons among age classes indicate that sites with high initial browsing pressure are typically released from that pressure and recover to commercially valuable stands based on stocking rate.

2. At least 3 commercial species accounted for ≥50% of the species composition within each age class, the majority of which were classified as light to no damage. The proportion of non-commercial species declined as age class increased.

3. The proportion of plots containing a dominant commercial tree classified as hardwood declined with age class from 83 to 49%. Conversely, the proportion of plots containing a commercial dominant softwood stem increased with age class from 17 to 51%, possibly indicating a shift to softwood-dominated stands from selective over-browsing of hardwood species. It is possible a shift from hardwood to softwood may be the natural successional trend for these sites.

4. The proportion of dominant commercial trees >3.05 m (beyond browse height) and without severe damage (expected to recover during future growth) increased with age class to 39% in the 16-20 year age class; however, these values were less than in nearby New Hampshire where the average value was 71% in the oldest age class. This growth rate is likely reflective of higher moose density in Vermont.
5. Further assessment is warranted to evaluate compensatory tree growth in response to a reduction in browsing due to forest aging and/or moose population density.

Chapter 2: Analysis of physical characteristics of bull moose harvested in Maine, 1980-2009

6. There was no evidence of a measurable decline in the physical parameters (body weight and antler spread) of adult bull moose harvested in Maine from 1980-2009, as also measured in Vermont and New Hampshire.

7. Between 1980-1987 and 2005-2009 there was a 4-10% increase in mean body weight in the 4 youngest age classes ($P \leq 0.024$), and minimal change (1-2%, $P >0.05$) in the $\geq 5.5$ year old classes.

8. There was a slight increase (4.0-8.3%, $P \leq 0.014$) of mean antler spread in the 4 youngest age classes, with some variability but no clear trend in bulls $\geq 5.5$ years old.

9. Maximum mean weight of yearlings (225 kg) occurred in the 2005-2009 time period ($P \leq 0.002$). Yearlings were the only age class in which the current (2005-2009) mean antler spread ($60 \pm 15.9$ cm, $\bar{X} \pm SD$) exceeded the 30 year mean. The slight increase in physical characteristics of yearlings differs from the trend in New Hampshire and Vermont where it is speculated that parasitism by winter ticks affects recruitment and growth rate. Moose in northern Maine may be less affected due to longer winters that temper tick impact and density.

10. The proportion of trophy bulls (spread $\geq 137$ cm) in the harvest declined somewhat as harvest increased from 1980-1987 to 2005-2009 (8.8 to 5.9%). The mean spread of
trophy bulls declined by only 2% ($P = 0.003$) from 1980-1987 to 2005-2009, which presumably is biologically irrelevant.

11. There were no differences ($P >0.05$) in the proportion of harvested bulls within each age class between the 1980-1987 and 2005-2009 time periods; some variation occurred in the intermediary time periods.

12. The relatively stable proportion of mature bulls (>5 years old) in the harvest across time periods (30-44%) does not indicate increasing selective harvest towards older, trophy bulls. The majority (86-92%) of trophy bulls were between 5.5 - 12.5 years old in all time periods, indicating that the proportion of trophy bulls in each age class is likely not influenced by harvest pressure, but corresponds with expected maximum growth and senescence.

13. In the face of the declining regional population, continued monitoring of harvested moose is warranted to best manage the largest and longest harvested population in the northeastern United States.

Chapter 3: Using aerial survey observations to identify winter habitat use of moose in northern Maine

14. Habitat variables associated with locations of moose collected during aerial surveys were compared to available habitat at multiple landscape scales; variables included land cover classes, elevation, slope, aspect, proximity to cuts, and proximity to mature conifer. Mixed forest was the most used land cover type at both the location and 5 ha scales (35.1% and 31.3%, respectively).
15. Proximity to recent clearcuts, light partial cuts, and heavy partial cuts was an important predictor of moose location. However, regenerating forest habitat (recent clearcuts, partial cuts, regenerating forest, and scrub-shrub) was used in proportion to availability, although cut areas represented ~25% of the landscape overall.

16. Model selection performed with a mixed effects logistic regression model indicated moose presence was associated with a higher proportion of deciduous forest, shorter distance to cut, and smaller proportion of coniferous forest; this indicates abundance of food resources, not availability of cover, is likely the most important factor in predicting habitat use during the study period.

17. Elevation was higher (~11m), on average, for used units than available units. This may reflect avoidance of wetlands in winter as locations were associated with a smaller proportion of wetlands in comparison to available habitat. However, this minimal difference in elevation is likely biologically insignificant in the survey area.

18. The used proportion of coarse habitat variables (i.e., mature and regenerating forest) were similar to those available in each survey block, indicating that heterogeneous and good moose habitat is widely available across the commercial forest landscape of northern Maine.

19. Using moose locations derived from aerial surveys could provide further insight about the spatial distribution across the landscape, local density in areas with concern about forest regeneration, and temporal relationships between population responses and commercial forest management.


Bates, D.M. & Maechler, M. 2012. Lme4: Linear mixed-effects models using S4 classes. R Package Version 0.999999-0. http://cran.r-project.org/package=lme4


Carvell, K. L. 1967. The response of understory oak seedlings to release after partial cutting. West Virginia University Agricultural Experiment Station, Bulletin 553. Morgantown, West Virginia, USA.


______. 2012. Maine's Moose Population Estimated at 76,000 After New Survey. Maine Department of Inland Fisheries and Wildlife, Augusta, Maine, USA.

______. 2013. Report to the Joint Standing Committee on Inland Fisheries and Wildlife: Proposed Actions For Moose Management in Regards to the Number of Permits Issued, the Length and Timing of the Annual Moose Hunting Season. Maine Department of Inland Fisheries and Wildlife, Augusta, Maine, USA.


Wattles, D. W. 2011. Status, Movements, and Habitat Use of Moose in Massachusetts. M.S. Thesis. University of Massachusetts Amherst, Amherst, Massachusetts, USA.

### Regeneration Survey Data Sheet

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**Observer:** 

**Cut ID:** 

**Date:** 

**Cut Year:** 

**Cut Size:**

**Start Time:** 

**End Time:** 

**Start Coordinates:**

- **East:** 
- **North:** 
- **Start Bearing:** 
- **90°:**

**Plot**

**Commercial**

**Damage**

**Height**

**Non-Commercial**

**Damage**

**Height**

**Comments:**

---

**APPENDIX A. REGENERATION SURVEY DATA SHEET**

---

---
APPENDIX B. SPECIES COMPOSITION (%) AND BROWSE DAMAGE CATEGORY OF
DOMINANT STEMS BY AGE CLASS IN CLEARCUTS IN NORTHEAST VERMONT.

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APPENDIX C. MEAN (±SD) FIELD-DRESSED BODY WEIGHT (kg) OF BULL MOOSE HARVESTED IN MAINE BY TIME PERIOD AND AGE CLASS, 1980-2009.

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<th>1.5 yr</th>
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<td></td>
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<td>n</td>
<td>Mean Weight</td>
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<td>1988-1998</td>
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<td>316±37.3</td>
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</table>
APPENDIX D. MEAN (±SD) ANTLER SPREAD (cm) OF BULL MOOSE HARVESTED IN MAINE BY TIME PERIOD AND AGE CLASS, 1980-2009.

<table>
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<th>Time Period</th>
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<th>2.5 yr</th>
<th>3.5 yr</th>
<th>4.5 yr</th>
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<tbody>
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<td></td>
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<td>Mean Spread</td>
<td>n</td>
<td>Mean Spread</td>
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<td>82±14.1</td>
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<td>60±15.9</td>
<td>896</td>
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<td>805</td>
<td>92±14.9</td>
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APPENDIX E. CRITERION C (POPULATION COMPOSITION) OF THE MAINE MOOSE MANAGEMENT SYSTEM (MORRIS 2002).

CRITERION C: population composition

The third step needed to meet population goals is to determine if the composition of the herd is at the desired level. Two levels have been specified. WMD 11 is to have at least 38% bulls (60 bulls : 100 cows). In WMDs 1-10, 12-14, and 18, 19, 28, and 29 the population is to have 17% mature (over 4 years old) bulls.

Determine the composition of the moose herd from moose sightings reported by deer hunters and the ages of harvested animals using the following equations.

\[
\begin{align*}
\text{Eq. 5 } S &= \frac{B}{B+C} \times 100 \\
\text{Eq. 6 } A &= \frac{F}{T} \times 100 \\
\text{Eq. 7 } P &= \frac{B}{B+C} \times \frac{F}{T} \times 100
\end{align*}
\]

For equations 5-7,

\( S \) = Percentage of bulls in the population. Initially, use proportion of bulls to cows in sightings by deer hunter (pers. com. Bontaites and Gustafson).
\( A \) = Percentage of mature bulls\(^6\) among antlered bulls.
\( B \) = number of bulls seen by deer hunters
\( C \) = number of cows seen by deer hunters
\( T \) = number of bulls over 2 in the harvest
\( F \) = number of bulls over 5 in the harvest
\( P \) = Percentage of mature bulls\(^7\) in population.

Determine the status of the population structure.

For WMD 11:
If \( S < 38\% \) there are too few bulls in the population.
If \( S \geq 38\% \) the sex composition of the population is acceptable.

For WMDs 1-10, 12-14, and 18, 19, 28 and 29:
If \( P < 17\% \) there are too few mature bulls in the population.
If \( P \geq 17\% \) the sex and age composition of the population is acceptable.

\[\text{Eq. 7 } P = \frac{B}{B+C} \times \frac{F}{T} \times 100\]

\(^1\) Ideally, this is the percent of bulls over 4 years of age among adult and yearling bulls. However, because hunters select against yearlings, the percent of 2+ bulls in the harvest that are over 5 years old will be used as an estimate.
APPENDIX F. DESCRIPTION OF THE 7 LAND COVER CATEGORIES/HABITAT TYPES USED FOR ANALYSIS OF MOOSE LOCATIONS IN EARLY WINTER IN NORTHERN MAINE (MELCD 2004).

<table>
<thead>
<tr>
<th>Land Cover/Habitat Category</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crops/Grasslands/Blueberry</td>
<td>Areas of grasses, legumes or mixtures planted for grazing or crop production; areas dominated (&gt;80% total vegetation) by grasses or herbaceous vegetation, fields dominated by production of low-bush blueberries</td>
</tr>
<tr>
<td>Deciduous Forest</td>
<td>Dominated by trees greater than 5 meters tall and greater than 20 percent of total vegetation cover; more than 75% deciduous trees; frequent species include maple (Acer spp.), hickory (Carya spp.), oaks (Quercus spp.), and aspen (Populus tremuloides)</td>
</tr>
<tr>
<td>Coniferous Forest</td>
<td>Dominated by trees greater than 5 meters tall and greater than 20 percent of total vegetation cover; more than 75% coniferous trees; frequent species include pine (Pinus spp.), spruce (Picea spp.), and balsam fir (Abies balsamea)</td>
</tr>
<tr>
<td>Mixed Forest</td>
<td>Dominated by trees greater than 5 meters tall and greater than 20 percent of total vegetation cover; neither deciduous nor coniferous species account for more than 75% of total tree cover</td>
</tr>
<tr>
<td>Recent Cuts/Regenerating Forest/Scrub-Shrub</td>
<td>Areas harvested with &gt;90% canopy cover removal and expected to regenerate to forest; regenerating forest indicates previously harvested forested areas that have begun to regenerate and may include seedling to sapling sized trees with some residual trees present (forest loss and subsequent regrowth must have occurred after 1995); scrub-shrub areas are dominated by shrubs less than 5 meters tall with shrub canopy typically greater than 20% of total vegetation</td>
</tr>
<tr>
<td>Wetland</td>
<td>Palustrine scrub-shrub/emergent wetlands, estuarine scrub-shrub/emergent wetlands, and non-tidal wetlands dominated by woody vegetation</td>
</tr>
<tr>
<td>Partial Cuts</td>
<td>Light partial cuts (&lt;50% overstory removal) including improvement thinning, light shelterwood, and light selection harvests; heavy partial cuts (&gt;50% overstory removal) including heavy shelterwood and heavy selection harvests; forest loss must have occurred after 1995</td>
</tr>
</tbody>
</table>