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

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ABSTRACT: Winter habitat use by moose (*Alces alces*) is typically comprised of regenerating forest and softwood cover in the northeastern United States, and globally, high winter densities are of concern relative to forest damage. Habitat variables associated with winter locations of moose collected during aerial surveys in Maine in 2011 and 2012 were compared to available habitat at multiple landscape scales. Mixed forest was the most used land cover type at both the location and 5 ha scales (35.1% and 31.3%, respectively). Although regenerating forest habitat was used only in proportion to availability, the proximity to recent clearcuts, light partial cuts, and heavy partial cuts was an important predictor of moose location. The used proportion of coarse habitat variables (i.e., mature and regenerating forest) were similar to those available in each aerial survey block, indicating that heterogeneous and productive moose habitat is widely available across the commercial forest landscape of northern Maine. Moose locations derived from aerial surveys can provide insight about spatial distribution and habitat use across the landscape, identify local density in areas where forest regeneration is of concern, and monitor population responses to commercial forest management practices.

Key words: aerial surveys, *Alces alces*, winter, habitat use, moose, Maine

Moose (*Alces alces*) 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 selective use of certain habitats 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 forage and cover for moose (Leptich and Gilbert 1989, Scarpitti et al. 2005).

Although moose are reasonably mobile in typical winter conditions in northern New England, habitat use is influenced by weather, snow depth, forage availability, and cover. Moose minimize energy expenditure and reduce home range in winter (Peek 1997, Renecker and Schwartz 1997b), 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). The most significant landscape characteristic influencing winter locations in northeast Vermont was proximity to forest openings/timber cuts that presumably

provide important seasonal browse (Millette et al. 2014). 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 were associated with heavy browsing, limited growth, and regeneration of birch (*Betula spp.*) in Newfoundland (Bergerud and Manuel 1968), and low regeneration in specific cutover sites adjacent to traditional wintering areas in New Hampshire (Bergeron et al. 2011). It was predicted that such sites were shifting from hardwood to coniferous dominance in both northeast Vermont (Andreozzi et al. 2014) and northern New Hampshire (Bergeron et al. 2011).

Winter aerial surveys conducted by The Maine Department of Inland Fisheries and Wildlife (MDIFW) in 2011 and 2012 measured moose abundance in specific northern Wildlife Management Districts (WMD) with presumed high moose density (Kantar and Cumberland 2013), and additional surveys determined sex-age composition. Each observation had an associated GPS location providing the ability to identify and assess 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 populations.

This GIS analysis was conducted to measure habitat and landscape characteristics associated with locations of moose observed during winter aerial surveys in northern Maine. Millette et al. (2014), who originally measured moose abundance, used a similar approach to identify winter habitat use relationships in northern Vermont. The primary objectives were to identify the habitat type 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 encompassed those WMDs flown in each survey year: WMDs 2, 3 and 6 were flown in winters 2010 and 2011, and WMDs 1, 2, 3, 4, 5, 8, 11 and 19 in winters 2011 and 2012 (Fig. 1). The survey area totaled ~32,950 km^2 and included Aroostook County and northern portions of adjacent Franklin, Hancock, Penobscot, Piscataquis, Somerset, and Washington Counties which are 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), and 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 1; L. Kantar, unpublished data).

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 except
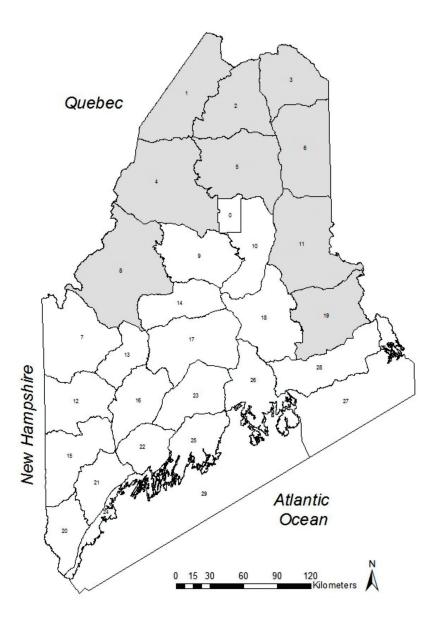
Fig. 1. Maine Wildlife Management Districts (shaded) used for double-count aerial surveys and sex-age composition surveys during winters 2011 and 2012, northern Maine, USA.

WMD 11 which was surveyed to evaluate the reliability of the survey technique at lower density. Survey blocks were 15 × 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 in the WMD. The double-count survey occurred

when moose mobility was unrestricted (snow depths <61 cm), ambient temperature was relatively cold (<−12 °C), and no obvious group-ing was evident (Kantar and Cumberland 2013); the same conditions were met during the composition surveys. Moose locations (n = 481; ≥1 moose/location) were acquired during abundance surveys in 2011

Table 1. Forest composition (%) of survey blocks within Wildlife Management Districts (WMD) flown in double-count and age-sex composition aerial moose surveys during winters 2011 and 2012, northern Maine, USA.

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

(28 January – 1 February) and 2012 (13 December 2011 – 8 February 2012), and composition surveys in 2012 (13 December 2011 – 3 February 2012) (Table 2). The GPS coordinates were collected at each observation location; the number of moose at each location ranged from 1 (n = 215, 45%) to 16 (n = 1), with groups >5 restricted to composition surveys.

Habitat Use

All GPS locations were defined as used locations and mapped in 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 2011) to represent available locations within each flight survey block. Because most moose were moving (disturbed) from the helicopter, and to evaluate a reasonable spatial scale of habitat use, a circular buffer (4.9 ha) was placed around each used and available location as a conservative estimate of diurnal habitat use; this buffer also accounted for any GPS error. The ~5 ha scale is representative of a circular polygon with a radius of 125 m that was the average

distance moved by moose in a 2-hour period in northwest Wyoming (Becker 2008).

Land cover types were identified using the Maine Landcover Dataset 2004 (MELCD:

Table 2. Survey dates and number of locations collected during aerial double-count and composition count surveys by WMD during winters 2011 and 2012, northern Maine, USA.

Date	WMD	Locations (n)
Double-count		
28-Jan-11	2	33
31-Jan-11	3	24
1-Feb-11	6	13
13-Dec-11	2	27
8-Jan-12	5	11
9-Jan-12	4	40
11-Jan-12	1	26
22-Jan-12	19	21
26-Jan-12	8	17
2-Feb-12	4	31
8-Feb-12	11	4
Composition count		
13-Dec-11	2	66
28-Dec-11	3	63
22-Dec-11	4	55
3-Feb-12	8	50

Maine Office of Geographic Information System 2004), and applied to 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 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 the U.S. Geological Survey was used to assess elevation, slope, and aspect.

Statistical Analysis

General linear mixed model (GLMM) analysis was performed using JMP software (SAS Institute, Cary, North Carolina, 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 habitat differences within WMDs. 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 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$_c$) scores; top competing models were those with ΔAIC$_c$ <2.0 and the best fitting model was determined by identifying the model with the lowest AIC$_c$ score and highest Akaike weight (Burham and Anderson 2002). Model parameter coefficients were averaged for top competing models (i.e., ΔAIC$_c$ <2.0) 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 $\overline{X} \pm SE$.

RESULTS

Habitat composition of used units was dominated (~95%) by 5 habitat variables that were similar (0–4% different) at the location and 5 ha scale. The primary composition 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 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 were found between used and available units at locations

and the 5 ha scale in the individual GLMM analyses of habitat variables. Used locations included more deciduous forest (7.3%, F = 8.92, P = 0.003) than 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. 2). 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. 2) 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. 2).

Used locations were in closer proximity to cuts (299.4 ± 66.8 m) than available locations (410.4 ± 66.8 m, P < 0.0001); similarly, at the 5 ha scale (P < 0.0001; Fig. 3) used units were closer to cuts (215.1 ± 62.2 m) than available units (319.1 ± 62.2 m). 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 (291.6 ± 39.4 m) than available locations (280.1 ± 39.4 m; P = 0.012), and likewise at the 5 ha scale (291.3 ± 39.6 m vs. 280.1 ± 39.6 m, P = 0.014). Directional aspect was
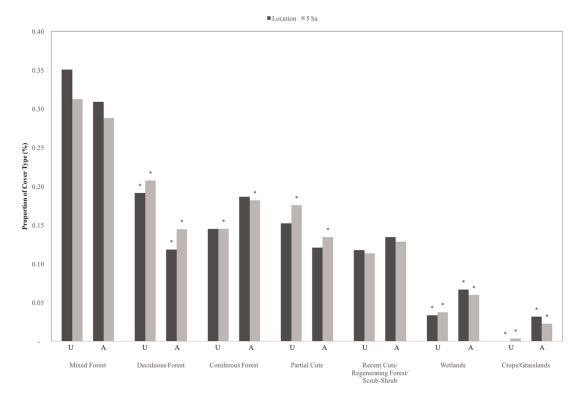

Fig. 2. Proportion (%) of cover types within used (U) and available (A) units for locations and the 5 ha landscape scale during winters 2011 and 2012 in northern Maine, USA. Units are starred (*) that are different (P < 0.05) within each cover type at the location and the 5 ha scale.
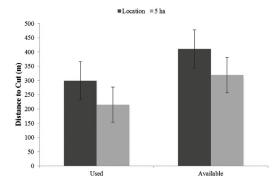
Fig. 3. Mean distance (m) to cuts of used and available units at locations and the 5 ha landscape scale during winters 2011 and 2012, northern Maine, USA. Distance was less ($P < 0.05$) at both used scales; bars reflect the SE.

not different ($P > 0.05$) at either scale, with the exception of northeast-facing slopes used less than available at locations (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 the analysis. There was no detectable difference in slope ($P > 0.05$) at either scale.

The habitat parameters used in the logistic regression mixed effects models were deciduous forest, coniferous forest, wetlands, distance to cuts, and elevation. The model that best explained (lowest AIC_c score) moose presence included deciduous forest, distance to cut, and wetlands at both the location and 5 ha scales (Table 3). Specifically, locations were most influenced by a higher proportion of deciduous forest ($\beta = 0.516$, $SE = 0.179$), shorter distance to cuts ($\beta = -0.269$, $SE = 0.072$), and smaller proportion of wetlands ($\beta = -0.596$, $SE = 0.318$); likewise, at the 5 ha scale used areas were most influenced by deciduous forest ($\beta = 0.180$, $SE = 0.066$), distance to cuts ($\beta = -0.197$, $SE = 0.054$), and wetlands ($\beta = -0.107$, $SE = 0.069$; Table 3). Models with ΔAIC_c <2.0 also included smaller

proportions of coniferous forest and elevation at both the location ($\beta = -0.209$, $SE = 0.184$ and $\beta = -0.029$, $SE = 0.071$, respectively) and 5 ha scales ($\beta = -0.086$, $SE = 0.069$ and $\beta = -0.044$, $SE = 0.072$, respectively; Table 3).

DISCUSSION

The collection of accurate moose locations during winter aerial surveys in Maine resulted in a robust dataset that, while time-specific, was efficient, relatively cheap compared to long-term collaring efforts, and repeatable. The number (n = 481) of locations (i.e., moose) and 5 ha areas analyzed in this study over a ~2 month time period was 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 km²) in early and late winter, respectively.

This modeling exercise indicated that proximity to regenerating forests in the form of recent clearcuts, light partial cuts, or heavy partial cuts is an important predictor of the location of moose during winter in northern Maine (Table 3, Fig. 3). 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), regenerating stands were used more than available in early winter in Massachusetts (Wattles 2011), and moose locations were influenced by the relative distance to forest openings associated with timber harvest in Vermont (Millette et al. 2014). Unlike in summer when high quality forage is available

Table 3. The total number of parameters (K), log likelihood statistic (logLik), AIC$_c$ score, delta AIC$_c$, and model weight for top competing location and 5 ha landscape scale models (i.e., delta AIC$_c$ scores <2), and the estimates and standard error (SE) for the model-averaged coefficients.

Locations					
Model selection based on AIC$_c$	K	logLik	AIC$_c$	Delta	Weight
Deciduous + Distance to Cut + Wetlands	5	−652.41	1314.87	0	0.40
Coniferous + Deciduous + Distance to Cut + Wetlands	6	−651.76	1315.61	0.73	0.28
Deciduous + Distance to Cut	4	−654.26	1316.55	1.68	0.17
Deciduous + Distance to Cut + Elevation + Wetlands	6	−652.32	1316.73	1.86	0.16
Model-averaged coefficients	Estimate	SE			
(Intercept)	−0.060	0.081			
Deciduous	0.516	0.179			
Distance to Cut	−0.269	0.072			
Wetlands	−0.610	0.318			
Coniferous	−0.209	0.184			
Elevation	−0.029	0.071			
5 ha Landscape Scale					
Model Selection based on AIC$_c$	K	logLik	AICc	Delta	Weight
Deciduous + Distance to Cut + Wetlands	5	−653.79	1317.65	0	0.24
Deciduous + Distance to Cut	4	−654.96	1317.96	0.31	0.21
Coniferous + Deciduous + Distance to Cut + Wetlands	6	−652.96	1318.00	0.36	0.20
Coniferous + Deciduous + Distance to Cut	5	−654.27	1318.60	0.95	0.15
Deciduous + Distance to Cut + Elevation + Wetlands	6	−653.64	1319.36	1.72	0.10
Coniferous + Deciduous + Distance to Cut + Elevation + Wetlands	7	−652.73	1319.57	1.92	0.09
Model-averaged coefficients	Estimate	SE			
(Intercept)	−0.032	0.066			
Deciduous	0.180	0.070			
Distance to cut	−0.197	0.054			
Wetlands	−0.107	0.069			
Coniferous	−0.086	0.069			
Elevation	−0.044	0.072			

in more habitat types (Scarpitti 2006), regenerating forests are preferentially used in winter because concentrated, abundant browse allows moose to forage efficiently (Belovsky 1981).

While the distance to cut was shorter for used than available units at both the location and 5 ha scales (Fig. 3), 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. 2).

Deciduous forests were preferentially used and were important in predicting locations (Fig. 2, Table 2). Winter habitat use in Maine is primarily influenced by food availability until snow depth becomes restrictive, and moose are commonly located where sufficient hardwood browse is available (Morris 1999). Moose feed mostly on deciduous vegetation (Renecker and Schwartz 1997a) 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). 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 in used than available units throughout the study area. The slightly higher elevation (~11 m) may reflect avoidance of wetlands in winter as used locations had a smaller proportion of wetlands than available habitat (Table 3). Wetland habitats at lower elevations may be important predictors of moose locations from late spring through autumn when insects, thermoregulation, and aquatic forage influence habitat use, but play no role in winter habitat selection (Peek et al. 1976, Peek 1997). Previous research in Maine found that moose moved from lowland (<305 m) into mid-elevation areas (367–427 m) in early winter, and occurred at slightly higher elevations later in winter (Thompson et al. 1995). However, the ~11 m difference in elevation that we measured is probably biologically insignificant.

Trends in used habitat variables were similar at 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 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 4). Northern Maine is considered high quality moose habitat due to commercial timber harvesting that produces stands of varying age and size providing adequate forage and cover throughout the region, and this heterogeneous

Table 4. A comparison of the mean proportion (%) ± SE of coarse cover types (i.e., mature and regenerating forest) within used units at locations and within the 5 ha landscape scale and the proportions within survey blocks during winters 2011 and 2012, northern Maine, USA.

	Proportion Mature Forest (%)		
WMD	Location (used)	5 ha (used)	Survey block
1	73.1 ± 8.9	70.7 ± 6.8	68.0
2	73.0 ± 4.0	75.8 ± 3.1	72.6
3	80.5 ± 4.3	77.5 ± 3.1	72.4
4	57.8 ± 5.2	57.8 ± 4.2	55.4
4	54.8 ± 9.1	50.0 ± 7.3	55.9
5	90.9 ± 9.1	70.1 ± 11.5	70.4
6	53.8 ± 14.3	62.6 ± 11.6	65.0
8	52.8 ± 5.9	52.4 ± 4.5	65.9
11	100.0 ± 0.0*	80.2 ± 7.7	69.8
19	76.2 ± 9.5	73.9 ± 7.9	71.2

	Proportion Regenerating Forest (%)		
WMD	Location (Used)	5 ha (Used)	Survey block
1	26.9 ± 8.9	25.7 ± 6.9	28.1
2	24.6 ± 3.9	22.3 ± 3.0	22.8
3	17.2 ± 4.1	17.6 ± 3.0	13.6
4	41.1 ± 5.2	40.9 ± 4.2	35.6
4	35.5 ± 8.7	42.9 ± 7.5	37.2
5	9.1 ± 9.1	23.2 ± 11.0	23.4
6	15.4 ± 10.4	9.6 ± 6.1	8.7
8	40.3 ± 5.8	40.5 ± 4.4	31.5
11	0.0 ± 0.0	18.1 ± 8.0	19.5
19	19.0 ± 8.8	20.9 ± 6.9	18.9

*Small sample size (n=4) likely influenced proportions.

habitat is key to the current high regional population (MDIFW 2012).

Because moose browsing can substantially alter plant communities and affect the structure and dynamics of forest ecosystems (McInnes et al. 1992, Renecker and Schwartz 1997a), 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 scale (Dussault et al. 2005, Månsson et al. 2007). Integrated management of an abundant moose population with commercial forestry in northern Maine requires balancing moose density with their potential post-harvest influence on forest regeneration and stand composition (Bergeron et al. 2011, Andreozzi et al. 2014).

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). 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 about the effects of heavy clearcutting in the 1970s and 1980s, particularly in response to a substantial spruce budworm (*Choristoneura fumiferana*) outbreak (Griffith and Alerich 1996), resulted in the Maine Legislature passing The Maine Forest Practices Act in 1989 (Maine Forest Service 1999). This act limited the size of clearcuts (<250 acres) and led to a dramatic shift from clearcutting to partial harvests beginning in the early 1990s; for example, ~93% of the 444,339 acres harvest in Maine was defined as partial harvest in 2011 (Maine Forest Service 2011). This harvest practice will presumably produce abundant and patchily distributed 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/km^2; Kantar and Cumberland 2013) may reflect such habitat change.

Analyses and modeling with data from single locations of individuals, rather than continuous locations from radio-collared animals, pose some concern and limitation for application across spatial and temporal scales. However, our habitat use information was analogous with past regional studies, and importantly, was labor efficient and provided added value to annual surveys. Subsequent surveys in the same WMDs should identify temporal changes in moose abundance and distribution important in developing management strategy. Expansion and continuation of such analyses should also prove useful in examining the spatial distribution of moose across the landscape, the concentration of moose in habitat vulnerable to browsing damage, and long-term temporal relationships between moose population responses and timber harvesting practices in northern Maine.

REFERENCES

ANDERSON, D. R., W. A. LINK, D. H. JOHNSON, and K. P. BURNHAM. 2001. Suggestions for presenting the results of data analyses. The Journal of Wildlife Management 65: 373–378.

ANDREOZZI, H. A., P. J. PEKINS, and M. L. LANGLAIS. 2014. Impact of moose browsing on forest regeneration in northeast Vermont. Alces 50: 67–79.

BARTON, K. 2013. MuMIn: multi-model inference. R package version 1.9.0 http://cran.r-project.org/package=MuMIn (accessed July 2013).

BATES, D. M., and M. MAECHLER. 2012. Lme4: linear mixed-effects models using S4 classes . R Package Version 0.999999-0 http://cran.r-project.org/package=lme4 (accessed July 2013).

BECKER, S. A. 2008. Habitat selection, condition, and survival of Shiras moose in northwest Wyoming. M.S. Thesis. University of Wyoming, Laramie, Wyoming, USA.

BELOVSKY, G. E. 1981. Food plant selection by a generalist herbivore: the moose. Ecology 62: 1020–1030.

BERGERON, D. H., P. J. PEKINS, H. F. JONES, and W. B. LEAK. 2011. Moose browsing and forest regeneration: a case study in northern New Hampshire. Alces 47: 39–51.

BERGERUD, A. T., and F. MANUEL. 1968. Moose damage to balsam fir-white birch forests in central Newfoundland. The Journal of Wildlife Management 32: 729–746.

BURHAM, K., and D. ANDERSON. 2002. Model Selection and Multivariate Inference: A Practical Information–Theoretical Approach. Springer-Verlag, New York, New York, USA.

DUSSAULT, C., R. COURTOIS, J. P. OUELLET, and I. GIRARD. 2005. Space use of moose in relation to food availability. Canadian Journal of Zoology 83: 1431–1437.

——, C., and J. OUELLET. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. Ecoscience 11: 321–328.

ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute. Redlands, California, USA.

GRIFFITH, D. M., and C. L. ALERICH. 1996. Forest Statistics for Maine, 1995. USDA Forest Service Northeastern Forest Experiment Station Resource Bulletin NE-135. Radnor, Pennsylvania, USA.

HEIKKILA, R., P. HOKKANEN, M. KOOIMAN, N. AYGUNEY, and C. BASSOULET. 2003. The impact of moose browsing on tree species composition in Finland. Alces 39: 203–213.

HUNDERTMARK, K. J. 1997. Home range, dispersal and migration. Pages 303–336 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institute Press, Washington, D.C., USA.

JMP. 2012. Version 10. SAS Institute Inc., Cary, North Carolina, USA.

KANTAR, L. E., and R. E. CUMBERLAND. 2013. Using a double-count aerial survey to estimate moose abundance in Maine. Alces 49: 31–39.

KARNS, P. D. 1997. Population distribution, density and trends. Pages 125–140 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institute Press, Washington, D.C., USA.

LEPTICH, D. J., and J. R. GILBERT. 1989. Summer home range and habitat use by moose in northern Maine. The Journal of Wildlife Management 53: 880–885.

MAINE FOREST SERVICE. 1999. Forest Regeneration and Clearcutting Standards: MSF Rules, Chapter 20. Augusta, Maine, USA.

——. 2011. Silvicultural Activities Report: Including Annual Report on Clearcutting and Precommercial Activities. Department of Agriculture, Conservation and Forestry, Forest Policy and Management Division, Augusta, Maine, USA.

MAINE OFFICE OF GEOGRAPHIC INFORMATION SYSTEM. 2004. Maine Land Cover Dataset. Augusta, Maine, USA.

MÅNSSON, J., H. ANDREN, Å. PEHRSON, and R. BERGSTRÖM. 2007. Moose browsing and forage availability: a scale-dependent relationship? Canadian Journal of Zoology 85: 372–380.

MASTENBROOK, B., and H. CUMMING. 1989. Use of residual strips of timber by moose within cutovers in northwestern Ontario. Alces 25: 146–155.

MCINNES, P. F., R. J. NAIMAN, J. PASTOR, and Y. COHEN. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73: 2059–2075.

MDIFW (MAINE DEPARTMENT OF INLAND FISHERIES AND WILDLIFE). 2012. Maine's Moose Population Estimated at 76,000 After New Survey. Maine Department of Inland Fisheries and Wildlife, Augusta, Maine, USA.

MILLER, B. K. 1989. Seasonal movement patterns and habitat use of moose in northern New Hampshire. M.S. Thesis. University of New Hampshire, Durham, New Hampshire, USA.

MILLETTE, T. L., E. MARCANO, and D. LAFLOWER. 2014. Winter distribution of moose at landscape scale in northeastern Vermont: a GIS analysis. Alces 50: 17–26.

MORRIS, K. I. 1999. Moose Assessment. Maine Department of Inland Fisheries and Wildlife, Augusta, Maine, USA.

PEEK, J. M. 1997. Habitat Relationships. Pages 351–375 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American Moose. Smithsonian Institute Press, Washington, D.C., USA.

——, D. L. URICH, and R. J. MACKIE. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildlife Monographs 48: 3–65.

R DEVELOPMENT CORE TEAM. 2013. R: a language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/ (accessed July 2013).

RENECKER, L. A., and C. C. SCHWARTZ. 1997a. Food habits and feeding behavior. Pages 403–439 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American Moose. Smithsonian Institute Press, Washington, D.C., USA.

——, and ——. 1997b. Nutrition and energetics. Pages 403–439 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American

Moose. Smithsonian Institute Press, Washington, D.C., USA.

SCARPITTI, D. 2006. Seasonal home range, habitat use, and neonatal habitat characteristics of cow moose in northern New Hampshire. M.S. Thesis. University of New Hampshire, Durham, New Hampshire, USA.

——, C. HABECK, A. R. MUSANTE, and P. J. PEKINS. 2005. Integrating habitat use and population dynamics of moose in northern New Hampshire. Alces 41: 25–35.

TELFER, E. S. 1970. Winter habitat selection by moose and white-tailed deer. Journal of Wildlife Management 34: 553–559.

THOMPSON, M. E., J. R. GILBERT, G. J. MATULA, JR., and K. I. MORRIS. 1995. Seasonal habitat use by moose on managed forest lands in northern Maine. Alces 31: 223–245.

VIVAS, H. J., and B.-E. SAETHER. 1987. Interactions between a generalist herbivore, the moose (*Alces alces*), and its food resources: an experimental study of winter foraging behaviour in relation to browse availability. Journal of Animal Ecology 56: 509–520.

WATTLES, D. W. 2011. Status, movements, and habitat use of Moose in Massachusetts. M.S. Thesis. University of Massachusetts Amherst, Amherst, Massachusetts, USA.

WESTWORTH, D., L. BRUSNYK, J. ROBERTS, and H. VELDHUZIEN. 1989. Winter habitat use by moose in the vicinity of an open pit copper mine in north-central British Columbia. Alces 25: 156–166.