COMPOSITIONAL ANALYSIS OF MOOSE HABITAT IN NORTHEASTERN MINNESOTA

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ABSTRACT: It is well accepted that moose (*Alces alces*) often use early successional habitats in the boreal forest. It is not clear, however, whether use of disturbed habitats represents a preference or simply that moose are more detectable. Previous research based on visual observations assumed that moose were equally detectable in all cover types. We evaluated habitat selection of moose in northeastern Minnesota using telemetry locations and Land-Use Land-Cover (LULC) type information. We calculated measures of habitat selection within their home range (third-order) and selection of habitats to create a home range (second-order) using a technique called composition analysis. The analyses indicated that the Cutover cover type ranked highest in summer and winter in both second- and third-order selection and its rank generally was significantly higher than most other cover types. Selection for aquatic habitats during the summer was not evident in our analysis. Cover types that could provide lower operative temperatures from shade ranked higher than aquatic cover types. Inferences from these analyses should be treated with caution because of inherent weaknesses of use-availability analyses and biases associated with VHF telemetry locations.

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Habitat management for moose (*Alces alces*) in the boreal forest is predicated on the inference that early successional habitats created by disturbance (e.g., forest fire, logging, and wind or insect damage) are preferred habitats and that they result in higher moose numbers (Aldous and Krefting 1946, Spencer and Chatelain 1953, Krefting 1974, Peek et al. 1976). While it is clear that moose often use disturbed habitat, it is not clear whether this use represents a preference or simply that moose are more detectable in this cover type. Early successional habitats tend to be more open which can increase the visibility of moose and present a bias. It is likely that the high quality forage available in early successional habitats should benefit moose if the population is food limited. However, even with good hypothetical explanations of why moose would benefit from this association, until this preference can be demonstrated empirically, continued repetition has the potential of leading to dogmatic thinking (Romesburg 1981). To more clearly evaluate the importance of disturbance to moose habitat, analyses require data in which animals have an equal probability of being detected in all habitats.

Aquatic habitat has also been noted as preferred habitat in much of the boreal forest because moose are commonly observed feeding in ponds and lakes from late May to mid-August (Murie 1934, Peterson 1955, DeVos 1956). While not ubiquitous in the boreal forest, most authors suggest that these habitats are preferred (Peek 1997). As with early successional habitats, aquatic habitats tend to be more open resulting in a higher detection rate for moose. It has been reasoned that moose use these habitats for the high quality forage, the sodium content of this forage, insect relief, and possibly for relief from warmer temperatures (Ritcey and Verbeek 1969, Peek et al. 1976, Jordan 1987, Peek 1997).

Cover for shade may also be important to moose in summer. Based on metabolic research, Renecker and Hudson (1986) indicated that moose are intolerant of heat but superbly adapted to cold and that summer temperatures may well define their southerly distribution. Recent research has suggested that warming temperatures associated with climate change may be linked to the increased mortality observed in moose populations found along the southern edge of their distribution (Murray et al. 2006; Lenarz et al. 2009, 2010). Microclimate can vary substantially in different cover types (Ackerman 1987, Schwab and Pitt 1991, Demarchi and Bunnell 1993, Dussault et al. 2004, McGraw 2011) and moose shift to more shaded habitats as temperatures rise above some metabolic threshold (Ackerman 1987).

Habitat selection can take place at several different scales. The geographic range of a species, for example, represents first-order selection (Johnson 1980), and second-order selection determines the home range of an individual or social group within that range. The use of various habitat components within the home range represents third-order. Based on the preceding interpretations, moose should select summer home ranges that contain early successional habitats and aquatic habitat for food and shaded habitat to prevent overheating. During the winter, moose should select primarily for early successional habitats as a source of food.

A clear understanding of how moose utilize their habitat is needed for management. This information is difficult to determine entirely from direct observations which are subjected to visibility biases. Even during winter under ideal snow and light conditions, visual obstruction due to forest cover results in many moose being missed (e.g., roughly 50% of moose were missed during helicopter surveys in Minnesota; Giudice et al. 2011, Lenarz, unpubl. data). Unbiased determination of habitat utilization requires the use of VHF or GPS telemetry.

In the following we report from results of a VHF telemetry study in northeastern Minnesota. Although the study was designed to document annual adult moose mortality, the telemetry locations of radioed individuals should provide insights into moose habitat use in northeastern Minnesota. The primary objective of this analysis was to determine whether this regional moose population displayed third-order seasonal selection for specific cover types. We also examined whether moose exhibited second-order seasonal selection relative to the cover types available in northern Minnesota.

METHODS

Study Area

The 3,953 km^2 study area was defined by telemetry locations for moose in northeastern Minnesota (47°30'N, 91º21'W; Fig. 1). The forests were transitional between Canadian boreal forests and northern hardwood forests common further south (Pastor and Mladenoff 1992). Wetlands, including bogs, swamps, small to medium-sized lakes, and small streams are interspersed throughout. The study area is on a low plateau that rises abruptly from Lake Superior and reaches about 700 m above sea level (Heinselman 1996). A northeast-southwest continental divide runs down the middle of the plateau with water flowing southeast into Lake Superior or northwest into Hudson Bay.

The study area was primarily a mosaic of mixed wood (39%), conifer (23%), and bog (11%, Table 1) classified as the Northern Superior Upland section (Minnesota Department of Natural Resources [MNDNR] 2007). The main conifer species were northern white cedar (*Thuja occidentalis*), black spruce (*Picea*

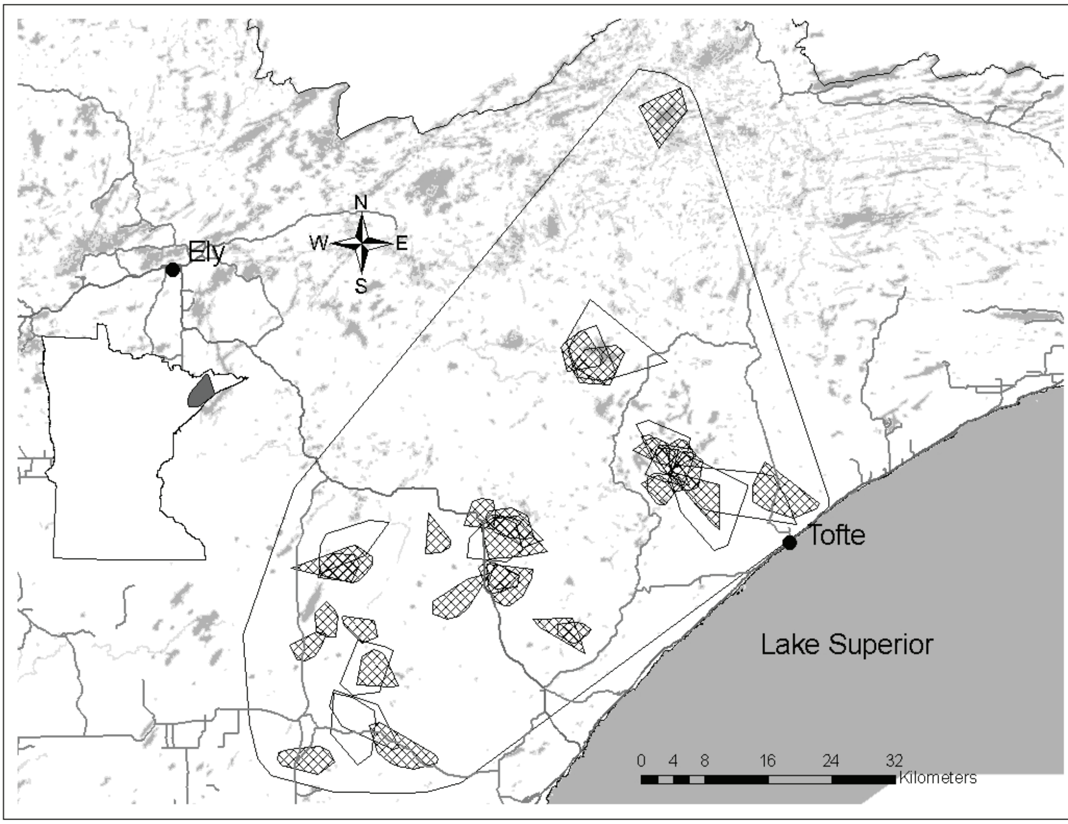

Fig.1. Study area used in composition analysis of moose in northeastern Minnesota, USA, 2002-2010. The large polygon represents available habitat for second-order analysis. Small open polygons represent 95% MCP home ranges during the winter; cross-hatched polygons represent 95% MCP home ranges during the summer.

mariana), and tamarack (*Larix laricina*) on the lowlands and balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and jack (*Pinus banksiana*), white (*P. strobus*), and red pine (*P. resinosa*) on the uplands. Deciduous species, primarily quaking aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*), occurred on the uplands in hardwood stands or were intermixed with the conifers.

The majority of land within the study area (74%) fell within the Superior National Forest with the balance in state, county, or private ownership. The area was sparsely inhabited and communities within the study area contained <100 permanent residents. Hunting is restricted by permit and <2% of the estimated population is harvested annually (MNDNR 2011).

July is the warmest month in the study area with an average high temperature of 26° C and January the coldest with an average high temperature of -10° C (NOAA 2001-2010). Total annual precipitation averaged 71 cm with 55% occurring between June and September. Precipitation usually occurred as snow between late October and mid-April and snow sometimes accumulated >100 cm (NOAA 2001-2010).

Study Animals and Telemetry

We captured and handled moose according to methods described by Lenarz et al. (2009). Between 2002 and 2008, we captured adult male and female moose (≥1.7 yr old) in early February or March by helicopter net-gunning (2002, Wildlife Capture Services, Marysvale,

Table 1. Land Use Land Cover (LULC) data, cover types used in the analyses, and the proportion of each cover type within the study area in northeastern Minnesota.

LULC Cover Data	Cover Type	Proportion	Mean Patch Size (ha)	Final Cover Type	Proportion
Mixed-wood forest	Mixed Forest	38.60%	6.1	Mixed	38.60%
Conifer forest	Conifer Forest	22.50%	2.7	Conifer	22.50%
Wetlands - bogs	Bog	11.20%	6.8	Bog	11.20%
Regeneration/young forest	Cutover	6.90%	3.3	Cutover	6.90%
Open water	Water	6.10%	4.4	Aquatic	9.50%
Deciduous forest	Deciduous Forest	6.00%	6.9	Deciduous	9.00%
Marshes and fens	Marsh	3.40%	1.8	Aquatic	
Shrubby grassland	Shrub	0.20%	6.3	Other	2.30%
Grassland	Shrub			Other	
Gravel pits and open mines	Other	0.30%	0.5	Other	
Bare rock	Other			Other	
Cultivated land	Other			Other	
Farmsteads	Other			Other	
Other rural development	Other			Other	
Urban/Industrial	Other			Other	
	Hardwood Regen.*	3.00%	0.5	Deciduous	
	Blowdown*	1.30%	1.2	Other	
	Conifer Regen.*	0.50%	0.2	Other	

*Data from P. T.Wolters (unpublished data).

Utah) or darting (2003-2005 and 2008, Quicksilver Air, Inc., Fairbanks, Alaska). We fitted each moose with a VHF radiocollar (Advanced Telemetry Systems, Isanti, Minnesota). From February 2002-May 2009 we located each moose approximately once weekly ($\bar{x}$ = 7.7 days, SE = 0.177, n = 346) from fixed-wing aircraft and recorded a GPS location. Moose were observed visually on ~28% of the locations. Animal capture and handling protocols met the guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007).

The use of point data that ignores locational error increases the risk of drawing erroneous conclusions about relative preference (Retti and McLouglin 1999). To identify error, we conducted blind tests of locational error by positioning test collars in trees throughout the study area. The error distances were right-skewed, with a few large values (n = 50, median = 254 m, g_1 = 3.6) best represented by a log normal distribution. We estimated parameters of this distribution using maximum likelihood with built in non-linear optimizers in Program R (R Development Core Team 2006). Because mean patch size (Table 1) was generally quite small relative to the telemetry error, there was an increased probability of habitat misclassification at the telemetry location. As recommended by Samuel and Kenow (1992), we used a subsampling approach in which the error distribution (log normal) was used to simulate a subsample of all possible points surrounding each telemetry location. This procedure reduces the bias associated with misclassification (Samuel and Kenow 1992). For each telemetry location we simulated 100 points using a random angle between 0 and 360° and a random distance chosen from the fitted log normal distribution. Because of small patch size (Table 1) and potential GPS error (moose occasionally moved in response to the aircraft), we used this approach even when moose were observed visually.

Habitat Availability and Use

We classified telemetry locations according to season with locations dated 1 October-31 March assigned as "winter" and the remainder of the year as "summer." While these dates were not ideal from a life history standpoint, they did maximize the number of radioed moose that could be included in the seasonal analyses. We censored moose which dispersed out of the study area or displayed distinct migratory behavior from further analysis. We calculated 95% minimum convex polygon (MCP) seasonal home ranges based on telemetry points (not including simulated points) for each moose using Home Range Tools for ArcGIS (Rodgers et al. 2007). This procedure was used to identify outlier points (1 to 3 per seasonal MCP) by calculating the mean of all x and y coordinates for an individual moose and then selecting 95% of the points closest to this mean (Rodgers et al. 2007). We then censored moose with fewer than 30 seasonal telemetry points. We tested for differences in MCP size using a linear fixed effects model using Program R (R Development Core Team 2006).

For the third-order analyses, we used the cover type at the telemetry and simulated points to calculate proportional habitat "use" for each moose in each season. We calculated the seasonal MCP home range for each moose based on telemetry locations and simulated points. The proportion of each cover type within an MCP represented "availability" for an individual moose.

For the second-order analyses, we used the proportion of each cover type within a seasonal home range as "use" (availability in the third-order analyses). We defined "availability" as the proportion of each cover type within a polygon calculated as the MCP from the pooled points (both seasons, telemetry, and simulated) of all moose included in the analysis (Fig. 1). Hereafter, this polygon that represents "availability" for both seasonal second-order analyses (Fig. 1) is referred to as the study area.

To classify habitat we created a vegetative cover layer using a land use-land cover (LULC) raster layer provided by MNDNR (1998a, b). This source layer was derived from LANDSAT 30-meter thematic satellite imagery dated summers 1991-1996, divided into 16 LULC classes based on imagery dated 1995 and 1996, then further processed to replace Transportation class values with surrounding values (MNDNR 1998a, b). Overall classification accuracy was assessed at ≥95% (MNDNR 1998b). In ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) we used the Reclassify command to combine these 15 classes into 9 classes (Table 1). Forest disturbance data (unpublished) obtained from P. T. Wolters (University of Minnesota, Duluth) were comprised of 3 classes of regenerating forests: deciduous and coniferous logging activities (1975-2000) and blowdown that occurred during a 1999 windstorm. Incorporating these data using the Mosaic command with the Last option allowed us to further refine the vegetative cover layer. Finally, we used the ArcGIS Spatial Analyst Extract Values to Points command to identify the cover type at each telemetry location and simulated point.

The study area was composed primarily of the Mixed, Conifer, and Bog cover types and they made up >72% of the total area (Table 1). The Mixed cover type had a mature canopy that was composed of approximately equal amounts of hardwood and conifer species. Forest with a canopy ≥67% conifer species was classified as Conifer cover type and was primarily upland conifers including balsam fir and jack, white, and red pine. Bog was characterized as peat lands with a high water table and varying amounts of tree cover, typically white cedar, black spruce, or tamarack. The Deciduous forest included areas with at least 67% canopy cover of woody deciduous species, primarily white birch and quaking aspen. Cutover represented areas where commercial timber was removed in 1980-1995. The Marsh cover type was composed of grassy, wet areas with standing or slowly moving water. Water covered about 6% of the area and represented permanent water bodies such as lakes, rivers, and ponds. The Other cover type represented an amalgam of covers such as bare rock, gravel pits, and rural development and represented only 0.3% of the study area.

Habitat Selection

We used compositional analysis (Aebischer et al. 1993) to determine seasonal second- and third-order selection of 12 cover types by moose. This technique uses the individual animal as the sampling unit and compares proportional habitat use with proportional habitat availability. Hypothesis testing of the nonstandard multivariate data is done using MANOVA/MANCOVA-type linear models (Aitchison 1986). Aebischer et al. (1993) indicated that a minimum of 6 animals were necessary for statistical inferences; we combined sexes because we had data on 26 females but only 3 males (Table 2). Missing data occurred in 2 situations: 1) a particular habitat was available but not used, and 2) a particular habitat was not available for use by an individual. In the first case, Aebischer et al. (1993) recommended that zero use should be replaced with a small positive value, less than the smallest recorded nonzero proportion. In the first case, Bingham and Brennan (2004) and Bingham et al. (2007) found that replacing zero use with a small positive value increased the potential for Type I error and could lead to a systematic bias. The authors recommended reclassifying habitat categories so that no habitat categories with 0% use are included in the analysis. In our analysis, we combined cover types with no use to the most similar type with use. Hardwood regeneration was added to Deciduous (hereafter termed Deciduous), Conifer Regeneration, Shrub, and Blowdown were added to Other, and Water was added to Marsh to form the Aquatic category (Table 1). In the second case, Aebischer et al. (1993) indicated that one approach was to delete the animal but cautioned the resultant loss of information could induce bias. Because specific cover types were not available for 3 moose (1 moose had no Cutover and 3 moose had no Other cover type available), we dropped these individuals from the analyses. Analyses were conducted in SAS using the program BYCOMP.SAS (Ott and Hovey 1997).

RESULTS

Home range size as measured with the 95% MCP (not including simulated points) varied according to season and sex with the largest home ranges occurring among males and during winter (Table 2). Only 4% of the 90 radioed moose (for which we had ≥30 telemetry locations) in northeastern Minnesota were classified as migratory (distinctly separated seasonal ranges); an additional 2% exhibited dispersal (permanent one-way shifts) and 18% displayed exploratory movements (returned to original home range) of up to 77 km. In female moose, the winter home range averaged 30.4 km^2 (SE = 6.0, n = 12) and during the summer 13.6 km^2 (SE = 1.9, n = 23). Average annual home range for females was 29.9 km^2 (SE = 3.3, n = 26). In male moose, the winter home range averaged 44.2 km^2 (SE = 13.3, n = 3), during the summer 29.4 km^2 (SE = 1.6, n = 3) and annual home range averaged 58.0 km^2 (SE = 15.1, n = 3). Home range size differed between seasons (t = 4.036, P = 0.002) and between sexes (t = -2.417, P = 0.002).

Third-order selection

Seasonal cover type selection was not random. During winter male and female

Table 2. Annual and seasonal home range size (95% MCP) of moose in northeastern Minnesota, USA, 2002-2009. Compositional analyses were conducted only on the seasonal data.

		Summer (n = 26)		Winter (n = 15)		Annual (n = 29)	
Moose ID	Sex	# Locations	95% MCP (km^2)	# Locations	95% MCP (km^2)	# Locations	95% MCP (km^2)
41430	F	43	18.9	47	72.2	86	69.9
41530	F	53	26.2	47	31.0	95	55.4
41620	M	39	32.2	42	70.8	77	87.8
41720	F	37	7.5	-	-	62	42.2
42030	F	43	13.5	-	-	66	42.7
43640	F	31	17.5	-	-	52	19.6
43840	F	-	-	30	36.1	61	64.3
44620	F	60	17.5	52	13.3	107	21.9
45020	F	46	8.3	47	12.3	89	13.0
45530	M	35	26.6	30	31.9	62	46.6
45830	F	35	9.3	-	-	59	36.1
46530	F	31	8.7	-	-	49	13.5
46740	F	52	23.7	50	70.1	97	47.0
47140	M	42	29.4	47	29.9	85	39.5
47522	F	36	21.9	30	13.1	61	17.1
48310	F	37	12.8	-	-	64	17.9
48430	F	32	9.3	-	-	48	16.4
49120	F	49	16.7	41	30.7	86	35.2
49430	F	32	6.0	36	23.5	65	18.3
49640	F	-	-	30	13.8	52	18.1
49820	F	34	8.0	-	-	51	8.9
50550	F	31	9.8	-	-	49	18.2
51120	F	31	9.7	-	-	50	20.1
51830	F	38	11.1	-	-	62	19.8
52030	F	58	15.8	52	21.8	105	26.0
52420	F	37	9.3	-	-	57	22.6
52630	F	33	19.8	-	-	58	52.4
52933	F	34	12.6	-	-	55	32.5
53440	F	-	-	32	26.4	62	27.2
Mean		40	15.5	41	33.1	68	32.8

moose used proportionately more Cutover and Mixed cover types than was available in their winter home ranges (Fig. 2). Proportional use of Bog, Conifer, and Other cover types was close to the proportion available. Proportional use of Deciduous and Aquatic cover types was substantially less than the proportion available. During summer proportional use of the Cutover cover type was substantially higher than available in the summer home range, and use of Conifer was slightly higher than availability (Fig. 2). Use of Mixed, Deciduous, Aquatic,

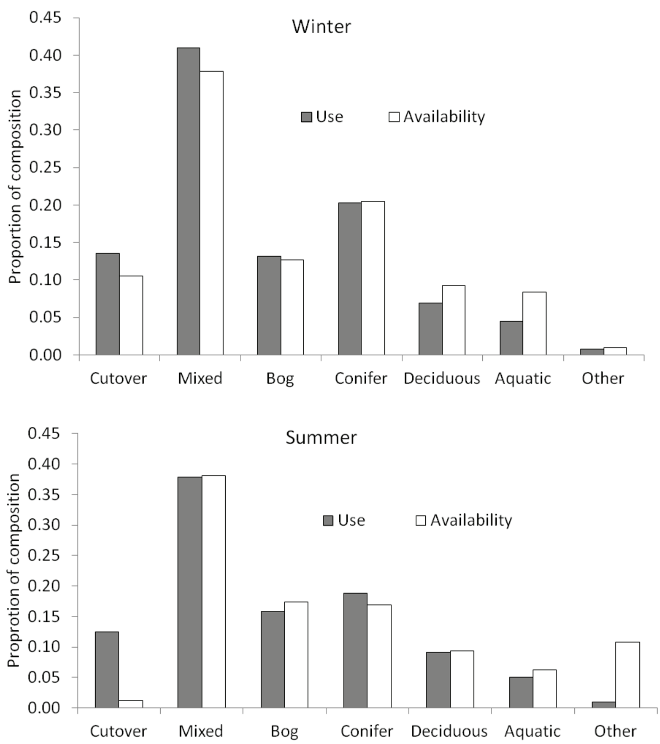

Fig. 2. Third-order selection (i.e., comparing cover type composition of simulated locations to the cover type composition of the individual home range) by moose in northeastern Minnesota, USA, 2002-2010. Habitats are arranged from most to least preferred for winter and summer. Gray bars indicate mean proportional utilization and white bars represent mean proportional habitat available.

and Bog cover types was slightly lower than the proportion available. Proportional use of the Other cover type was substantially lower than what was available.

Compositional analysis indicated that during winter Cutover had the highest rank among the 7 cover types, and the Aquatic cover type had the lowest rank (Table 3). There was no detectable difference between proportional use of Cutover and all of the remaining cover types except Deciduous and Aquatic, implying that the order of their assigned ranks (among Cutover, Mixed, Bog, Conifer, and Other) means little. The proportional use of the Aquatic cover type was significantly less than any other cover types except Other. During summer Cutover cover was used significantly more than all other cover types, and use of Other was significantly less than all other cover types.

Second-order selection

Analyses indicated the home ranges selected by northeastern moose were not random. In winter the average home range contained a substantially higher proportion of Cutover and a lower proportion of Conifer and Other cover types than was available in the study area (Fig. 3). The other cover types were present in about the same proportion as their availability. During summer the average home range contained more Cutover and Bog than available, and both Mixed and Deciduous cover types were found in proportions similar to their availability (Fig. 3). There was less Conifer, Aquatic, and Other cover types in the average summer home range than was found in the summer study area.

Compositional analysis indicated that Cutover again had the highest rank in winter home ranges, and was significantly higher than all other cover types (Table 4). In contrast, Other had the lowest rank and its presence was significantly less than all other cover types. A similar pattern existed in summer; Cutover had the highest rank and was significantly higher than all other cover types except Bog, whereas Other had the lowest rank and was significantly lower than Cutover, Bog, Mixed, and Conifer cover types.

DISCUSSION

The area of MCP seasonal and annual home ranges for moose in northeastern Minnesota were comparable to those reported for non-migratory moose found elsewhere in North America (Hundertmark 1997), but larger than those of moose in northwestern Minnesota

Table 3. Simplified ranks and randomized P values of third-order selection of moose in northeastern Minnesota, USA, 2002-2010. Gray cells represent $P < 0.05$. The order of cover types represents rank with cutover having the highest rank

Winter	Cutover	Mixed	Bog	Conifer	Deciduous	Other	Aquatic	Rank
Cutover	*	0.745	0.770	0.184	0.004	0.060	0.001	1
Mixed	0.745	*	0.991	0.184	0.550	0.050	0.001	2
Bog	0.770	0.991	*	0.242	0.111	0.046	0.001	3
Conifer	0.184	0.184	0.242	*	0.207	0.132	0.001	4
Deciduous	0.004	0.550	0.111	0.207	*	0.699	0.029	5
Other	0.060	0.050	0.046	0.132	0.699	*	0.053	6
Aquatic	0.001	0.001	0.001	0.001	0.029	0.053	*	7

Summer	Cutover	Conifer	Mixed	Deciduous	Aquatic	Bog	Other	Rank
Cutover	*	0.001	0.001	0.001	0.001	0.001	0.001	1
Conifer	0.001	*	0.246	0.274	0.007	0.043	0.001	2
Mixed	0.001	0.246	*	0.618	0.095	0.184	0.001	3
Deciduous	0.001	0.274	0.618	*	0.480	0.434	0.001	4
Aquatic	0.001	0.007	0.095	0.480	*	0.796	0.001	5
Bog	0.001	0.043	0.184	0.434	0.796	*	0.001	6
Other	0.001	0.001	0.001	0.001	0.001	0.001	*	7

(Phillips et al. 1973). Moose habitat in northwestern Minnesota was highly fragmented by agricultural development and smaller home ranges might result if moose are restricted to smaller patches of habitat. Phillips et al. (1973) also found that approximately 20% of northwestern Minnesota moose migrated between seasonal ranges which contrasts with the 4% we identified in this study in northeastern Minnesota.

The inference that early successional habitats are preferred by moose was reinforced by our analyses. In both the second- and third-order analyses, Cutover was ranked highest among the 7 cover types in both seasons (Tables 3 and 4). In the third-order analysis the mean proportional use of Cutover exceeded its availability and in the second-order analysis, home ranges contained a higher proportion of Cutover than was available in the study area (Fig. 2 and 3). While early successional habitats may be preferred, these results do not necessarily imply that the availability of cutover results in higher moose numbers. Moose populations limited by predation, hunting, and or disease likely will not benefit from an abundance of early successional forest.

Selection for aquatic habitats during summer was not evident in our analysis. In both the second- and third-order analyses, the mean proportional use of the Aquatic cover type was less than its availability. In the third-order analysis, the rank of the Aquatic cover type was significantly lower than Cutover and Conifer (Table 3). In the second-order analysis, the rank of the Aquatic cover type was significantly lower than that for Cutover, Bog, and Mixed (Table 4). Open water accounted for 6.1% of the area (Table 1) and included a few larger lakes up to 95 km^2. If the limnetic zone (open water beyond most plant growth) were excluded from both the second- and third-order analyses, the availability of the Aquatic cover type would decline and its rank would likely increase. The width of the littoral zone (open water containing plant growth) varies widely in the study area and was dependent in part on lake size, depth, and

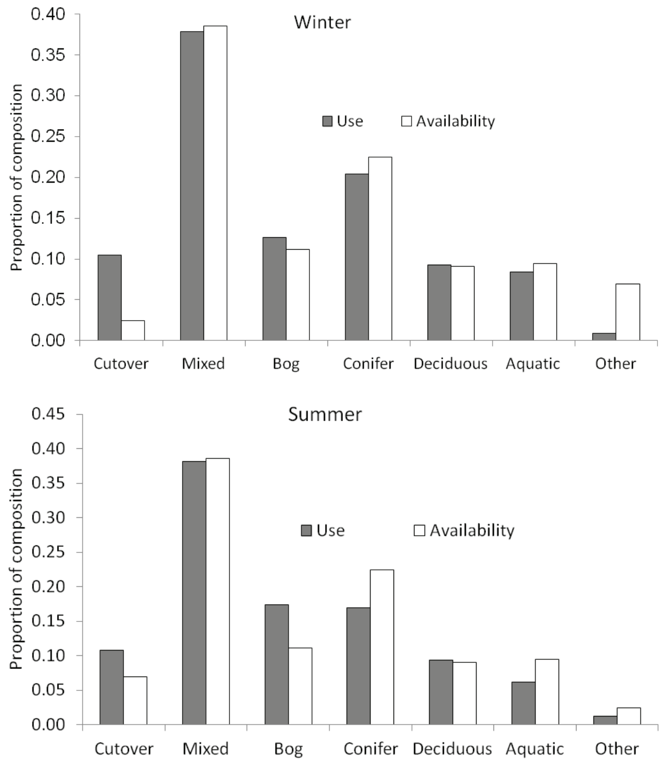

Fig. 3. Second-order selection (i.e., comparing cover type composition of individual home ranges to the cover type composition of the study area) by moose in northeastern Minnesota, USA, 2002-2010. Habitats are arranged from most to least preferred for winter and summer. Gray bars indicate mean proportional utilization and white bars represent mean proportional habitat available.

substrate; hence, it would be very difficult to accurately parameterize this sub-type for reanalysis. Most authors (Peterson 1955, DeVos 1958, Ritcey and Verbeek 1969, Peek et al. 1976) document that use of aquatic habitat is concentrated from June until August. Because our analysis treated summer as a much longer period (1 April-30 September), selection for the Aquatic cover type may have been eclipsed by selection for other cover types during the remainder of this season.

Traditionally, shaded habitats have been viewed as thermal habitat during summer (Parker and Gillingham 1990, Demarchi and Bunnell 1993, Cook et al. 1998, 2004) because shade will reduce solar radiation and the resultant operative temperature (Campbell and Norman 1998). The mature component of the Conifer, Mixed, and Deciduous cover types could produce such shade, and Aquatic and Bog cover types could also act as a thermal refuge because bedding in a wet bog or immersion in water could reduce body temperature through conduction and evaporation. In the third-order analysis (summer) the mean proportional use of Conifer exceeded availability while use of Mixed, Deciduous, Aquatic, and Bog cover types was slightly less than their availability (Fig. 2). Conifer was ranked significantly higher than either Aquatic or Bog, however, there were no significant differences among the ranks for Mixed, Deciduous, Aquatic, and Bog cover types. Assuming that moose behaviorally reduce their thermal load through habitat selection, it appears that moose prefer Conifer habitat over other cover types. Presumably, if we could have restricted analysis to days when temperature was above the thresholds identified by Renecker and Hudson (1986), there might have been a more refined preference of one cover type over another. Moreover, if use of Aquatic and Bog habitats is limited to early morning and evening, our analysis would obscure the importance of these cover types because most of the telemetry locations occurred during mid-day.

The second-order analysis suggests that moose selection of home ranges is not random. During summer moose selected home ranges containing a higher proportion of Cutover and Bog than their availability; conversely, Conifer, Aquatic, and Other cover types had significantly lower preference ranks. During winter Cutover again had a significantly higher rank and the Other cover type had a

Table 4. Simplified ranks and randomized P values of second-order selection of moose in northeastern Minnesota, USA, 2010. Gray cells represent P < 0.05. The order of cover types represents rank with cutover having the highest rank.

Winter	Cutover	Bog	Mixed	Conifer	Aquatic	Deciduous	Other	Rank
Cutover	*	0.001	0.001	0.002	0.001	0.002	0.001	1
Bog	0.001	*	0.777	0.271	0.254	0.296	0.001	2
Mixed	0.001	0.777	*	0.453	0.230	0.107	0.001	3
Conifer	0.002	0.271	0.453	*	0.471	0.645	0.001	4
Aquatic	0.001	0.254	0.230	0.471	*	0.927	0.002	5
Deciduous	0.002	0.296	0.107	0.645	0.927	*	0.001	6
Other	0.001	0.001	0.001	0.001	0.002	0.001	*	7

Summer	Cutover	Bog	Mixed	Conifer	Deciduous	Aquatic	Other	Rank
Cutover	*	0.405	0.023	0.001	0.012	0.002	0.001	1
Bog	0.405	*	0.325	0.005	0.122	0.002	0.001	2
Mixed	0.023	0.325	*	0.019	0.029	0.001	0.001	3
Conifer	0.001	0.005	0.019	*	0.794	0.097	0.001	4
Deciduous	0.012	0.122	0.029	0.794	*	0.393	0.058	5
Aquatic	0.002	0.002	0.001	0.097	0.393	*	0.125	6
Other	0.001	0.001	0.001	0.001	0.058	0.125	*	7

significantly lower rank.

The Cutover cover type identified in the LULC layer represented regenerating forest that was 7-22 years old at the beginning of our research (2002). Research has suggested that moose benefit most from regenerating forest when it is 11-30 years old (Kelsall et al. 1977, Schwartz and Franzmann 1989). We attempted to refine our analysis of cover type selection by including areas of hardwood regeneration, conifer regeneration, and blow down from a GIS layer provided by Wolters (unpubl. data). Although these data covered a wider span of time than the LULC data (1975-2000 vs. 1980-1995), they represented only a small subset of the overall Cutover cover type and represented a small proportion of the home ranges and study area. Ultimately we needed to combine them with other cover types to prevent Type I error (Bingham and Brennan 2004).

Problems exist in most analyses of habitat selection because of biases associated with the measurement of habitat use and availability and the interpretation of results (Garshelis 2000). In our third-order analysis, we attempted to improve the accuracy of our measures of habitat use by incorporating telemetry locations as well as simulated points to account for telemetry error. Nonetheless, recent research indicated that techniques used to incorporate telemetry error were inherently inaccurate with patch sizes < 20 ha (cf. Table1, Montgomery et al. 2010). Unless patches consistently encapsulate the telemetry polygon, it is questionable whether resource use studies such as third-order selection can be accurate (Saltz 1994, Rettie and McLoughlin 1999).

Analyses of second-order selection, however, are not dependent on the accuracy of telemetry locations but rather on the characterization of the home ranges used by individuals and the availability of important habitats. Garshelis (2000:123) argued that while "animals may be able to choose borders that encompass the best mix of habitats from what exists on the landscape; they cannot alter the mix to suit their needs." The 7 cover types used in this analysis were fairly ubiquitous and patches within the study area were typically quite small (Table 1). That only 3 moose were eliminated from the summer analysis because specific cover types were not available implies that virtually every moose had access to all cover types and was able to create a home range containing the most important habitat. That these 3 moose existed in home ranges not containing all 7 cover types further implies that none of the cover types is critical to moose survival.

MANAGEMENT IMPLICATIONS

The primary objective of this analysis was to determine whether moose in northeastern Minnesota display third-order selection for specific cover types previously identified as important – cutovers, aquatic habitat, and summer shade. While our results may indicate that the Cutover cover type is important, it is dangerous to make precise management prescriptions based on use-availability information because of inherent biases. The preferences identified here tend to represent fairly gross patterns and our results do not indicate anything about the relative size of cutover areas, the juxtaposition of other cover types, or specific resources within the cover type (e.g., forage) important to moose. Moreover, Osko et al. (2004) demonstrated that preferences are not fixed but change as the relative abundance of available habitat changes. Finally, any demonstration of preference identified in these results does not imply that any of these habitats are critical or that they are relevant to population productivity (Balsom et al. 1996, Osko et al. 2004).

It is important to remember that this study was not designed to evaluate habitat preferences in moose of northeastern Minnesota. Rather, it was designed to determine annual levels of adult mortality. As a result, the sample of VHF telemetry locations for each moose was generally small and the timing was generally limited to mid-day. Clearly, a study that incorporates GPS locations with much larger sample sizes would have been preferable. Nonetheless, the general preferences observed tend to support selection for (not a requirement for) early successional habitat.

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