Effect of Temperature on Habitat Use by Moose in Voyageurs National Park in the Summer

Ronald Moen, Ph.D.
Center for Water and Environment, Natural Resources Research Institute
Department of Biology, Swenson College of Science and Engineering
University of Minnesota, 5013 Miller Trunk Hwy, Duluth, MN 55811-1442

Michael Joyce, M.S.
Center for Water and Environment, Natural Resources Research Institute
University of Minnesota, 5013 Miller Trunk Hwy, Duluth, MN 55811-1442

Steve K. Windels
National Park Service, Voyageurs National Park, 360 Highway 11 E, International Falls, MN 56649

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Summary

Moose (*Alces alces*) are an integral part of biological processes and a favorite sight of visitors to Voyageurs National Park (VNP). In the face of global climate change moose may also become a bellwether species for the persistence of northern species in VNP and the surrounding area. Climate change will affect national parks like VNP in many ways, ranging from changes in vegetation and possible loss of wildlife species to altered visitation rates by people. Minnesota is at the southern edge of moose distribution. Climate change predictions are for a 3^{o} to 4^{o} C increase in average summer temperatures by 2100, which would result in an increased number of summer days during which moose would be heat stressed. We deployed GPS collars on moose in VNP to evaluate changes in habitat use and activity as related to fine-scale changes in ambient temperature. We captured and radiocollared 21 moose by aerial darting or net-gunning. We measured black globe temperatures in habitats across VNP. The annual Minimum Convex Polygon home range area was about 15 km^2, while seasonal home ranges were about 10 km^2. Home range size was slightly less than in adjoining areas of northeast Minnesota. There was no difference in proportional cover type in the home range among annual, winter, and summer home ranges, and cover type use was similar to cover type use by moose in northeast Minnesota. Wet bog and wet marsh/fen cover types were preferred in hot summer temperatures, while open water was not used very much, with less than 1% of locations in water when temperatures were above 30 C. Use of almost all cover types was similar whether temperature, dew point, or heat index were used as the metric. For future analysis of cover type use ambient or black globe temperature should be an adequate metric. Habitats that are of most use to moose in hot temperatures have a wet substrate and some canopy cover during the day. At night moose seemed to be less limited by heat dissipation because of colder temperatures and the lack of solar radiation. Monitoring the population status of moose at Voyageurs National Park is of critical importance in order to make contrasts with the declining moose populations in other regions of Minnesota.

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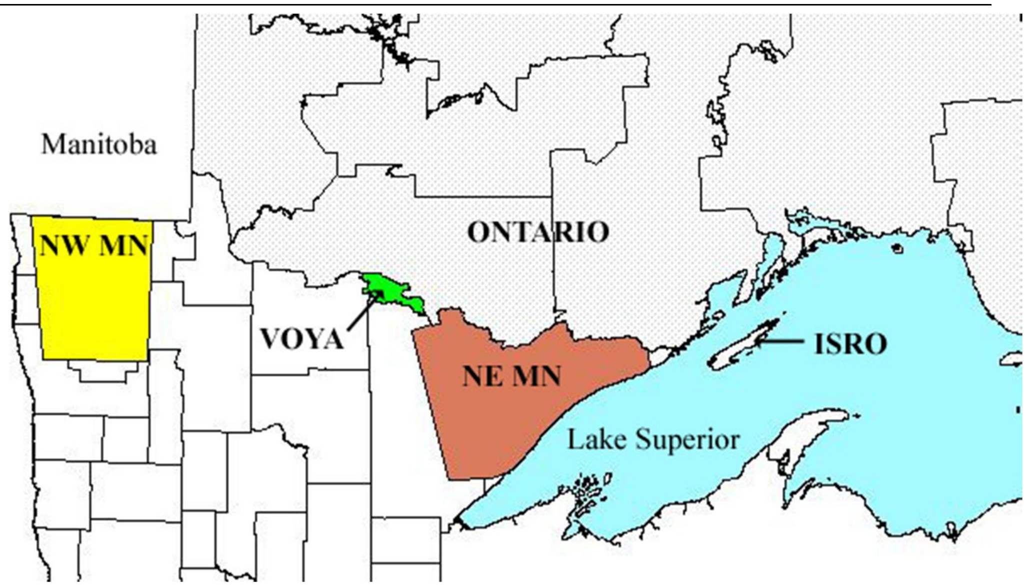
Introduction

Moose (*Alces alces*) are an integral part of biological processes and a favorite sight of visitors to Voyageurs National Park (VNP). In the face of global climate change moose may also become a bellwether species for the persistence of northern species in VNP and the surrounding area. Climate change will affect national parks like VNP in many ways, ranging from changes in vegetation and possible loss of wildlife species to altered visitation rates by people (NPCA 2007). The National Park Service, and Voyageurs National Park in particular, is uniquely positioned to both study the effects of climate change on northern species and provide refugia for populations of northern species such as moose, given the general lack of fragmentation and human disturbance in National Parks (NPCA 2007).

Minnesota is at the southern edge of moose distribution (Franzmann and LeResche 1978, Franzmann et al. 1978). The MN DNR manages moose as two disjunct populations in the northwest (NW) and northeast (NE) portions of the state (Fig. 1). The northwest population declined in the 1990's, and the northeast population declined in the 2000's (Murray et al. 2006, Lenarz et al. 2010). Voyageurs National Park is geographically between these two populations, but closer to the northeast population. Moose in VNP are not surveyed as part of the MN DNR's moose management program (Lenarz et al., 2007). The moose population in VNP has remained relatively steady based on periodic aerial surveys since 1991 (Windels 2014). Moose populations in NE MN and VNP are contiguous with moose in Ontario, which are managed by the Ontario MNR. One moose radiocollared in VNP in the 1990s had part of its home range in adjacent Ontario (Cobb et al. 2004).

Figure 1. General locations of moose in Minnesota relative to VNP. The NE MN population is contiguous with moose in VNP, and there are moose in Ontario north of the Minnesota border. Isle Royale National Park (ISRO) could be a logical extension of this project in the future.



The motivation for this project is in large part based on projected future increases in temperature for this region. Climate change predictions are for a 3^{o} to 4^{o} C increase in average summer temperatures by 2100 (IPCC 2007), which would result in an increased number of summer days during which moose would be heat stressed. Moose are able to survive very cold conditions (Kelsall and Telfer 1974), can be heat-stressed in winter at temperatures above 0^{o} C, and can be heat-stressed in summer at temperatures of only 15-20^{o} C (60-70^{o} F) (Renecker and Hudson 1986). If temperatures rise above -5^{o}C, in winter or 17-24^{o} C in summer (Renecker and Hudson 1986, McCann et al. 2013) moose may respond with behavioral and physiological changes. Summer and winter temperatures increased as the moose populations declined in northwestern Minnesota (Murray et al., 2006). Survival of moose radiocollared in Minnesota was negatively correlated with ambient temperatures in January and in the spring months (Lenarz et al., 2009).

Reasons why the VNP moose population has not declined significantly is unknown. The decline of moose in Minnesota may be caused in part by increasing temperatures, although the increase in average temperatures is small. However, despite rising temperatures in the 1990s, moose populations increased in Maine, New Hampshire, Vermont, New York, and Massachusetts (Timmerman 2003). Even data from Minnesota illustrate that the problem is complicated: the moose population in northwestern Minnesota almost disappeared from 1990 to 2007, while the population in northeast Minnesota was stable until about 2003 and then declined (Lenarz et al. 2009, DelGiudice 2014). North Dakota moose populations show a similar inconsistency, the population closest to the NW MN moose population is declining while 2 other populations in ND are stable or increasing (Maskey and Sweitzer, 2006). Aerial survey counts of moose in Ontario adjacent to VNP declined between 2000 and 2003 (Hilborn, 2004).

Both moose and woodland caribou (*Rangifer tarandus*) were present in the VNP area in pre-settlement times (Peterson 1955, Peek et al. 1976). White-tailed deer (*Odocoileus virginianus*) appeared around 1900, caribou were extirpated from the region around 1930, and moose were present throughout the 1900s (VNP unpublished records), with more recent presence documented by aerial counts in the 1980s and 1990s (Gogan et al. 1997). Moose densities in VNP were 0.25 to 0.50 / km^2 from the time of the park's establishment in 1975 through the 1990s (Gogan et al. 1997); VNP unpublished data), which is a population of 40 to 80 moose. After an 11-year hiatus a moose survey in VNP found the population was similar to previous years (Windels 2014). If moose in VNP had followed the NE MN population trend (DelGiudice 2014) there should have been about 20 to 40 moose in the 2009 survey.

Moose and white-tailed deer have been sympatric since at least the 1930s in VNP (Gogan et al. 1997). White-tailed deer are increasing at the northern edge of their range in Minnesota due to mild winters that are associated with recent changes in climate. The total deer population in the northern forest region increased from 800,000 in 1997 to 1,250,000 in 2004 (Erb and Benson 2004). After application of sightability correction factors used in the nearby Superior National Forest, deer densities approaching 8.0/km^2 were estimated in VNP in 1992 (Gogan et al. 1997). MNDNR estimated spring deer population densities in the deer management unit adjacent to VNP ranged from 5.1-8.6/km^2 in 2005.

The probability of moose and deer co-existing appears to decline if deer density is > 5 deer / km^2, although evidence is circumstantial and high variance indicates other factors also affect co-existence (Whitlaw and Lankester 1994). VNP is a case in point: despite presence of meningeal worm and high deer densities, there is only one confirmed case of *Parelaphostrongylus tenuis* (March 2008) for adult moose in VNP (Gogan et al. 1997, VNP unpublished records). Meningeal worm (*P. tenuis*) and liver flukes (*Fascioloides magna*) have been implicated in moose mortality in Minnesota between 1972 and 2014 (Spears et al. 2005, Murray et al. 2006, Wunschman et al. 2014). Meningeal worm is a parasite that does not affect deer but usually thought to be fatal to moose. In the 1980's *P. tenuis* was found in 80% of deer pellet groups and in 80% of adult deer examined in and adjacent to VNP. In NE MN, 18 of 109 moose were sero-positive for antibodies against *P. tenuis* using an ELISA test (Ogunrimi et al. 2002). However, only 5 of these 18 moose died from unknown causes (i.e., possible *P. tenuis* mortality) in the 2 to 5 years following blood collection (Lenarz et al. 2007).

Liver flukes were the greatest source of mortality in the NW Minnesota moose population (Murray et al. 2006) and may be associated with some mortalities in the NE Minnesota moose population Reduced physical condition associated with parasite loads may affect population level variables by reducing calf:cow ratios and changing bull:cow ratios.

In this research project we deployed GPS collars on moose in VNP to evaluate changes in habitat use and activity as related to fine-scale changes in ambient temperature. Moose GPS collar locations were the link we used to understand how cover types were used differentially as ambient temperature increases in summer. At the population level we repeated an aerial survey of the moose population in VNP. We used data collected from captured moose to determine productivity from blood samples, fecal pellets, and also included data from the aerial survey. These data were combined with information from a separately funded project that assessed the prevalence, intensity, and distribution of liver flukes and meningeal worm in white-tailed deer in the park (Cyr et al. 2014, VanderWaal et al. *in press*). These parasites are often fatal to moose but are generally non-lethal to deer, the primary vector in our study area. Finally, we will use results from this research project, historical research in VNP, and other recent research on moose in Minnesota to develop a stochastic simulation model of moose demographics, building on the model developed by Murray et al. (2006) for moose in northwestern Minnesota.

Methods

Study Area. Voyageurs National Park covers an area of 882 km^2 and is located along the United States-Canada boundary (48°30′N 92°53′W). The park primarily consists of two major landmasses and 4 large lakes. Maximum topographic relief is 80 to 90 m. Moose radiocollared in this study were located on the Kabetogama Peninsula. Vegetation includes southern boreal forest characterized by balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*) and quaking aspen (*Populus tremuloides*), and northern hardwood forest characterized by red maple (*Acer rubrum*), green ash (*Fraxinus pennsylvanica*), red pine (*Pinus resinosa*) and white pine (*P. strobus*) (Kurmis et al. 1986). Annual temperatures range from −43°C to 36.6°C and average −6.1°C in January and 18.6°C in July (2010, National Weather Service, International Falls, MN). Lakes in the park are usually ice-covered by late November, and ice break-up occurs around 1 May (Kallemeyn 1987).

GPS radiocollars. We captured and radiocollared 21 moose by aerial darting or net-gunning following protocols used by the NE MN moose project from 2002-2007 (Lenarz et al. 2009, 2010). Moose were anesthetized by aerial darting (Kreeger et al. 2002, Gogan et al. 1997) or manually restrained when captured with a net gun (Carpenter and Innes 1995). Moose were captured in January and February 2010 and 2011. Moose were darted with a mixture of 1.2 ml (4.0 mg/ml) carfentanil citrate (ZooPharm, Laramie, WY) and 1.2 ml (100 mg/ml) xylazine HCl (Midwest Veterinary Supply, Inc., Burnsville, MN). The drugs were reversed with 7.2 ml (50 mg/ml) naltrexone HCl (ZooPharm) and 3 ml (5 mg/ml) yohimbine HCl (Midwest Veterinary Supply). Animal capture and handling protocols met the guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007). Each moose was fitted with a GPS radiocollar from Sirtrack (Havelock North, New Zealand). Location data were collected every 15 minutes (2010) or 20 minutes (2011-2012). We programmed collars to obtain locations every 15 minutes in 2010, and then in the following years we used a 20-minute interval between locations. Collars would have recorded about 35,000 locations per year from each radiocollared moose in 2010, and about 25,000 locations in 2011 and 2012. Collars also recorded temperature and activity with each GPS location attempt.

We collected blood and fecal samples to assess condition and pregnancy following methods described in Murray et al. (2006). Results are directly comparable to analyses of blood and fecal samples from 150 moose captured in NE MN for a VHF collar study because the same methodology and analyses will be conducted. These data are being analyzed by the MN DNR as part of their moose mortality project.

Aerial Surveys. Aerial counts followed standard protocols already in use by the MN DNR and tribal wildlife biologists in Minnesota (Lenarz 2007, DelGiudice 2014) when possible. One difference is that a fixed-wing aircraft was used instead of a helicopter (Windels 2014). These protocols were consistent with previous surveys in VNP to the extent possible. Because of similar methodologies moose population characteristics in VNP in the 1980s and 1990s, including calf:cow ratios, bull:cow ratios, and estimates of population size (Gogan et al. 1997, VNP unpublished records) were compared to current data.

Mortality checks for collared moose were conducted based on the mortality signals sent by the collars. Cause of death was determined when possible using techniques developed in the Northeast Minnesota Moose Project (Lenarz et al. 2009, 2010). With a small sample size of radiocollared moose, and the expectation that 1 or 2 of these animals might die in a year, cause of mortality is unlikely to be of much value from a statistical perspective.

Temperature measurements. Temperature measurements in specific habitats were conducted by Bryce Olson as part of his M.S. research (Olson 2014). The sampling design was stratified by vegetation cover type, canopy cover, and slope/aspect with temperature loggers placed at an intensity of 1 temperature logger for every 333 ha in the study area.

Black globe temperature loggers consisted of a data-logging thermocouple (Onset Computer Corporation, Bourne, Massachusetts, USA) inserted into a copper toilet tank float painted matte black (Olson et al. 2014). We calibrated loggers for a minimum of 96 h to verify accuracy and resolution as compared to the stated equipment specifications of the logger (±0.21°C from 0°-50°C). All loggers were synchronized and programmed to record temperatures every 15 minutes for 1 year.

At each sample point, we hung loggers 0.75 m above the ground and 15 cm from the trunk. Loggers were placed on the northeast side of trees to minimize direct solar radiation during the warmest time of day (Fig. 1). We used handheld field computers with GPS to verify that logger placement in the field was consistent with identified cover type and location within the cover type polygon. We used real-time GIS and measurements in the field to ensure we were within the identified cover type, canopy cover class, and slope/aspect category before we deployed loggers. Loggers were deployed from June 2010 to July 2011, with periodic downloads to reduce risk of data loss. Data were screened to remove biased or failed measurements (e.g., faulty logger, damaged globe or logger, and snow-covered loggers). We deployed an additional set of loggers from August 2011 to January 2012 to test for differences in position on slope. We randomly deployed 3 loggers in each of 9 combinations of cover type (deciduous, evergreen, and mixed), canopy cover class (<70%, 70-80%, >80% forested canopy), and slope position (top, mid-slope, and base). Slopes tested ranged from 17-47%.

We also downloaded weather data for the International Falls, MN weather station (KINL) from MesoWest (http://mesowest.utah.edu/). These data included hourly temperature (°C), relative humidity, and dewpoint (°C) readings. We then used the relative humidity (rh) and temperature in °F (T) to calculate a heat index value using Eq. 1 (www.srh.noaa.gov/epz/?n=wxcalc):

$$HeatIndex = -42.379 + 2.04901523 * \mathrm{TC} + 10.14333127 * \mathrm{rh} - 0.22475541 * \mathrm{TC} * \mathrm{rh} - 6.83783 * 10^{-3} * TC^2 - 5.481717 * 10^{-2} * rh^2 + 0.00122874 * TC^2 * rh + 8.5282 * 10^{-4} * rh^2 - 1.99 * TC^2 * rh^2 \quad \text{Eq. 1}$$

GIS analysis. Annual and seasonal home ranges were calculated using the package adehabitatHR (Calenge 2006) in R statistical software (version 3.0.2). We used location data sub-sampled to approximately one location every 7-10 days to match VHF location data collected from 1989-1992. Locations from each moose were divided into annual and seasonal location sets. Annual location sets started at the beginning of each May and ended the following April to correspond with the biological year of moose with calving in May. Seasonal location sets included winter (November 1 to April 15) and summer (April 16 to October 31) seasons. Season dates were selected to correspond to changes in environmental conditions (i.e., temperature and snow cover) and plant phenology (i.e., leaf-on vs. leaf-off). Annual and seasonal home ranges were calculated using the minimum convex polygon (MCP). We removed 5% of locations that were farthest from the arithmetic mean coordinate for that location set prior to generating an MCP home range (Rodgers and Kie 2011). Seasonal MCP home ranges were calculated for all seasonal location sets with ≥20 locations, while annual MCP home ranges were calculated for annual location sets with ≥30 locations over ≥200 days.

We also calculated annual home ranges and core areas using fixed-kernel density estimators (Worton 1987, 1989). Various methods exist for selecting the bandwidth or smoothing parameter for kernel home range calculation, and choice of bandwidth selection method can influence how well the estimated home range matches the true utilization distribution of the animal (Gitzen et al. 2006, Kie 2013). We used the 'ad hoc' bandwidth selection protocol described by Kie (2013) to select bandwidth values to use for each annual location set. Kie (2013) found this method had had less bias and lower Type I and Type II errors compared to other standard methods (e.g., reference bandwidth [Worton 1989] or least-squares cross-validation [Worton 1989, Gitzen and Millspaugh 2003] algorithms) when estimating home range size of elk (*Cervus elaphus*). Kernel home ranges were calculated using the 95% probability volumetric contour (i.e., 95% isopleth). We defined a core area as the part of a moose's home range used at maximum intensity and estimated core areas using the methods described by Vander Wal and Rodgers (2012). A grid size of 30 m was used for kernel density home range estimates.

We used ArcMap to determine cover type use with the Land Use-Land Cover classified LandSat data from the mid-1990s that have been successfully used in a lynx project in NE MN (Moen et al. 2006, Burdett et al. 2007, McCann 2006). The area and cover-type composition was calculated for each home range estimate. Cover-types were also calculated from a vegetation map layer from the Voyageurs National Park Vegetation Mapping Project produced from interpretation of fall 1995 and 1996 1:15,840-scale color infrared aerial photographs with a minimum resolution of 30 m (USGS-NPS Vegetation Mapping Program 2001, Faber-Langendoen et al. 2007).

Results

The annual Minimum Convex Polygon home range area was about 15 km^2, while seasonal home ranges were about 10 km^2 (Table 1, 2). There was little difference in area between winter and summer MCP home ranges. These home ranges are based on a subsample of GPS collar locations taken every 7 to 10 days to be comparable with home ranges calculated for moose in NE MN (Moen et al. 2010, Lenarz et al. 2011). Kernel home ranges calculated on the same points had a 95% kernel home range area of about 25 km^2, and a core kernel home range area at the 59% isopleth of 8 km^2.

Table 1. Annual home range measurements for 19 adult moose in Voyageurs National Park, 2010 to 2012. Minimum Convex Polygon (MCP) and Kernel home ranges are calculated. Areas are in km^2.

Variable	Mean	SEM
Days	333	10
Locations	36	2
100% MCP Area	17	2
95% MCP Area	14	1
95% Kernel home range area	25	2
Core Kernel home range area	8	1
Core Kernel home range isopleth	59	0

Table 2. Seasonal home range measurements for 19 adult moose in Voyageurs National Park, 2010 to 2012. Minimum Convex Polygon (MCP) and Kernel home ranges are calculated. Areas are in km^2.

Variable	Summer		Winter	
	Mean	SEM	Mean	SEM
Days	165	2	177	8
Locations	22	1	18	1
100% MCP Area	11	1	12	2
95% MCP Area	9	1	9	2

There does not appear to be a biological difference in proportional cover type in the home range among annual, winter, and summer home ranges in the LULC cover type classification (Fig. 2). The mean cover type for an annual MCP home range (Fig. 2) is what we will use as amount of “Available” cover type when we are determining if the moose used cover types out of proportion to availability. This is one possible version of available cover types. Other possible "available" cover types we could have used include the available cover types in the entire Kabetogama peninsula or available cover types based on buffers around a home range. 92% of the area is composed of Mixed Forest, Wet Bog/Marsh/Fen, Water, and Shrub categories (Table 3).

Figure 2. Percent of LULC cover type within the annual, summer, and winter home range of moose (Table 1, 2, 3). Cover types include Mixed Forest (Mix), Wet Bog and Wet Marsh/Fen (WetBMF), Water, Regenerating Forest and Shrubby grassland (Shrub), Deciduous forest (Decid), Coniferous forest (Conif), and other categories. Annual home ranges are not the average of Summer and Winter home ranges because of spatial overlap.

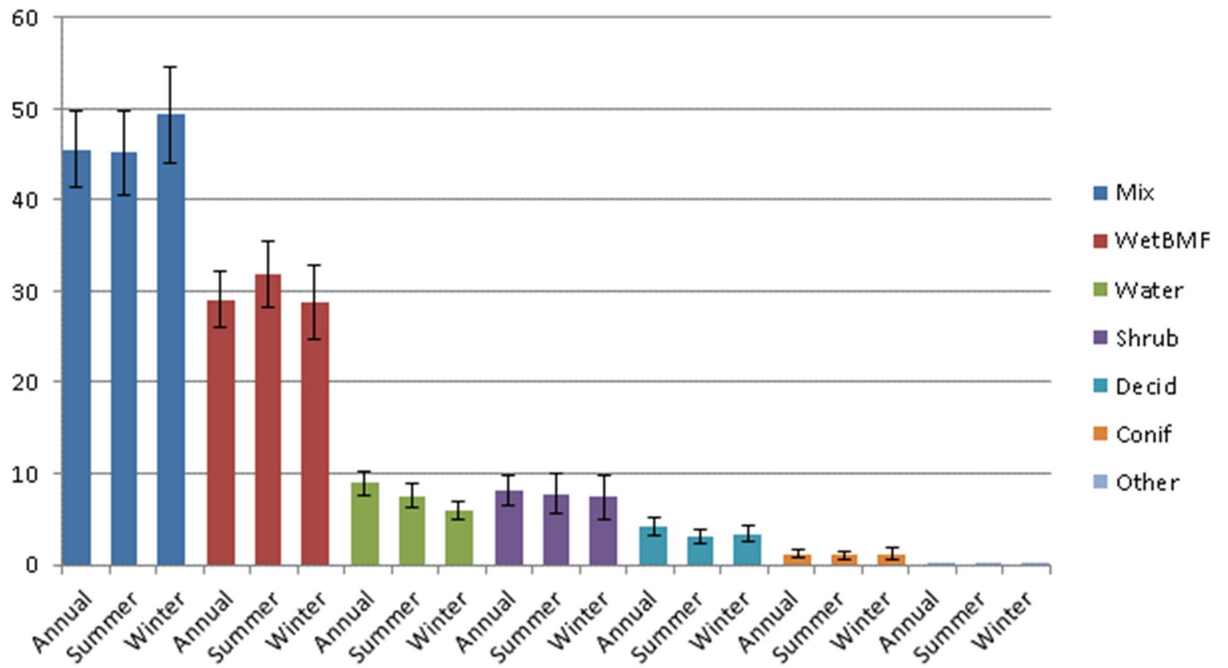
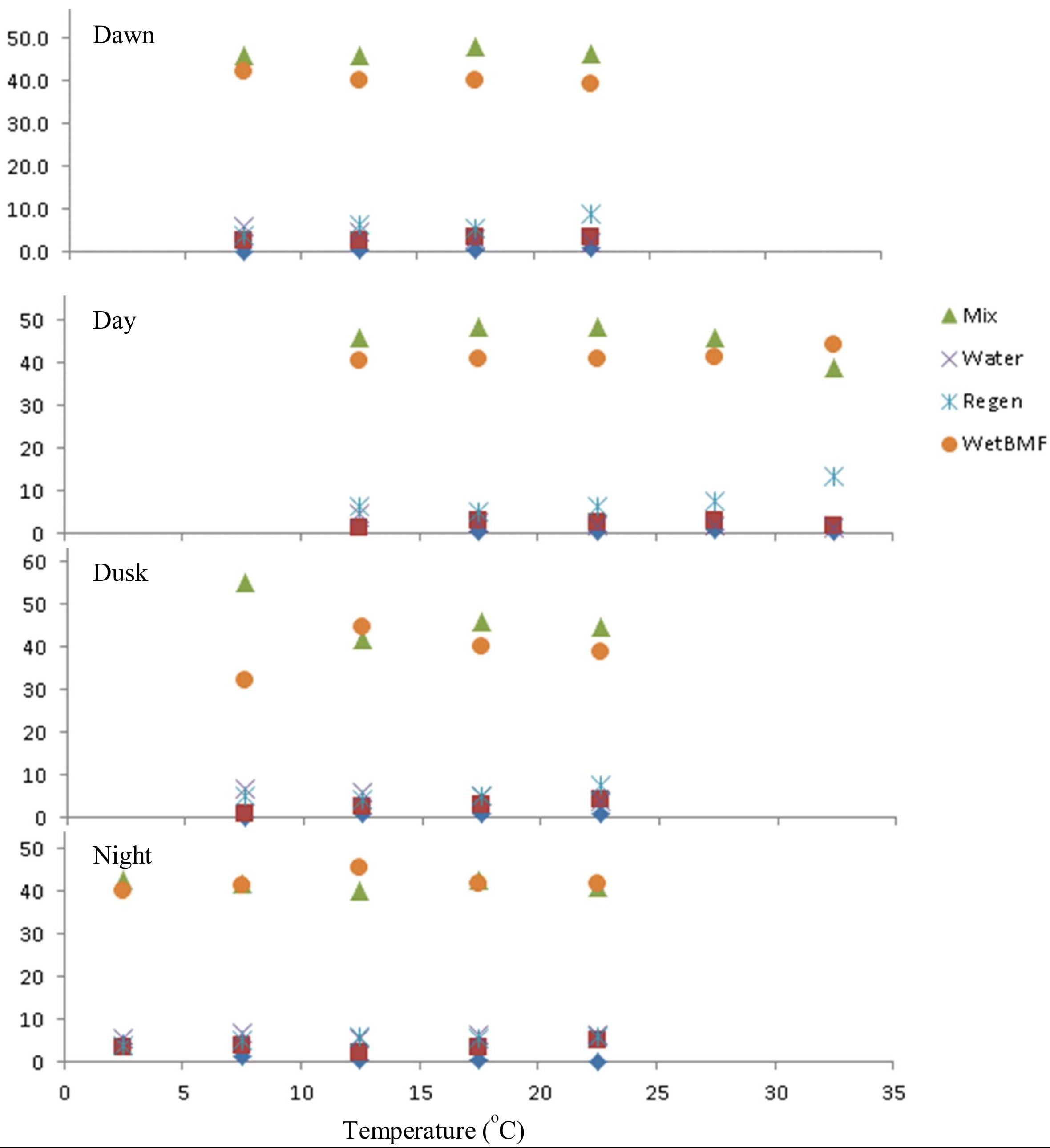


Table 3. Percent of LULC cover type within the annual, summer, and winter home range of moose (Fig. 2). Mean and SEM based on 20 to 27 home ranges.

Cover Type	**Annual**		**Summer**		**Winter**	
	Mean	SEM	Mean	SEM	Mean	SEM
Mixed Forest	46	4.1	45	4.6	49	5.3
Wet Bog/Marsh/Fen	29	3.1	32	3.6	29	4.1
Water	9	1.3	8	1.3	6	1.0
Shrub	8	1.7	8	2.2	7	2.3
Deciduous Forest	4	1.0	3	0.8	3	0.8
Coniferous Forest	1	0.4	1	0.5	1	0.7
Other	0	0.0	0	0.0	0	0.0

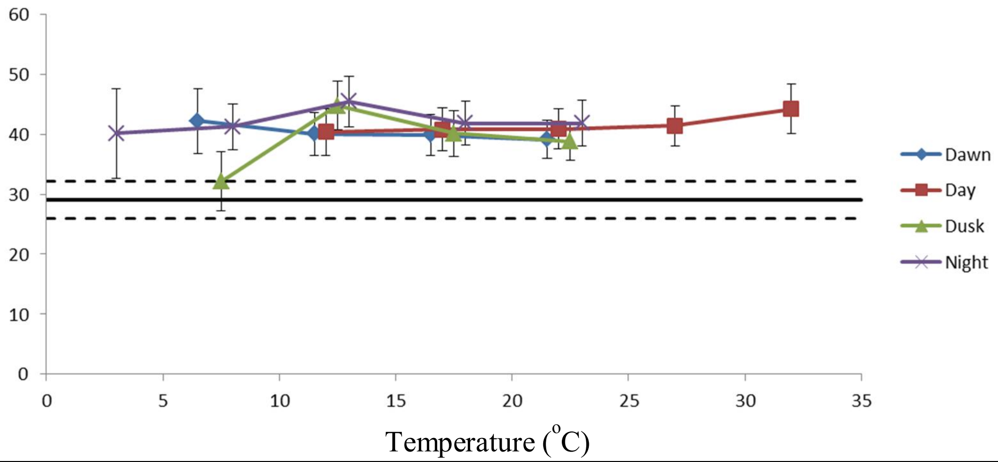
The pattern in cover type use was relatively constant across time periods and across temperatures (Fig. 3) at the broad scale. Differences that seemed to be present were a very slight decline in Wet Bog/Marsh/Fen use at dawn as temperatures increased, with an increase in use of Shrub/Regenerating Forest cover type. During the day there was a decline in the use of Mixed forest as temperatures increased, with an increase in the use of Shrub/Regenerating Forest cover type. At dusk at the coldest temperature bin there seemed to be a decrease in the use of Wet Bog/Marsh/Fen and an increase in the use of the Mixed forest cover type. At night there were not strong trends across temperature bins.

Figure 3. Mean cover type composition in dawn, day, dusk, and night across temperature range. Mean is based on different moose as the averaging unit, rather than all of the points as the averaging unit. Temperature was binned in 5 degree increments. There had to be at least 20 locations from a moose to include it in a temperature bin, and there had to be at least 10 moose to include the moose in the average for a cover type.



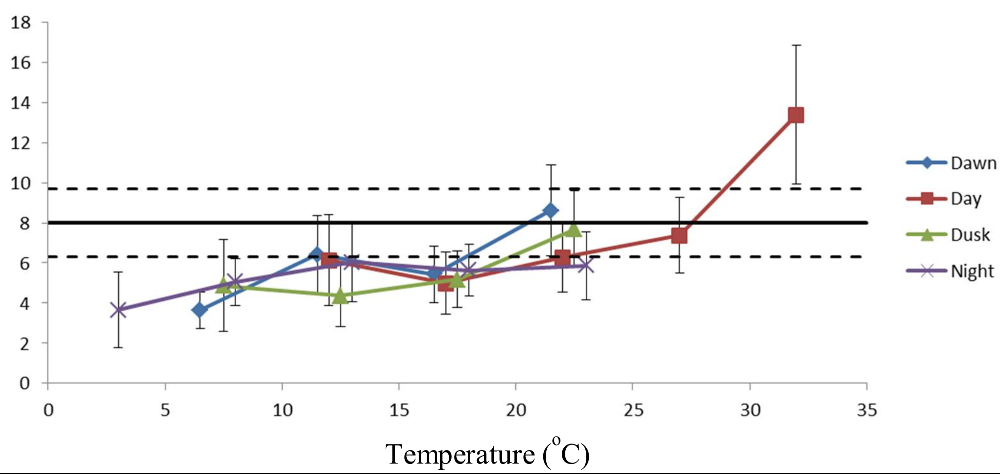
Wet Bog/Marsh/Fen cover type. The Wet Bog/Marsh/Fen cover types were used about 40% of the time, while the availability across the home ranges was about 30%, indicating selection for this cover type across all temperatures (Fig. 4). There was relatively little change in proportion of use across the temperature range combined, and no clear pattern here across temperatures.

Figure 4. Percent of Wet Bog/Marsh/Fen cover type used by moose based on GPS locations in 5 degree temperature bins, compared to the percent of the Wet Bog/Marsh/Fen cover type available to moose based on annual home range cover types (Table 3). Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



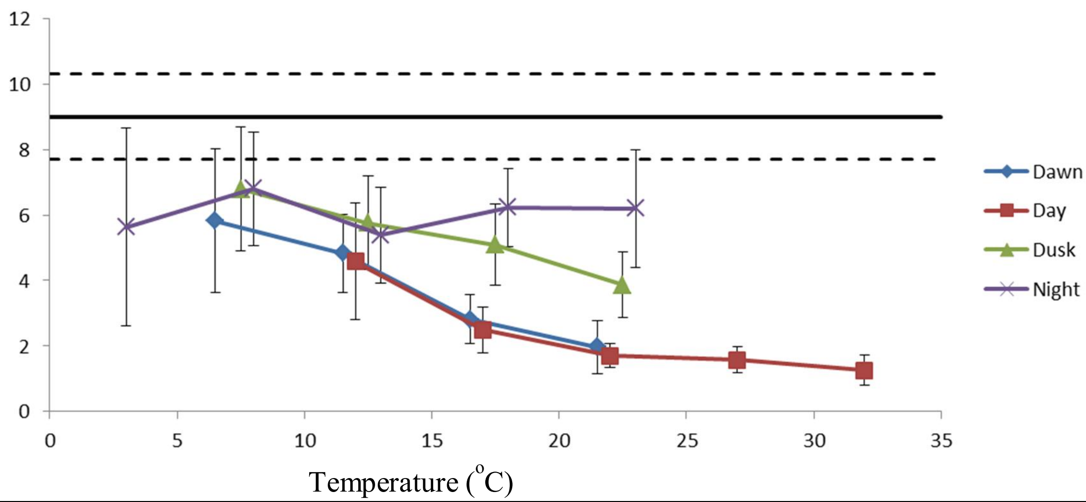
Regenerating Forest / Shrubby Grass cover type. The Regenerating Forest / Shrubby Grass cover type includes the rock openings in VNP as well as shrubby areas. Outside of VNP it would include regenerating forest. There is an increase in use of this cover type in the day at high temperatures, which is a surprising because the moose would likely be in the sun (Fig. 5). However, 14% of the locations are still relatively small compared to use of other types. It is also a little surprising that this cover type is used less than it is available at almost all temperatures, because it would be expected to have browse availability within reach of moose.

Figure 5. Percent of Regenerating Forest / Shrubby Grass cover type used by moose based on GPS locations in 5 degree temperature bins, compared to the percent of the Regenerating Forest / Shrubby Grass cover type available to moose based on annual home range cover types (Table 3). Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



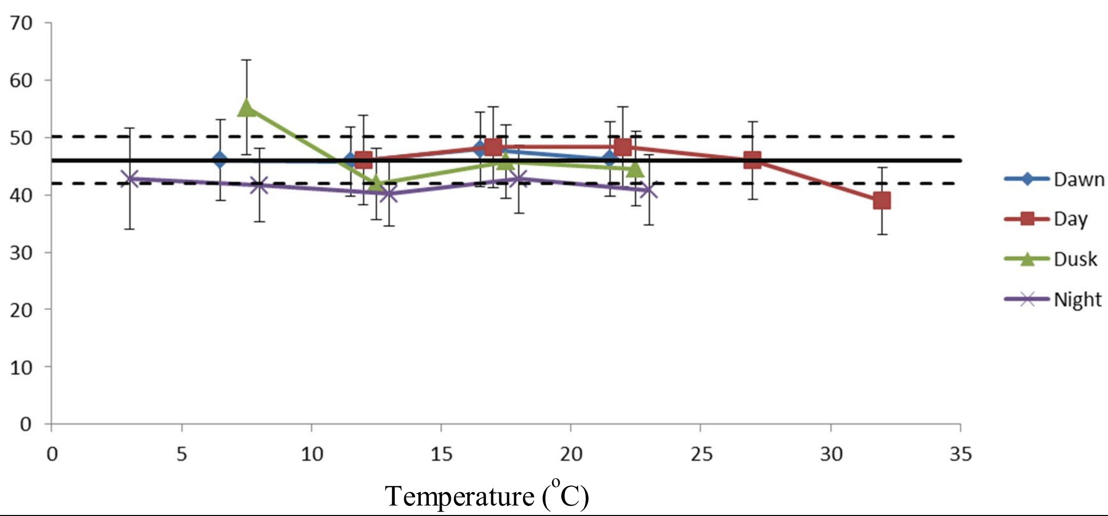
Water cover type. Open water is used less than it is available in all time periods, with a relative use of about 5% while the availability is about 9% across moose home ranges (Fig. 6). The decline in use at hot temperatures in dawn and day time periods is unexpected if moose are going to open water sources to cool down. There is possibly a slight decline in use of water at dusk as temperature increases.

Figure 6. Percent of water cover type used by moose based on GPS locations in 5 degree temperature bins, compared to the percent of the water cover type available to moose based on annual home range cover types (Table 3). Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



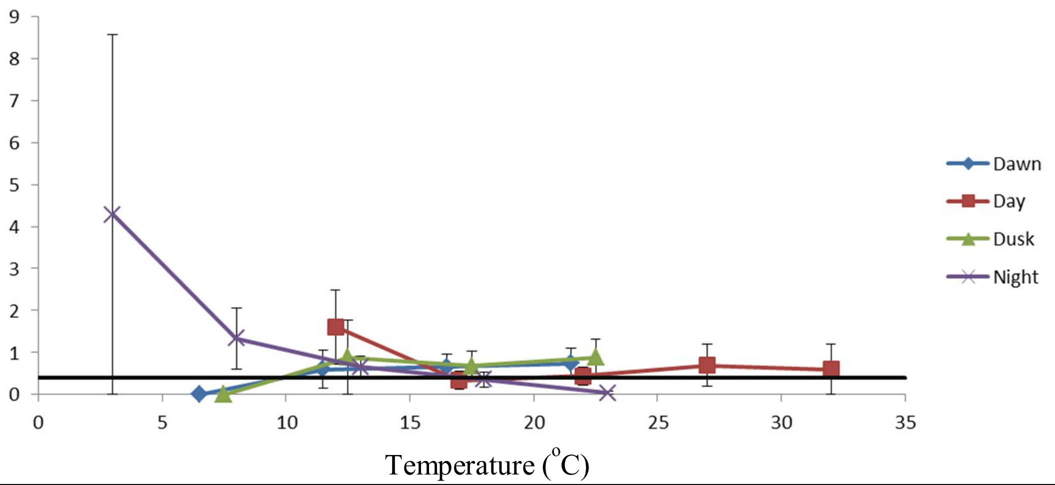
Mixed forest cover type. The Mixed forest cover type is the most common cover type, and it is used in proportion to availability (Fig. 7). There is a declining trend in use of the Mixed Forest cover type at hotter temperatures. The high use of the Mixed forest type at the cold temperatures at dusk may be an anomaly, as it is only on that temperature bin and not a trend across temperatures.

Figure 7. Percent of Mixed forest cover type used by moose based on GPS locations in 5 degree temperature bins, compared to the percent of the Mixed Forest cover type available to moose based on annual home range cover types (Table 3). Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



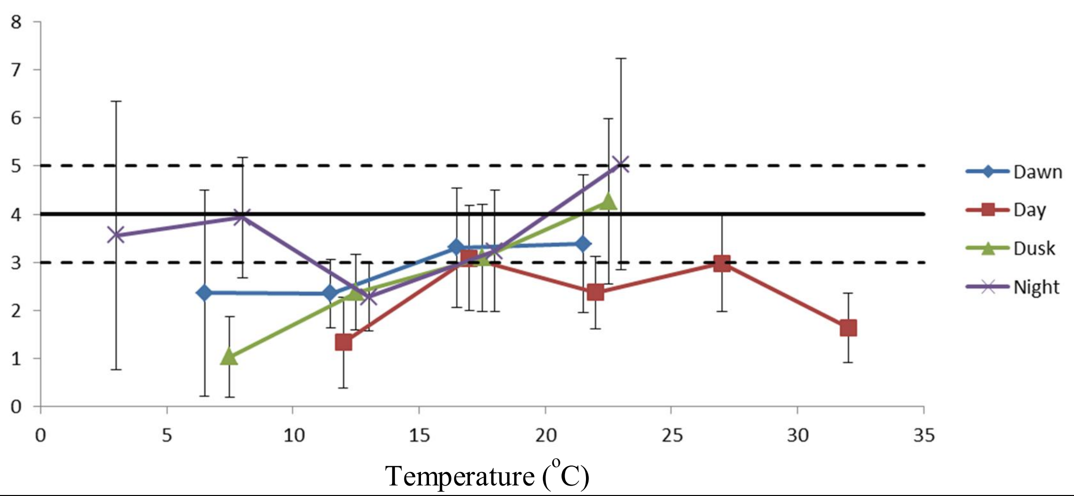
Coniferous Forest cover type. There is very little coniferous forest on VNP within moose home ranges, and it was used essentially in proportion to availability (Fig. 8). The exception to this is that use was higher at night for 1 moose (which is why the SEM is so large) at the coldest temperature.

Figure 8. Percent of Coniferous Forest cover type used by moose based on GPS locations in 5 degree temperature bins, compared to the percent of the Coniferous Forest cover type available to moose based on annual home range cover types (Table 3). Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



Deciduous Forest cover type. There is relatively little deciduous forest within moose home ranges on VNP, and it is more variable among moose than the other cover types, as indicated by the larger SEM (Fig. 9). Use is approximately in proportion to availability, although as with the mixed forest there may be a decline in use during the day at the hottest temperature bin.

Figure 9. Percent of Deciduous Forest cover type used by moose based on GPS locations in 5 degree temperature bins, compared to the percent of the Deciduous Forest cover type available to moose based on annual home range cover types (Table 3). Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



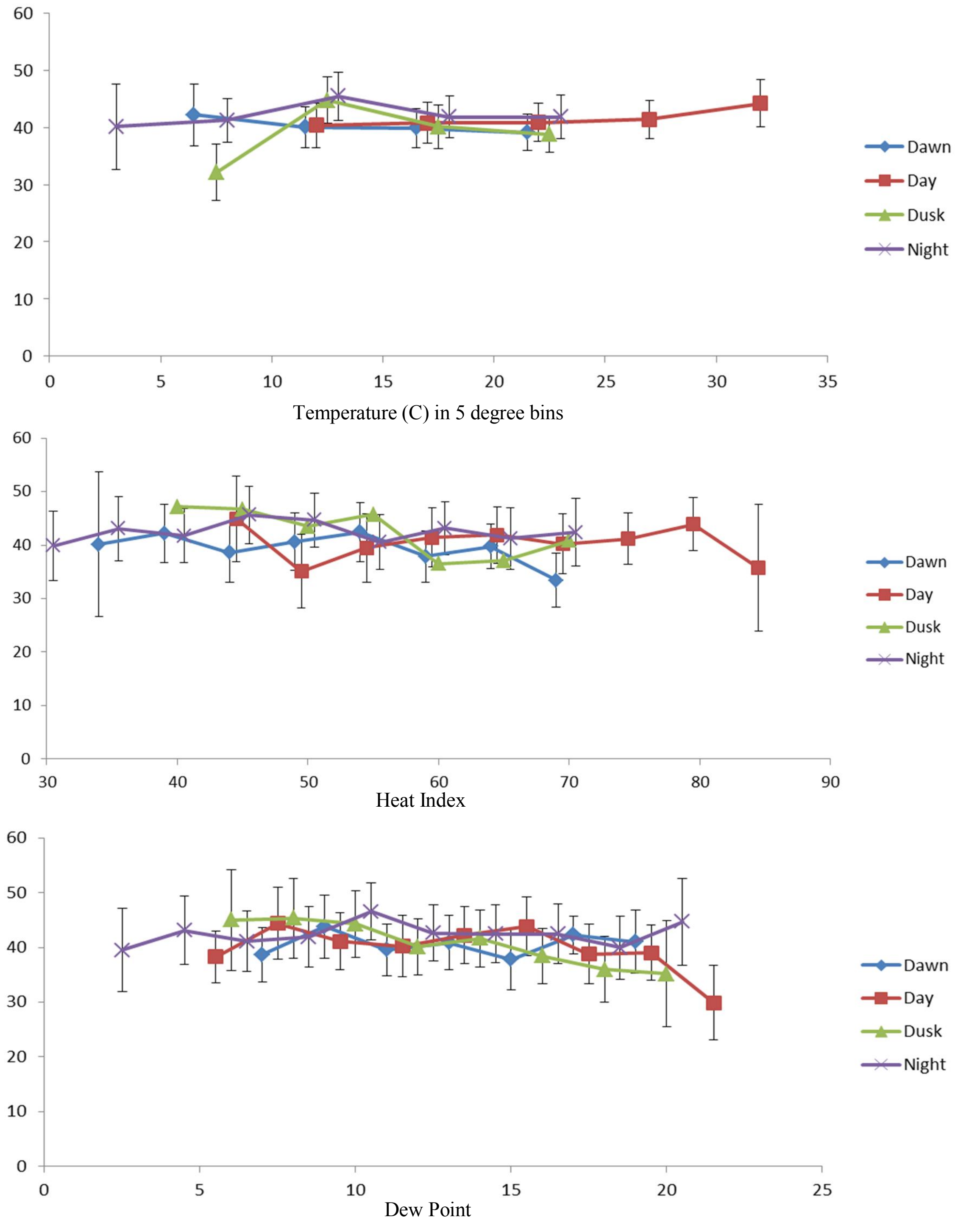
We also evaluated alternative heat indices to determine if they might better represent a moose response to changes in temperature. We calculated the Dew Point and the Heat Index (NWS) based on the temperature and relative humidity at the start of each GPS location interval. After calculating the Dew Point and the Heat Index we used a binning procedure similar to binning temperature into 5 degree increments. We then compared the index values for Temperature, Dew Point, and Heat Index in each cover type and at different times of the day (Dawn, Day, Dusk, and Night).

Overall, the general conclusion that can be drawn from this comparison are that the percent use of each cover type is correlated for the 5 degree temperature bins, Dew Point, and the Heat Index (Figs. 10 - 15). This is not unexpected, because Dew Point is calculated in part based on temperature (www.srh.noaa.gov/images/epz/wxcalc/heatIndex.pdf) and Heat Index is calculated from relative humidity and temperature (Eq. 1). Variance in cover type use for the 5 degree bins seems to be lower than variance for the Dew Point and Heat Index.

There are some differences at low and high temperature extremes because of how the bins are divided. Temperature was divided into 7 bins, while dew point and heat index were divided into 11 bins. This, and the possibility that GPS locations could switch bins (e.g., a high temperature with a high humidity would be in a different heat index bin than a high temperature with low humidity) mean that we can't do statistical correlations among cover type percentages for temperature, heat index, and dew point. However, visual interpretation indicates that there are not major differences between temperature, heat index, and dew point cover type use.

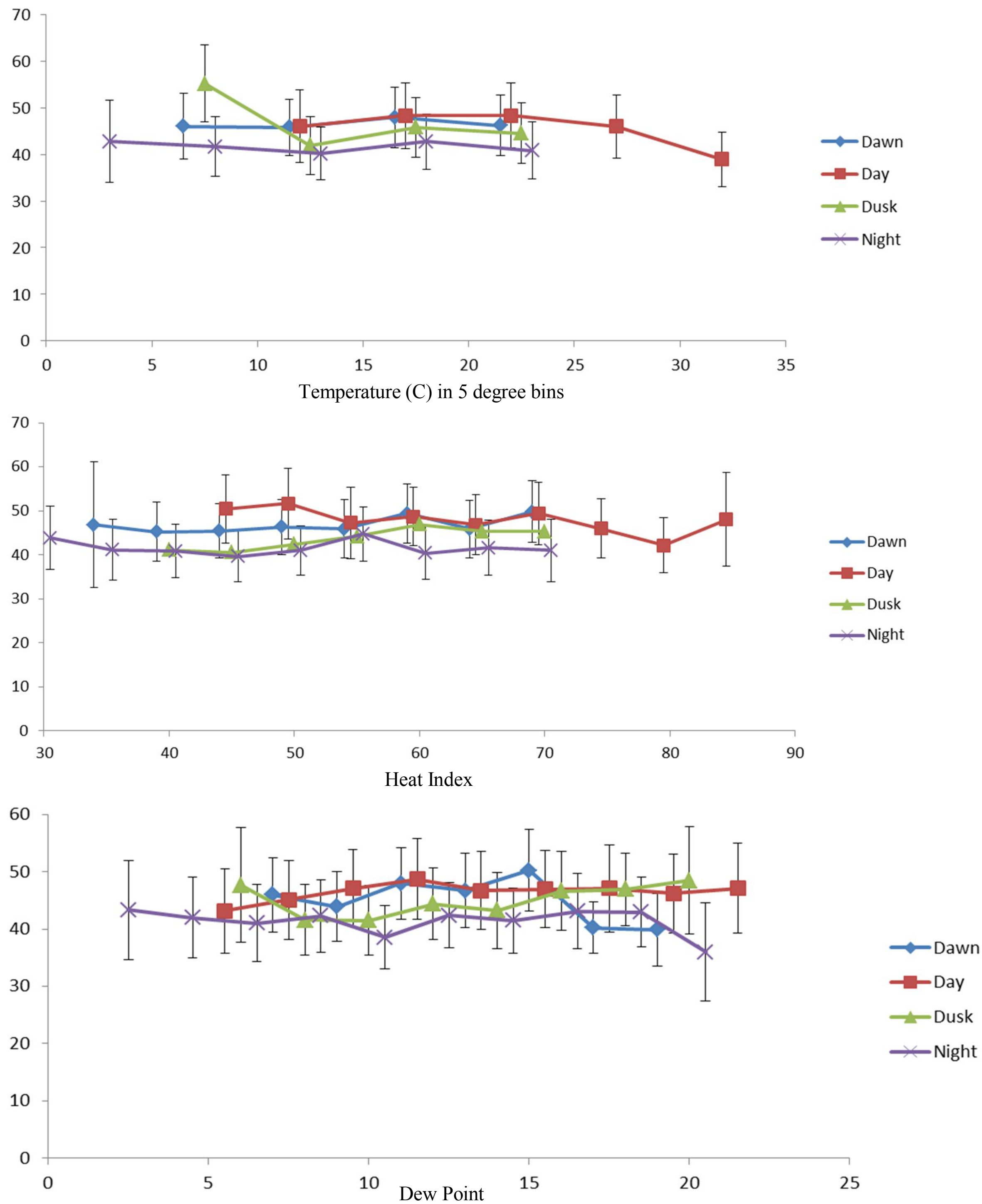
Wet Bog/Marsh/Fen cover type. This cover type is most different among indices, with a low temperature at dusk and no decline in day at high temperatures (Fig. 10). The difference at high temperatures among indices may be related to bin size. There are 5 bins for temperature and 9 bins for RH and HI. However, the general pattern is relative consistency across indices.

Figure 10. Percent use of Wet Bog/Marsh/Fen cover type for temperature in 5 degree (C) bins, Dew Point, and Heat Index at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose



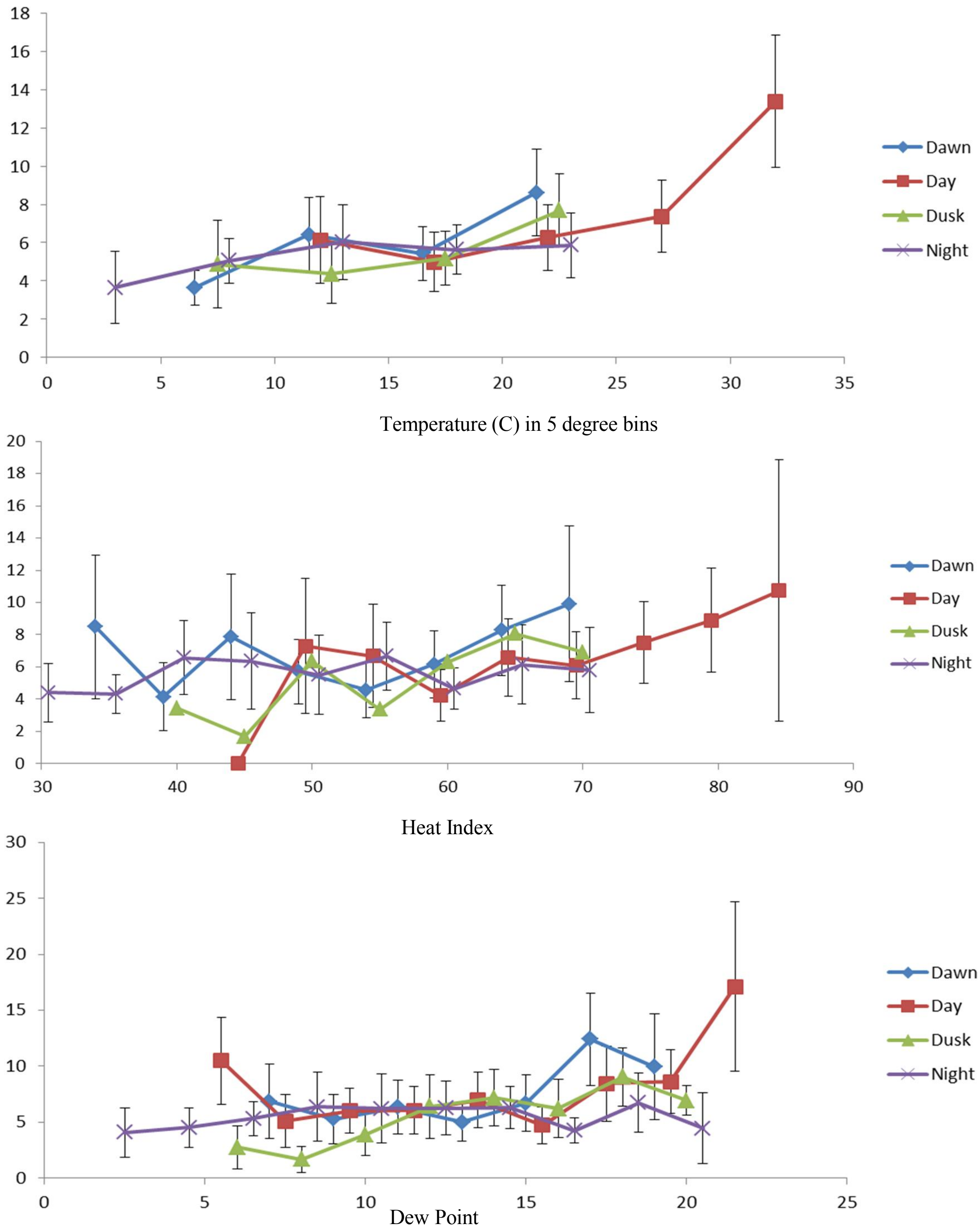
Mixed forest cover type. There was no pattern in indices in the mixed forest cover type except for the decline with highest temperatures in temperature bins compared to Heat Index and Dew Point bins (Fig. 11). This contrasts with the WetBMF cover type pattern. There was also relative consistency across the heat stress range.

Figure 11. Percent use of Mixed Forest cover type for temperature in 5 degree (C) bins, Dew Point, and Heat Index at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose



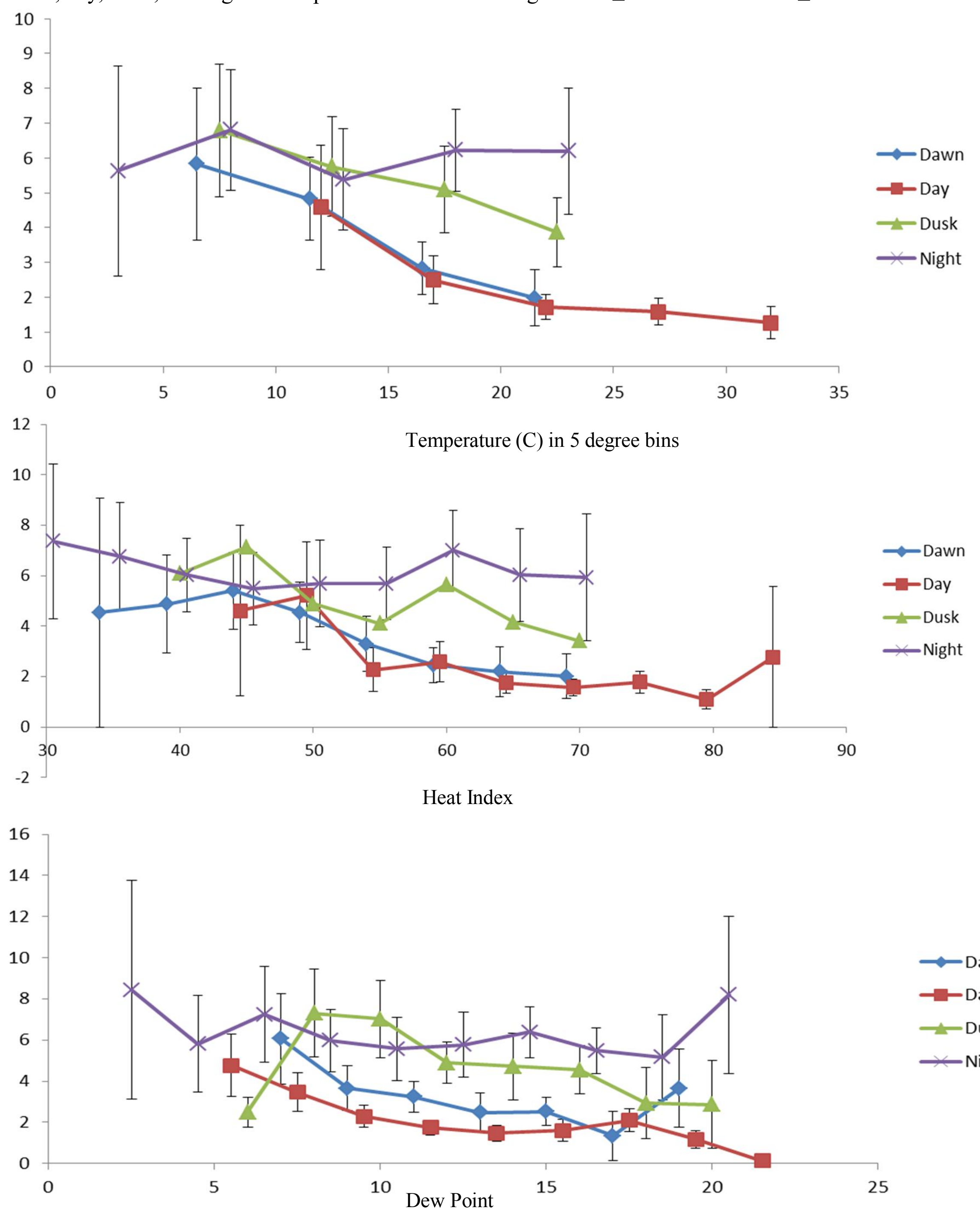
Regenerating Forest and Shrubby Grassland cover type. Use of Regenerating Forest / Shrubby Grassland with increasing ambient temperature shows a similar trend for temperature bin, dew point, and heat index (Fig. 12). All indices show the increase in the index during the day at hot temperatures. The increase at other time periods was also consistent among indices.

Figure 12. Percent use of Regenerating Forest and Shrubby Grassland cover types for temperature in 5 degree (C) bins, Dew Point, and Heat Index at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose



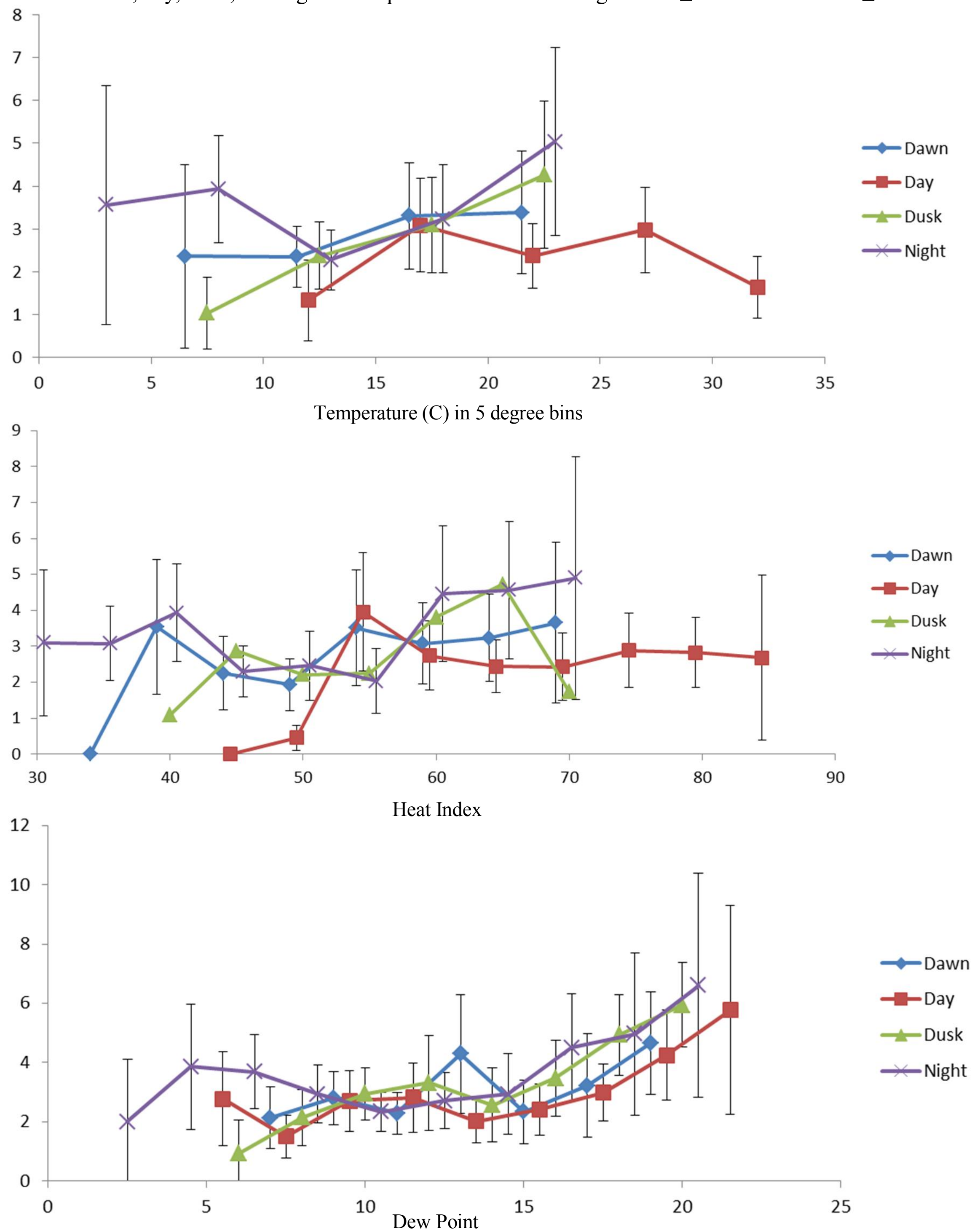
Open Water cover type. The Open Water cover type use shows consistent patterns across the temperature range (Fig. 13). All indices show the decline in use during the dawn and day as temperature increases. Use at night is relatively constant, while use at dusk also declines but is at a slightly higher percent use than during the day or at dawn.

Figure 13. Percent use of Open Water cover type for temperature in 5 degree (C) bins, Dew Point, and Heat Index at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose



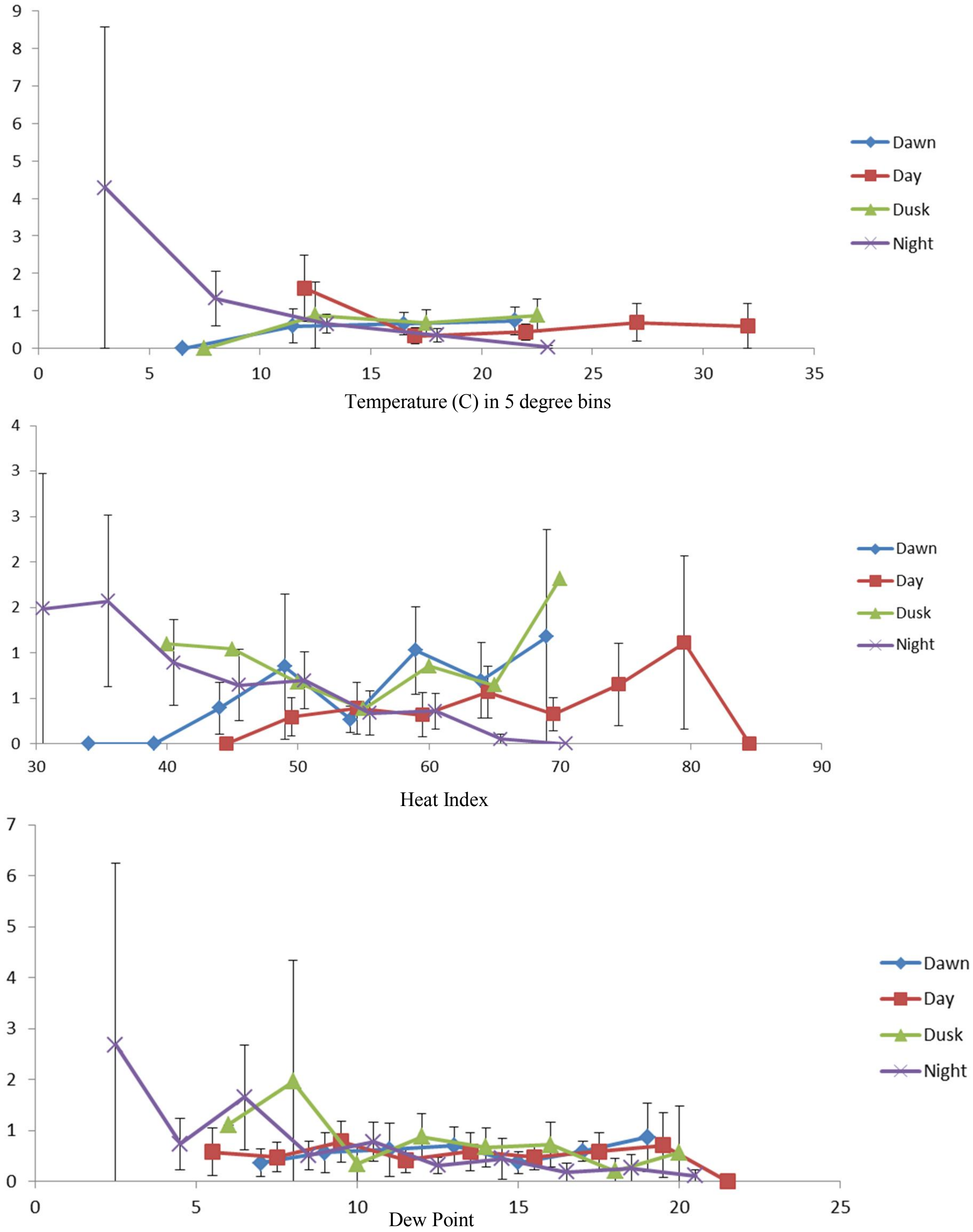
Deciduous Forest cover type. There is no clear pattern in cover type use for the Deciduous Forest cover type and high variance for all indices (Fig. 14), except that there is an increasing trend in use of this cover type at high temperatures for dew point. Variance is high on this increase, but this was the only comparison in which there was a disagreement among indices of this magnitude.

Figure 14. Percent use of Deciduous Forest cover type for temperature in 5 degree (C) bins, Dew Point, and Heat Index at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose



Coniferous Forest cover type. There is little Coniferous Forest within moose home ranges, and there was no clear pattern of use with temperature for any of these indices (Fig. 15). The increase in use of the coniferous forest cover type at low temperatures at night was due to 1 moose.

Figure 15. Percent use of Coniferous Forest cover type for temperature in 5 degree (C) bins, Dew Point, and Heat Index at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose



We used the EcoSubGroup field from the VNP National Vegetation Classification System (NVCS) (Faber-Landgendoen et al. 2007) to estimate available cover types within the MCP annual and seasonal home ranges (Figs. 16, 17, Table 4). As with LULC cover types, there are not clear seasonal patterns compared to cover type composition of the annual home range—at least at the level of contrasting percent cover type in the home range. One difference is that there are 14 cover types in the VNP NVCS instead of the 5 cover types that comprise most of the land area in the LULC classification. The top 7 cover types in the VNP NVCS comprise about 85% of the area (Fig. 16, Table 4).

Figure 16. Percent of VNP NVCS cover type within the annual, summer, and winter home range of moose (Table 1, 4) for cover types that are > 5% of area. Cover types are spelled out in the legend. Annual home ranges are not the average of Summer and Winter home ranges because of spatial overlap.

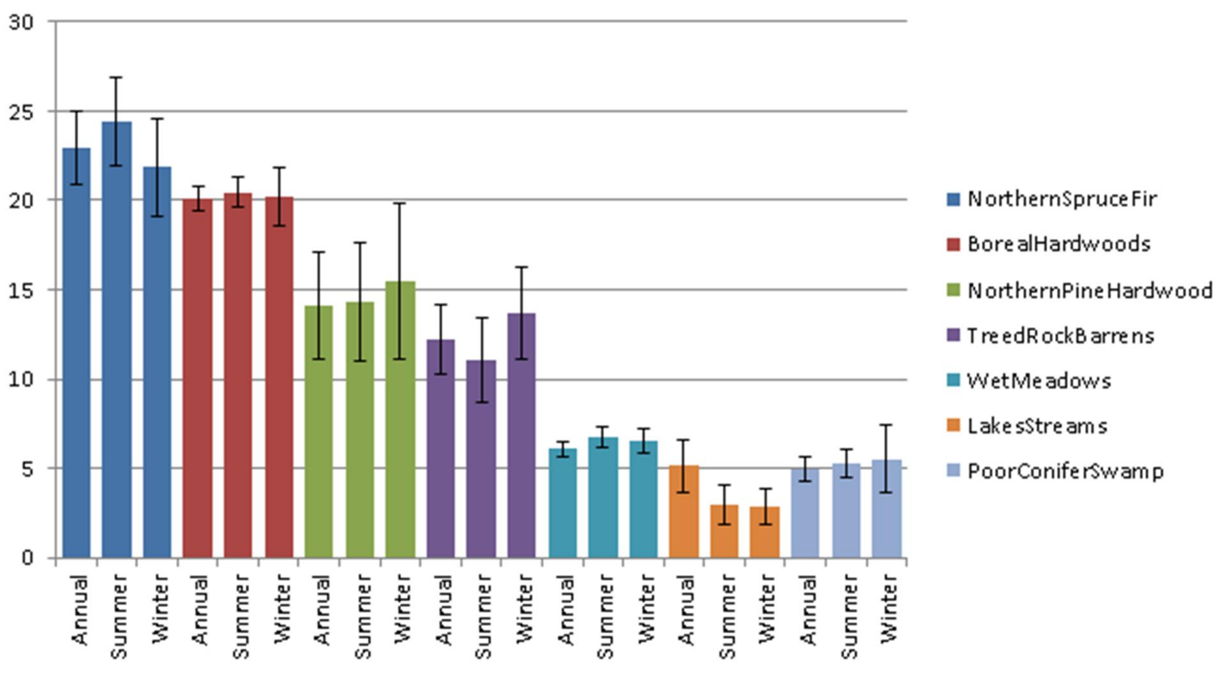


Figure 17. Percent of VNP NVCS cover type within the annual, summer, and winter home range of moose (Table 1, 4) for cover types that are < 5% of area. Cover types are spelled out except for Emergent Marshes (EmergMarshes). Annual home ranges are not the average of Summer and Winter home ranges because of spatial overlap.

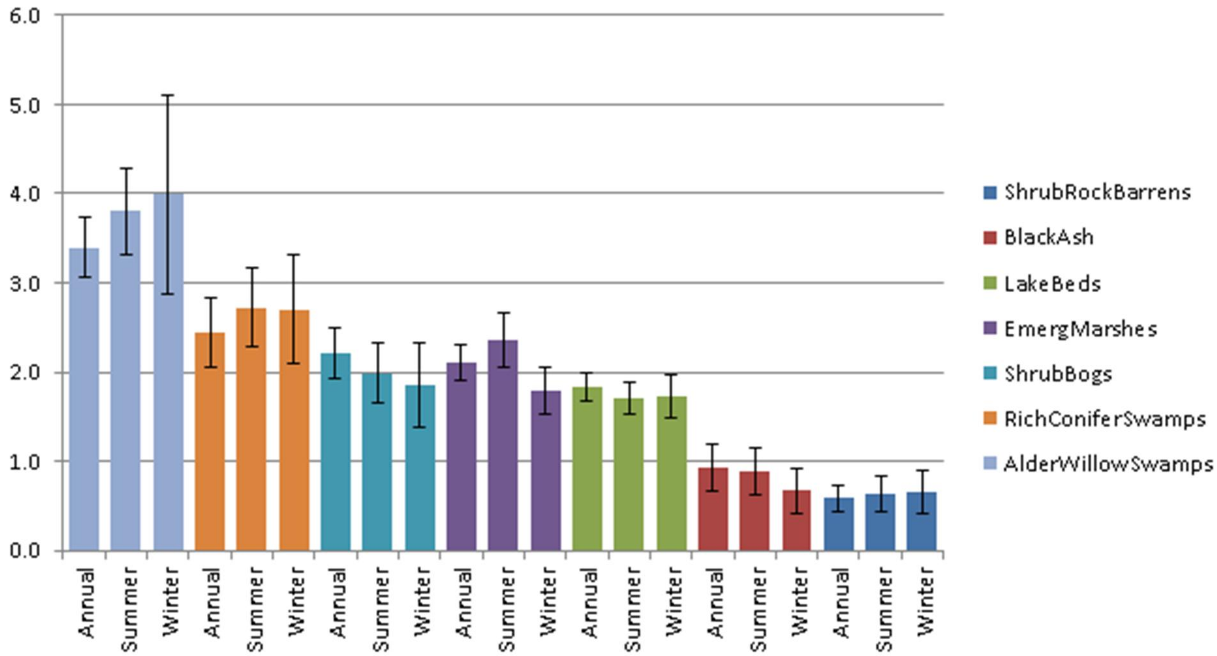
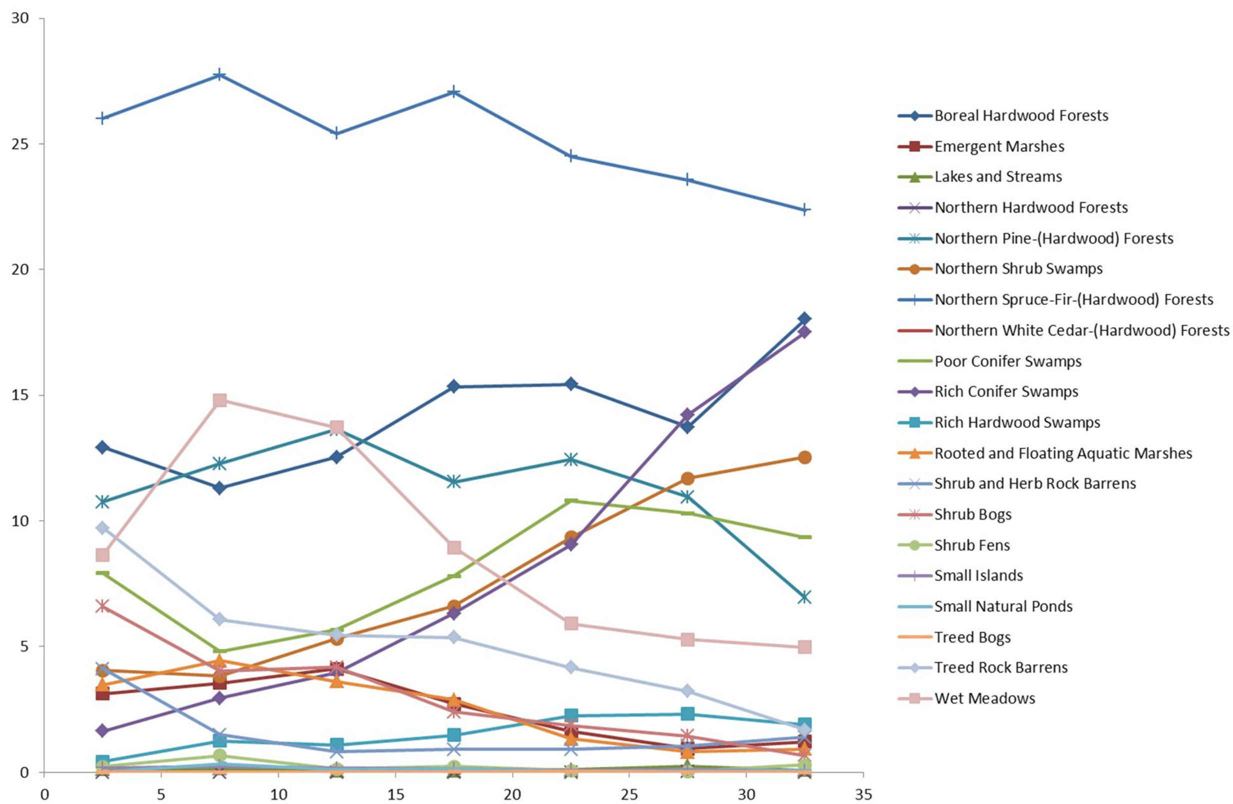


Table 4. Percent of Voyageurs National Park NVCS cover type within the annual, summer, and winter home range of moose (Fig. 2). Mean and SEM based on 20 to 27 home ranges. Areas are in km^2.

Cover Type	**Annual**		**Summer**		**Winter**	
	Mean	SEM	Mean	SEM	Mean	SEM
Northern Spruce Fir	23	2.0	24	2.5	22	2.8
Boreal Hardwoods	20	0.7	20	0.8	20	1.6
Northern Pine Hardwood	14	3.0	14	3.3	15	4.4
Treed Rock Barrens	12	2.0	11	2.3	14	2.6
Wet Meadows	6	0.4	7	0.6	7	0.7
Lakes Streams	5	1.5	3	1.1	3	1.0
Poor Conifer Swamp	5	0.7	5	0.8	6	1.9
Alder Willow Swamps	3	0.3	4	0.5	4	1.1
Rich Conifer Swamps	2	0.4	3	0.4	3	0.6
Shrub Bogs	2	0.3	2	0.3	2	0.5
Emergent Marshes	2	0.2	2	0.3	2	0.3
Lake Beds	2	0.2	2	0.2	2	0.2
Black Ash	1	0.3	1	0.3	1	0.3
Shrub Rock Barrens	1	0.2	1	0.2	1	0.2

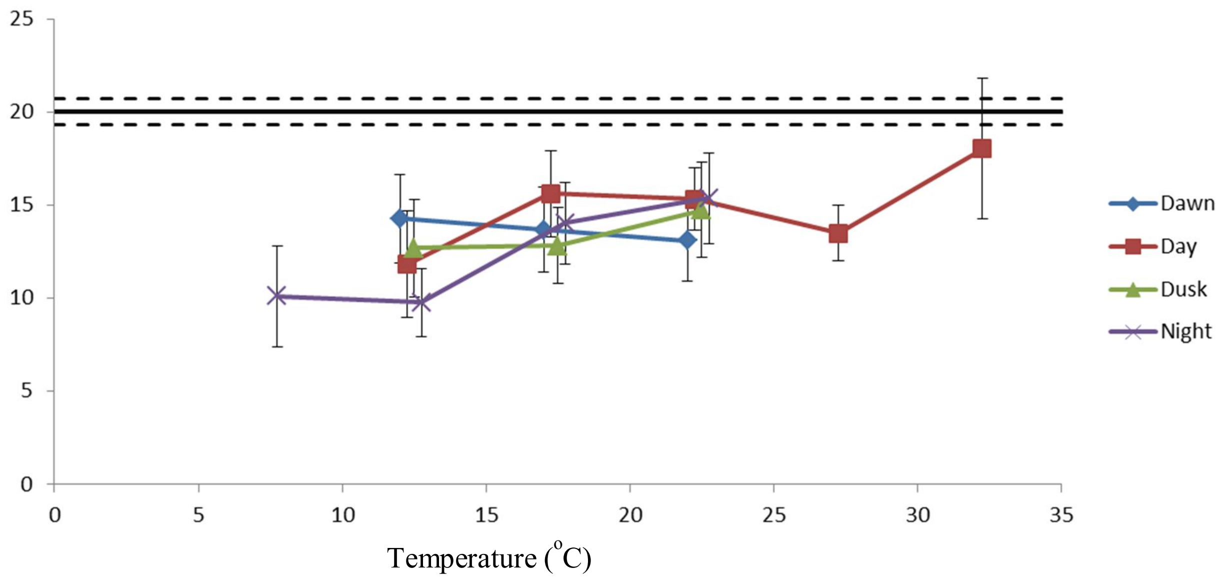
There were trends in use of some cover types with increasing temperatures based on moose GPS locations (Fig. 18). As the temperature class increased, the use of the Rich Conifer Swamp cover type increased to about 17% of locations at the hottest temperature class, even though this cover type composed only 3% of the home ranges. Northern Shrub swamp also increased, so that at hot temperatures these two cover types had 28% of the locations, even though they only comprised 8% of the home ranges. The Shrub Fen cover type use was highest at the middle temperature ranges and then decreased, but this may have been due to sample size. Moose preferred to use all of the wet cover types (except beaver meadows), with 40% of locations in the hottest temperature bin, while 10% of the home range area was in the wet cover types.

Figure 18. Percent of VNP National Vegetation Classification System (NVCS) cover type for GPS locations of moose as temperature increases. Points were placed into 5 degree bins. Variance is shown on later figures.



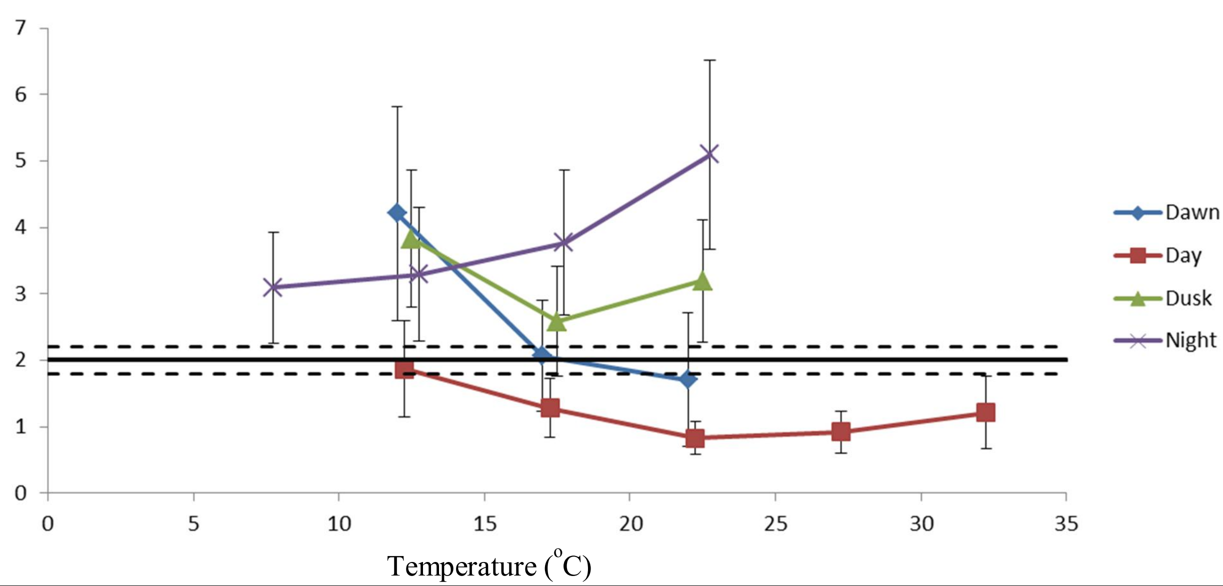
Boreal Hardwood Forests cover type. The Boreal Hardwood Forests cover type was used less than available, and generally showed a slight increase in use as temperature increased (Fig. 19).

Figure 19. Boreal Hardwood cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



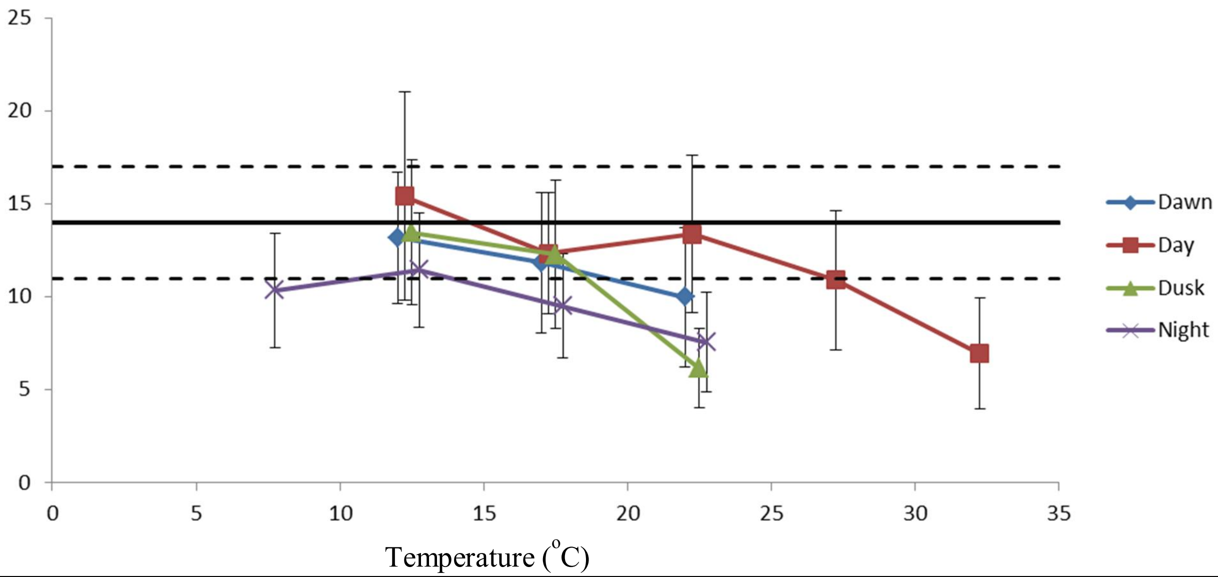
Emergent Marshes cover type. The Emergent Marsh cover type had low use during the day, and decreases in use at dawn and dusk. However, use increased at night at higher temperatures, although there was variability among moose (Fig. 20).

Figure 20. Emergent Marshes cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



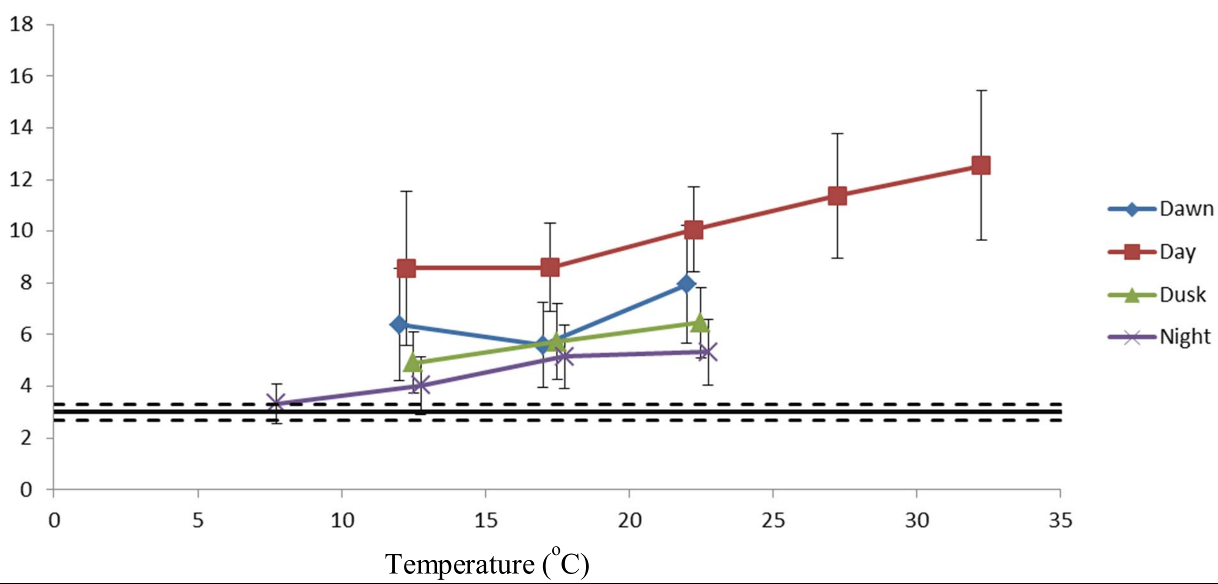
Northern Pine-(Hardwood) Forests cover type. The Northern Pine-(Hardwood) Forests cover type was used approximately in proportion to availability, and declined slightly as temperatures increased (Fig. 21). Declining trends during dawn, dusk, and night occurred about 10 degrees before declines during the day.

Figure 21. Northern Pine – (Hardwood) cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



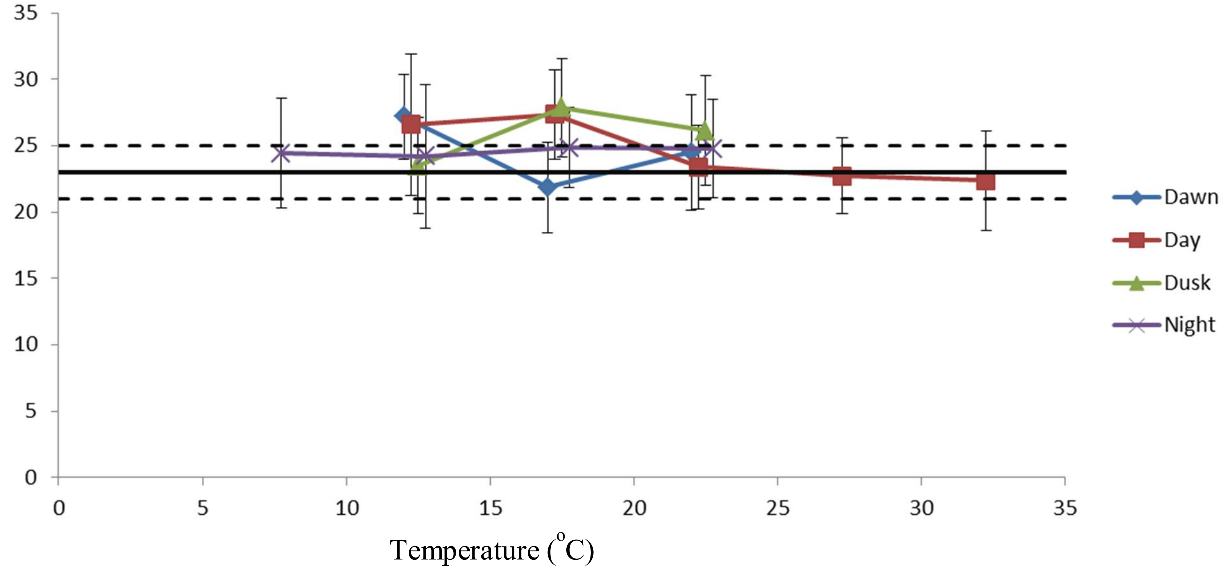
Northern Shrub Swamps cover type. The Northern Shrub Swamps cover type was used more than it was available, especially in daytime (Fig. 22). Use increased as temperature increased, to about 3 times availability at temperatures over 30 C.

Figure 22. Northern Shrub Swamps cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



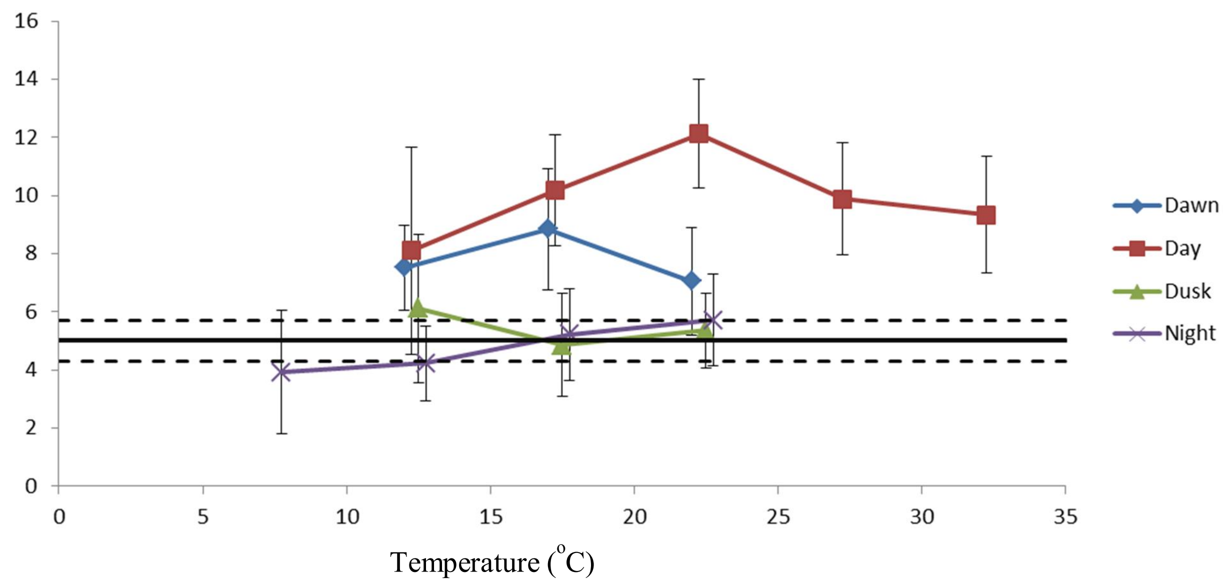
Northern Spruce-Fir-(Hardwood) Forests cover type. The Northern Spruce-Fir-(Hardwood) Forests cover type was used in proportion to availability, with a slight decline in use at higher temperatures, similar to the Mixed Forest cover type in the LULC classification (Fig. 23).

Figure 23. Northern Spruce-Fir-(Hardwood) Forests cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



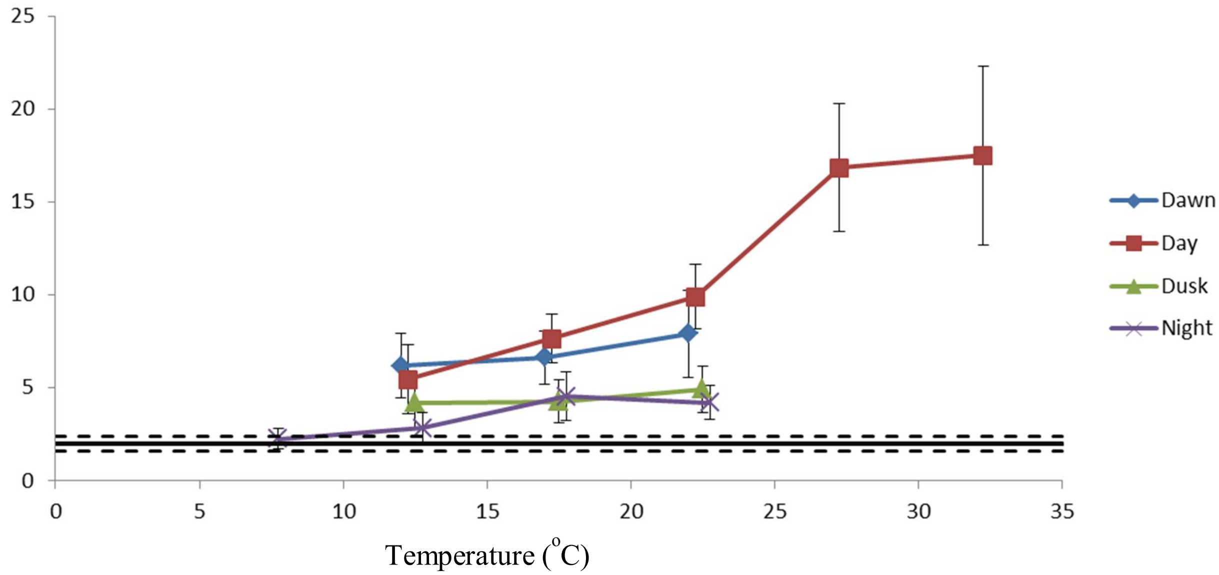
Poor Conifer Swamps cover type. The Poor Conifer Swamps cover type was used more during the day than expected, while at dusk and night it is used in proportion to availability (Fig. 24).

Figure 24. Poor Conifer Swamps cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



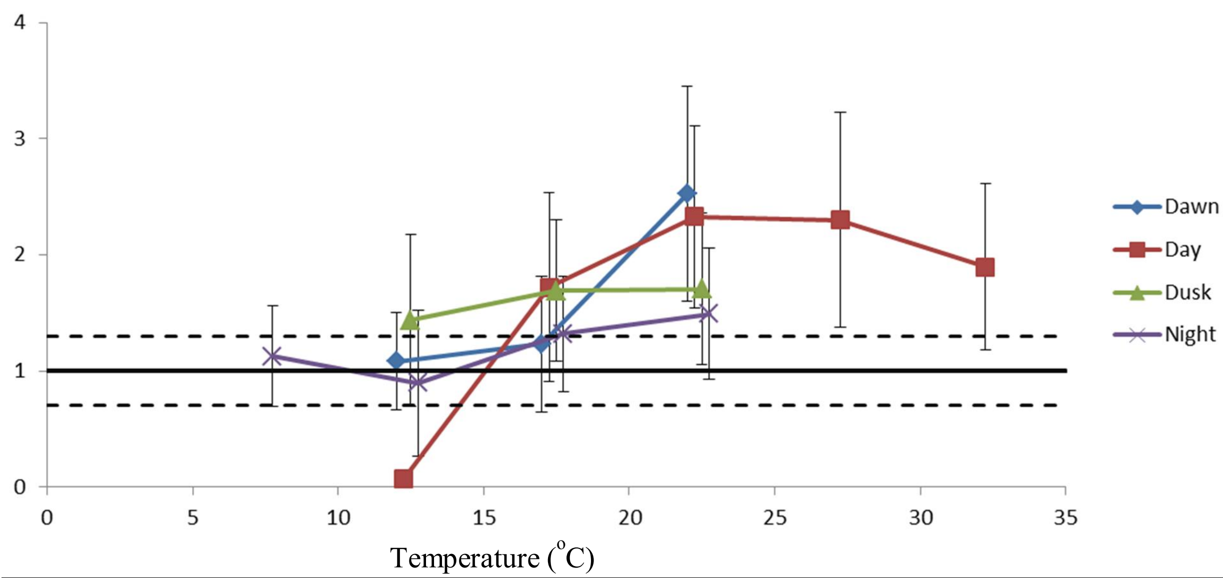
Rich Conifer Swamps cover type. The Rich Conifer Swamps cover type was used much more than available in all time periods and almost all days (Fig. 25). Use especially increased at hot temperatures, when this cover type was used about 6 times more than it was available.

Figure 25. Rich Conifer Swamps cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



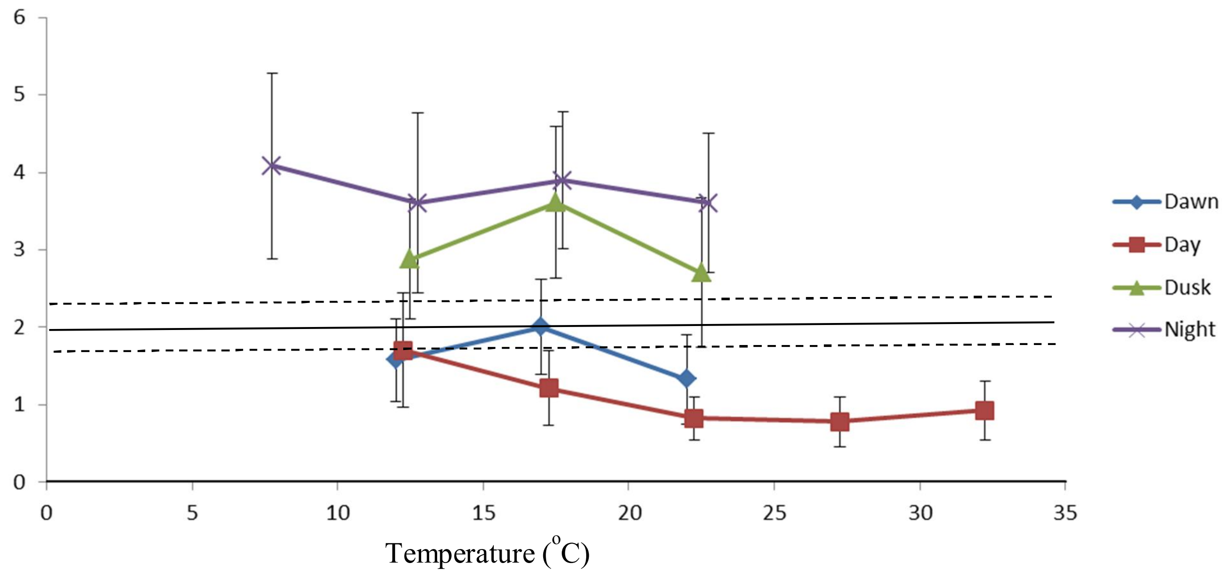
Rich Hardwood Swamps cover type. The Rich Hardwood Swamps cover type was used slightly more than available in hot temperatures, and showed at least slight increases in use in all time periods (Fig. 26).

Figure 26. Rich Hardwood Swamps cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



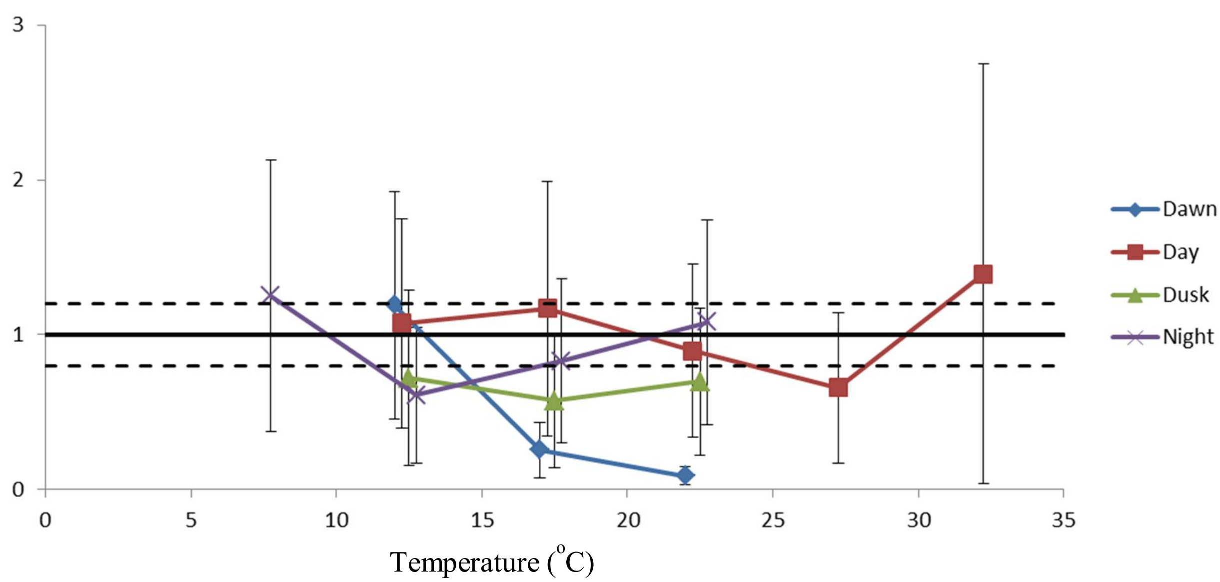
Rooted and Floating Aquatic Marsh cover type. Rooted and Floating Aquatic Marshes were used very little during the day, but were used at night (Fig. 27). There was a small decrease in use as temperatures increased.

Figure 27. Rooted and Floating Aquatic Marshes cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



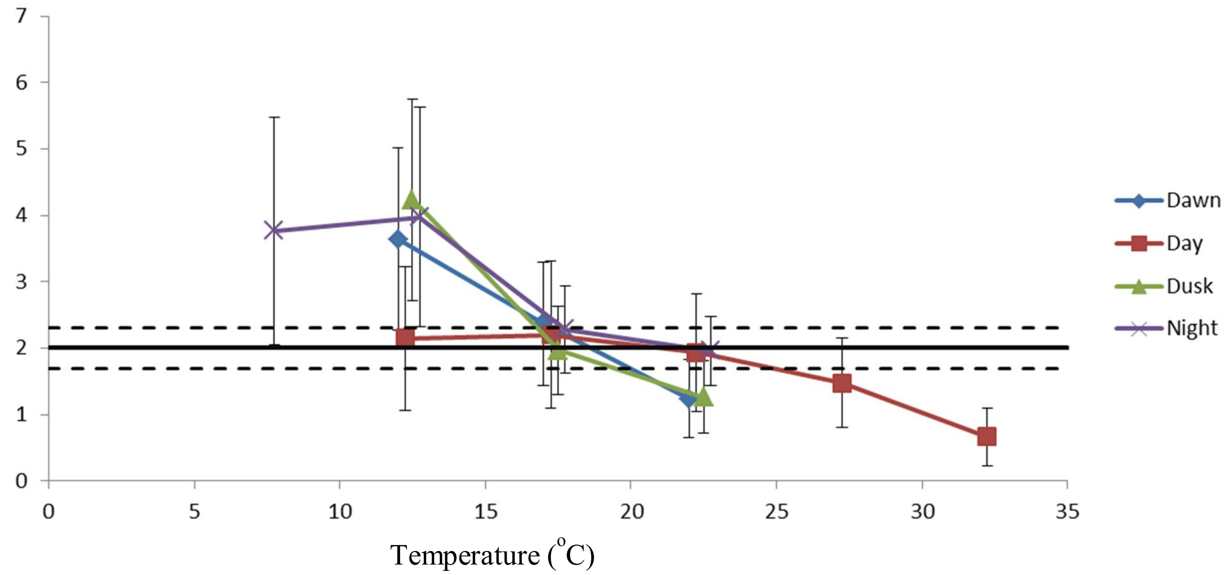
Shrub and Herb Rock Barrens cover type. The Shrub and Herb Rock Barrens cover type was used in proportion to availability, and there was little trend with temperature (Fig. 28).

Figure 28. Shrub and Herb Rock Barrens cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



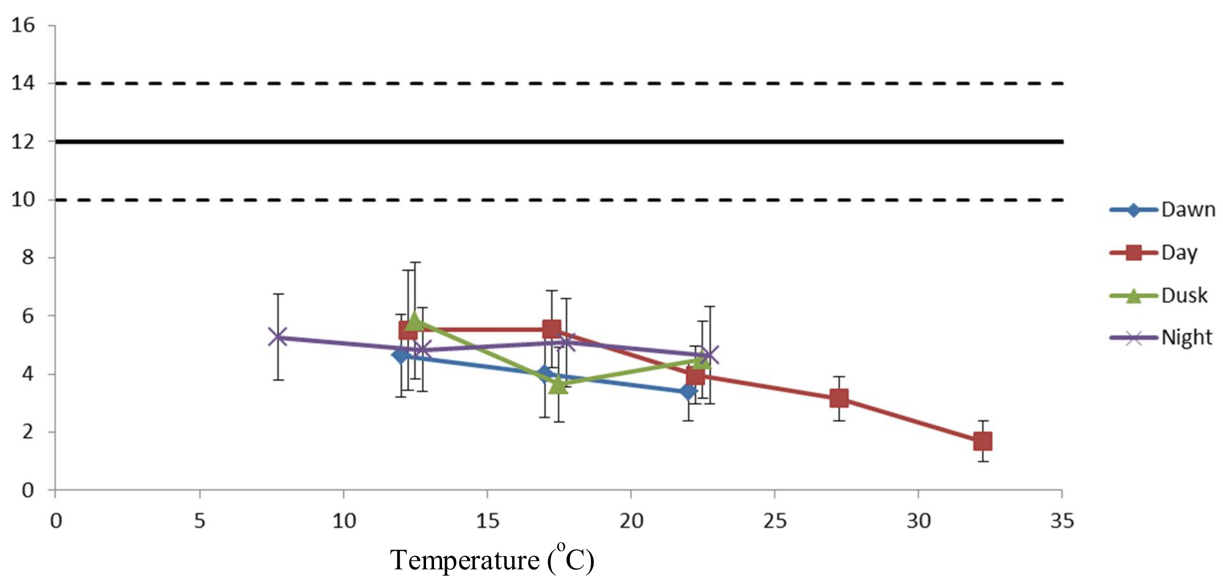
Shrub Bogs cover type. The Shrub Bogs cover type was used approximately in proportion to availability, but it did decline in use at all time periods as the temperature increased (Fig. 29).

Figure 29. Shrub Bog cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



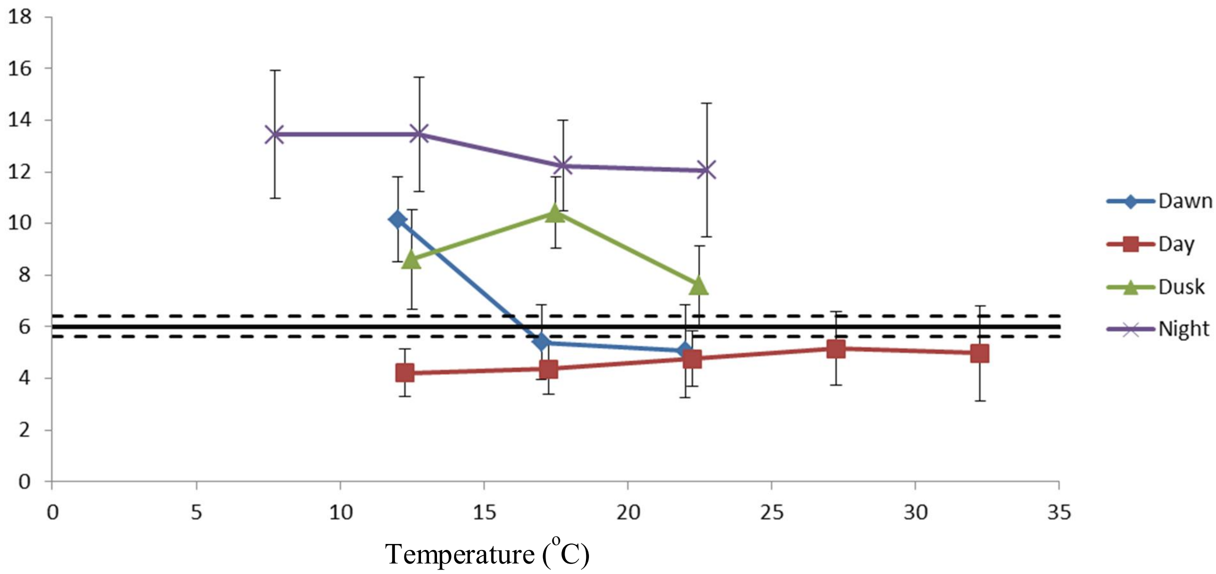
Treed Rock Barrens cover type. The Treed Rock Barrens cover type was used less than it was available, and there was a decreasing trend as temperatures increased (Fig. 30).

Figure 30. Treed Rock Barrens cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



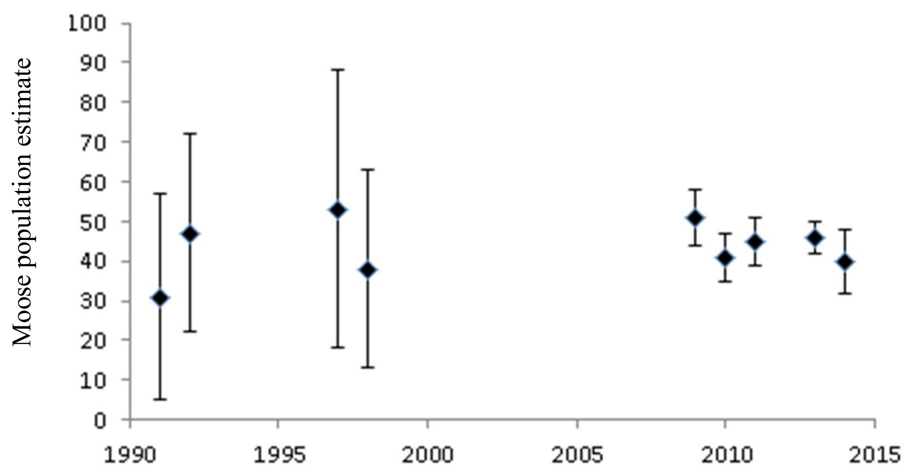
Wet Meadows cover type. The Wet Meadows cover type was used more than it was available at night and dusk. Use was similar to availability at dawn and during the day (Fig. 31).

Figure 31. Wet Meadow cover type in home range compared to the use by moose across temperature range at dawn, day, dusk, and night. Each point included in this figure had ≥ 20 locations from ≥ 10 moose.



Moose population estimates. Unlike the moose population in northeast and northwest Minnesota, the population in Voyaguers National Park has remained relatively constant from 1990 to the present (Windels 2014).

Figure 32. Estimates of the number of moose in VNP in the 1990's (Gogan et al. 1997) and in the 2010's (Windels 2014). Surveys in 2010's were done in GPS radiocollared moose used to estimate sightability, while surveys done in the 1990's were based on strip counts using a moose density strata of none and low with higher variance.



Discussion

Home Range. Annual home range size of moose in VNP from 2010 to 2012 was about 17 km^2, which was less than the average annual home range size of about 30 km^2 for moose in NE Minnesota (Moen et al. 2010, Lenarz et al. 2011). The moose in NE Minnesota included 2 females with home ranges over 100 km^2. Even after removing those two moose from the home range estimates, the VNP moose home range size is smaller than moose home ranges elsewhere in Minnesota, and in other parts of moose range.

Seasonal home ranges were also relatively small in VNP. In VNP, summer home range was about 9 km^2 in both summer and winter, while in NE Minnesota the average home range size was about 14 km^2 in summer and 30 km^2 in winter (Lenarz et al. 2011).

Cover type use at the home range scale was grossly similar between NE Minnesota and VNP, in part because there is a similar cover type composition available to moose in both areas. Differences existed for the LULC cover type because VNP is a national park without forest harvest, and because the area where moose are in VNP includes a significant amount of lowlands and beaver affected habitat (Johnston and Naiman 1990). The Mixed Forest cover type accounted for about 45% of the area of each home range, compared to about 40% in NE MN (Moen et al. 2010, Lenarz et al. 2011). The Wet Bog and Wet Marsh/Fen cover types accounted for about 28% of home ranges in VNP, and about 20% of home ranges in NE MN. The Regenerating Forest cover type, which was not present in VNP, made up the difference in NE Minnesota. Other cover types were < 10% and relatively similar between VNP and NE MN.

The VNP National Vegetation Classification System (NVCS) was composed of more cover types than LULC, but these could be collapsed into categories comparable to the LULC cover types. For example, Northern Spruce Fir, Boreal Hardwoods, and Northern Pine Hardwood accounted for about 56% of the area of an MCP range, similar to the about 60% of forested area in moose home ranges in NE MN (Moen et al. 2010, Lenarz et al. 2011).

One of the main conclusions from the cover type comparisons is that there was relatively little difference at the home range scale in seasonal cover type composition whether using the LULC or the NVCS system. There were no means that were more than 2 SEM's from the mean of the corresponding cover type in the other season. However, the similarity at the home range scale was in contrast to differences that occurred when the analysis was broken down by temperature and time of day in summer.

The Wet Bog and Wet Marsh/Fen cover types in LULC were used significantly more than available at all temperatures, and curiously use was constant across all temperatures. Moose spent about 40% of time in land classified as Wet Bog/Marsh/Fen no matter what the temperature, although the average amount of Wet Bog/Marsh/Fen in the annual home ranges was 30%. No other LULC cover type followed this pattern of constant use across temperatures and being used more than availability. For the VNP NVCS cover types, several wet cover types could be combined for an analysis with similar results. Wet cover types listed in Table 4 are about 23% of the annual home range area. Use of these wet cover types was much higher than availability, especially at high temperatures when use of these cover types comprised almost 50% of moose locations, twice the availability.

Use of the Mixed Forest cover type in LULC did not vary with temperature or time of day, except for a decrease in temperatures above 25 C. Use of the Mixed Forest cover type was also approximately in proportion to availability. The VNP NVCS classification separated forests into more specific categories, and there were trends in use and preference in forested cover types. The Boreal Hardwood Forest cover type was used less than it was available, and use increased with temperature. The Northern Pine (Hardwood) Forest cover type was used in proportion to availability, but use declined with increasing temperature. The Northern Spruce-Fir-Hardwood Forests cover type was used in proportion to availability, and use did not change with increasing temperature. Putting these three cover types together would account for about 55% of the area of moose home ranges, and about 50% of the use. Use of areas that are classified as Boreal Hardwood Forest were not preferred by moose, but were increasingly used as temperature increased.

Open Water was a cover type that was used less than it was available. Surprisingly, use decreased most at higher temperatures. It was expected that moose would be using water bodies to cool down either by convective heat loss while in the water or by evaporative heat loss when they left the water. However, availability of open water was about 9% of the home range, and in cooler temperatures moose use was about 6%. As temperatures increased above 25 C during the day moose use was < 2%. It is possible that moose were finding smaller bodies of water to dissipate body heat, but based on the increased use of wet cover types, it is more likely that moose are finding areas with a wet substrate to dissipate heat.

Use of the Regenerating Forest / Shrubby Grass cover type in LULC increased with temperature. Even during hot days when the sun would potentially be out there was increased use, especially above 20 C. Probably the most unexpected finding was that when temperatures were above 25 C moose spent 8% of the time in this cover type, and when temperatures increased to above 30 C, moose spent more than 12% of time in this cover type. One possibility is that moose are using this cover type when higher winds would allow increased convective and evaporative heat loss. However, it is unlikely that wind would have been high for 12% of the moose locations on hot days. The only possible analogous cover types in the VNP NVCS were the Northern Shrub Swamp and the Rich Conifer Swamp. Both of these cover types increased to about 12% use when temperatures were above 30 C during the day. What this means is that classification algorithms used by LULC were actually finding wetter habitats and placing them in Regenerating Forest or Shrubby Grass cover types.

The least common cover types in LULC were Coniferous Forest at < 0.5% and Deciduous Forest at about 4% . There were no comparable cover types in the VNP land cover, perhaps because conifer forests with subcanopy deciduous trees were not classified as conifer forests. These cover types were used very close to availability, with slightly less use of deciduous forests during the day at warmer temperatures.

The potential alternative heat stress indices of Heat Index and Dew Point did not improve the correlation between cover type use and temperature. Patterns were nearly the same for all cover type combinations and varied similarly with increasing temperatures. When percent use of a cover type increased with temperature, the corresponding values for Heat Index and Dew point also increased.

The single exception to this tight correlation was in the Deciduous Forest cover type where percent use of cover type was consistent between Temperature and Heat Index, but use increased at when Dew Point was greater than 15 C during all times of the day. The increase was to about 4% of locations, or about as much as the deciduous forest cover type was available in the home range. In order to fully understand this, we would need to consider whether the high dew point temperature was occurring on cooler times (e.g., 25 C ambient temperature and 20 C dew point, which would indicate nearly saturated air), or in hotter times (e.g., 32 C ambient temperature and 20 C dew point) which would indicate hot temperature but a low relative humidity and better heat dissipation. However, because this only happened < 4% of the time, it is probably not too important from an overall moose heat balance perspective.

For future analyses of moose response to temperature, we believe that the ambient temperature or the black globe temperature should be used. The ambient temperature is relatively easily available because it can be downloaded from weather stations, and avoids issues of calibrating collar temperatures or other devices. However, the black globe temperature may better represent the heat stress a moose is experiencing (McGraw et al. 2011, Olson et al. 2014).

Acknowledgements

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Literature Cited

Burdett, C.L., R. Moen, G.J. Niemi, and L.D. Mech. 2007. Defining space use and movements of Canada lynx with Global Positioning System telemetry. Journal of Mammalogy 88:457-467.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516-519.

Carpenter, L.H., and J.L. Innes. 1995. Helicopter netgunning: a successful moose capture technique. Alces 31:181-184.

Cobb, M.A., P.J.P. Gogan, K.D. Kozie, E.M. Olexa, R.L. Lawrence, and W.T. Route. 2004. Relative spatial distributions and habitat use patterns of sympatric moose and white-tailed deer in Voyageurs National Park, Minnesota. Alces 40:169-191.

Cyr, T., S.K. Windels, R. Moen, and J. Warmbold. 2014. Diversity and abundance of terrestrial gastropods in Voyageurs National Park: Implications for risk of individual moose to *Parelaphostrongylus tenuis* infection. Alces 50:121-132.

DelGiudice, G.D. 2014. Aerial moose survey. Minnesota Department of Natural Resources, St. Paul, USA.

Erb, J. and S. Benson. 2004. Distribution and abundance of wolves in Minnesota, 2003-2004. Minnesota Department of Natural Resources, St. Paul.

Faber-Landgendoen, D., N. Aaseng, K. Hop, and M. Lew-Smith. 2007. Field Guide to the plant community types of Voyageurs National Park. U.S. Geological Survey Techniques and Methods 2-A4.

Franzmann, A.W., and R.E. LeResche. 1978. Alaskan moose blood studies with emphasis on condition evaluation. Journal of Wildlife Management 42:334-351.

Franzmann, A.W., R.E. LeResche, R.A. Rausch, and J.L. Oldemeyer. 1978. Alaskan moose measurements and weights and measurement-weight relationships. Canadian Journal of Zoology 56:298–306.

Gannon, W.L., R.L. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809-823.

Gitzen, R.A., and J.J. Millspaugh. 2003. Comparison of least-squares cross-validation bandwidth options for kernel home-range estimation. Wildlife Society Bulletin 31:823-831.

Gitzen, R.A., J.J. Millspaugh, and B.J. Kernohan. 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. Journal of Wildlife Management 70:1334-1344.

Gogan, P.J.P., K.D. Kozie, E.M. Olexa, and N.S. Duncan. 1997. Ecological status of moose and white-tailed deer at Voyageurs National Park, Minnesota. Alces 33:187-201.

Hilborn, M. 2004. Moose population declining in east end of district. Fort Frances Times, Jan. 21, 2004.

Intergovernnmental Panel on Climate Change (IPCC). 2007. Climate change 2007: the physical science basis. Cambridge University Press, Cambridge, UK and New York, USA.

Johnston, C.A. and R.J. Naiman. 1990. The use of a geographic information system to analyze long-term landscape alteration by beaver. Landscape Ecology 4:5-19.

Kallemeyn, L.W. 1987. Correlations of regulated lake levels and climatic factors with abundance of young-of-the-year walleye and yellow perch in four lakes in Voyageurs National Park. North American Journal of Fisheries Management 7:513-521.

Kelsall, J.P., and E.S. Telfer. 1974. Biogeography of moose with particular reference to western North America. Le Naturaliste Canadien 101:117-130.

Kie, J.G. 2013. A rule-based *ad hoc* method for selecting a bandwidth in kernel home-range analyses. Animal Biotelemetry 1:13.

Kreeger, T.J., J.M. Arnemo, and J.P. Raath. 2002 Handbook of wildlife chemical immobilization. Fort Collins, CO: Wildlife Pharmaceuticals, Inc.

Kurmis, V., S.L. Webb, and L.C. Merriam. 1986. Plant communities of Voyageurs National Park, Minnesota, U.S.A. Canadian Journal of Botany 64:531-540.

Lenarz, M.S., M.W. Schrage, A.J. Edwards, and M.E. Nelson. 2007. Moose population dynamics in northeastern Minnesota, in: DonCarlos, M.W., R.O. Kimmel, J.S. Lawrence, and M.S. Lenarz, eds., Summaries of Wildlife Research Findings, 2005. Minnesota Department of Natural Resources, St. Paul, pp. 346-348

Lenarz, M.S., M.E. Nelson, M.W. Schrage, and A.J. Edwards. 2009. Temperature mediated survival in Northeastern Minnesota Moose. Journal of Wildlife Management, in press.

Lenarz, M.S., J. Fieberg, M.W. Schrage, and A.J. Edwards. 2010. Living on the edge: viability of moose in northeastern Minnesota. J Wildlife Management 74:1013-1023.

Lenarz, M.S., R.G. Wright, M.W. Schrage, and A.J. Edwards. 2011. Compositional analysis of moose habitat in northeastern Minnesota. Alces 47:135-149.

Maskey, J.J., and R.A. Sweitzer. 2006. Progress report: population ecology of moose in North Dakota: movements, habitat use, diets, and parasitic disease as a potential source of mortality. Unpublished progress report to North Dakota Game and Fish Department.

McCann, N. 2006 Using pellet counts to predict snowshoe hare density, snowshoe hare habitat use, and Canada lynx habitat use in Minnesota. University of Minnesota Duluth.

Moen, R., G.J. Niemi, C.L. Burdett, and L.D. Mech. 2006. Canada Lynx in the Great Lakes Region 2005 Annual Report 849.

Moen, R.A., J.M. Rasmussen, C.L. Burdett, and K.M. Pelican. 2010. Hematology, Serum Chemistry, and Body Mass of Free-Ranging and Captive Canada Lynx in Minnesota. Journal of Wildlife Diseases 46:13–22.

Murray, D.J., E.W. Cox, W.B. Ballard, H.A. Whitlaw, M.S. Lenarz, T.W. Custer, T. Barnett, and T.K. Fuller. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. Wildlife Monographs 116:1-30.

National Parks Conservation Association (NPCA). 2007. Unnatural disaster: Global warming and our national parks. Washington DC.

Ogunremi, O., M. Lankester, and A. Gajadhar. 2002. Immunodiagnosis of experimental Parelaphostrongylus tenuis infection in elk. Canadian Journal of Veterinary Research 66:1-7.

Olson, B. 2014. Measurement and modeling of thermal landscape for moose at Voyageurs National Park. M.S. Thesis. Bemidji State University.

Olson, B., S.K. Windels, M. Fulton, and R. Moen. 2014. Fine-scale temperature patterns in the southern boreal forest: implications for the cold-adapted moose. Alces 50:105-120.

Peek, J.M., D.L. Ulrich, and R.J. Mackie. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildlife Monographs 48.

Peterson, R.L. 1955. North American moose. University of Toronto Press, Toronto.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Renecker, L.A., and R.J. Hudson. 1986. Seasonal energy expenditures and thermoregulatory responses of moose. Canadian Journal of Zoology 64:322-327.

Rodgers, A.R., and J.G. Kie. 2011. HRT: Home range tools for ArcGIS®, version 1.1, user's manual. Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources.

Timmerman, H.R. 2003. The status and management of moose in North America circa 2000-2001. Alces 39:131-151.

U.S. Geological Society (USGS). 2001. Vegetation spatial database coverage for Voyageurs National Park. LaCrosse, WI: Vegetation Mapping Project, Upper Midwest Environmental Sciences Center.

Vander Wal, E., and A.R. Rodgers. 2012. An individual-based quantitative approach for delineating core areas of animal space use. Ecological Modelling 224:48-53.

VanderWaal, K.L., S.K. Windels, B.T. Olson, T. Vannatta, and R. Moen. 2014. Landscape influence on spatial patterns of meningeal worm and liver fluke infection in white-tailed deer. Parasitology in press.

Whitlaw, H.A., and M.W. Lankester. 1994. A retrospective evaluation of the effects of parelaphostrongylosis in moose populations. Canadian Journal of Zoology 72:1-7.

Windels, S.K. 2014. 2014 Voyageurs National Park moose population survey report. Natural Resource Data Series NPS/VOYA/NRDS-2014/645. National Park Service, Fort Collins, Colorado, USA.

Worton, B. J. 1987. A review of models of home range for animal movement. Ecological Modelling 38:277-298.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70(1):164-168.

Appendix 1. Other Deliverables

We had several graduate and undergraduate students at the University of Minnesota Duluth work on this project. Bryce Olson finished his M.S. Degree at Bemidji State in 2014. Other graduate students included Michael Joyce (Ph.D. student), Amanda McGraw (Ph.D. student), Tim Cyr (M.S. student), and Juliann Terry (M.S. student). All of these students have degrees in progress, with Cyr and Terry defending in December 2014 and finishing up their M.S. thesis changes in winter 2015. Joyce and McGraw will be finishing their degrees in the future. William Chen was a Ph.D. student who withdrew from the Ph.D. program before completing his degree. Undergraduate students who worked on this project include Cord Reno, Joshua Swanson, Nathan Ose, Richie Vang, Lucas O'Neil, Lee Austin, Rebecca Teigen, and Andrew Wizik.

Papers in the peer reviewed literature arising from this project include:

McGraw, A.M., J. Terry, and R. Moen. 2014. Pre-Parturition Movement Patterns and Birth Site Characteristics of Moose in Northeast Minnesota. Alces 50:93-103.

VanderWaal, K.L., S.K. Windels, B.T. Olson, T. Vannatta, and R. Moen. 2014. Landscape influence on spatial patterns of meningeal worm and liver fluke infection in white-tailed deer. Parasitology in press.

Olson, B., S. K. Windels, M. Fulton, R. Moen. 2014. Fine-Scale Temperature Patterns in the Southern Boreal Forest: Implications for the Cold-Adapted Moose. Alces 50:105-120.

Cyr, T., S.K. Windels, R. Moen, and J. Warmbold. 2014. Diversity and abundance of terrestrial gastropods in Voyageurs National Park: Implications for risk of individual moose to *Parelaphostrongylus tenuis* infection. Alces 50:121-132.

Papers in review arising from this project include:

McCann, N.P., R.A. Moen, S.K. Windels, and T. Harris. Influence of temperature on summer bed site selection by moose (*Alces alces*). Canadian Journal of Zoology, in review.

Papers to be in review within the next 3 months arising from this project include:

Moen, R., S.K. Windels, and S.A. Moore. Survival of moose in northeast Minnesota and implications for cause of death. To be submitted to Journal of Wildlife Management.

Joyce, M., S.K. Windels, B. Olson, M. Fulton, and R. Moen. Using a thermal landscape model to interpret bed site selection by moose in Voyageurs National Park. To be submitted to Ecological Modelling.

Moen, R., S.K. Windels, and M. Joyce. Home range size of moose in Voyageurs National Park over 3 decades. To be submitted to Oecologia.