DEPARTMENT OF NATURAL RESOURCES

ARE MOOSE GETTING WARM, AND HOW DO THEY RESPOND BEHAVIORALLY? VALIDATION OF AN APPROACH FOR REMOTELY MONITORING MOOSE BEHAVIORS

Andrew Herberg[1], Véronique St-Louis[1,2], Michelle Carstensen[3], James Forester[1]

SUMMARY OF FINDINGS

As part of an ongoing cause-specific mortality study of adult moose (Alces alces) in northeast Minnesota, and to better understand behavioral and physiological responses of moose to increasing ambient temperature, the Minnesota Department of Natural Resources (MNDNR) deployed Global Positioning System (GPS) collars on a total of 173 individuals from 2013-2015. This provided information on broad-scale animal movements and habitat use, but also fine-scale activity patterns using data from dual-axis activity sensors contained in the collars. In the portion of the research we present here, we wanted to test the efficacy of using dual-axis activity sensors for remotely predicting behavioral states of moose. Utilizing 10 captive female moose (>2 years old) at the Moose Research Center in Kenai, Alaska, fit with the same GPS collars as wild moose in Minnesota, we collected a total of 384 hours of behavioral observations during 4, 2-week windows distributed across seasons to evaluate if we can predict behavioral states using fine-scale activity data. Our results demonstrate that combining biotelemetry devices with modern statistical approaches allows researchers to examine the physiological and behavioral responses of moose to increasing ambient temperatures and changing landscapes, and at finer temporal and spatial scales than previously possible. Ultimately, results from this research will be applied to the data we obtained from Minnesota moose to better understand moose behavioral responses to increasing body temperatures.

INTRODUCTION

Moose are experiencing lower survival rates at the southern edge of their range compared to core geographic range (Dodge et al. 2004; Murray et al. 2006; Maskey 2008; Lenarz et al. 2010). In Minnesota, moose in the northwestern portion of the state are all but extirpated (Murray et al. 2006), and the northeastern population has declined from an estimated 8,840 in 2006 to 3,710 in 2016 – a reduction of 55% (DelGuidice 2017). Although the ultimate driver of the northeast population decline remains unknown, recent research has demonstrated that the majority of moose mortalities can be attributed to health-related causes (Murray et al. 2006; Carstensen et al. 2014). Moose are known to be physiologically sensitive to heat (Renecker and Hudson 1986; Renecker and Hudson 1989; McCann et al. 2013) and to alter the habitat types they use when ambient temperature increases (Schwab and Pitt 1991; van Beest et al. 2012; Street et al. 2015; Street et al. 2016) by selecting for habitats that act as thermal refuges (Dussault et al. 2004); i.e., to the potential detriment of spending less time in optimal foraging habitat (Street et al. 2016). Understanding not only where moose are in the landscape, but what they are doing in different areas of their range (e.g., resting, moving, foraging), is a critical step towards developing forest

[1]University of Minnesota, Department of Fisheries, Wildlife, and Conservation Biology, 2003 Upper Buford Circle, Ste. 135, St. Paul, MN, 55108
[2]Minnesota Department of Natural Resources, Wildlife Biometrics Unit, 5463-C West Broadway, Forest Lake, MN, 55025
[3]Minnesota Department of Natural Resources, Wildlife Health Program, 5463-C West Broadway, Forest Lake, MN, 55025

management practices that may benefit moose (e.g., enhance cover but also improves forage quality).

Between 2013-2015, the MNDNR deployed GPS collars equipped with dual-axis activity sensors 173 free-ranging adult moose in an effort to gain a better understanding of moose behavioral and physiological responses to ambient temperatures and habitat, among others (Carstensen et al. 2014). The activity sensors, besides recording an animal's geographic location, detect and record changes in neck movements as a measure of fine-scale activity (Ungar 2005); this provides a unique opportunity to understand and remotely predict behavioral states in free-ranging animals (Löttker et al. 2009, Ungar et al. 2010, Roberts et al. 2016). Few studies, however, have taken advantage of this technology in part due to a poor understanding of how activity sensor measurements correlate with specific behaviors. Understanding fine- and broad-scale spatial and temporal patterns in activity and habitat use has direct applications for the management and conservation of imperiled species (Gervasi et al. 2006).

The goal of this study was to develop an approach, based on observations of animals in a captive setting, to predict the proportion of time moose spend in different behavioral states over a given time period using activity sensor data. The ability to predict behavioral states from GPS-collars equipped with dual-axis activity sensors may offer insights into how moose behavior changes in response to its environment, and has direct applications to the GPS- and activity-collar data collected as part of the ongoing project of moose in Minnesota. Our specific objectives included:

1) Determine if dual-axis activity sensors can accurately classify behavioral states in moose,

2) Develop a predictive model that can be used to remotely infer behavioral states, and

3) Examine the potential for using remotely predicted behavioral states to investigate behavioral responses of moose to time of day, and changes in habitat and ambient temperatures.

STUDY AREA

The study was conducted at the Kenai Moose Research Center (MRC) located on the Kenai Peninsula, Alaska (Figure 1). The MRC, a 970-hectare captive facility operated by the Alaska Department of Fish and Game, was built in the 1960s to study moose's responses to their environment (Hundertmark et al. 2000). All moose in this study were maintained in outdoor enclosures approximately 240 ha in size and encompassed a mix of habitat types (Thompson et al. 2017). The moose were maintained at densities of 4-8 adult females per enclosure (30-60 ha/moose), depending on the time of year and conspecific aggression. Moose naturally foraged within the enclosures and were only supplemented during times of low nutritional condition, handling (e.g., weighing), or during specific studies. Moose had access to water from lakes and wetlands throughout the enclosures. To supplement water intake during the warm season (late spring to early fall) cattle troughs were available in enclosures with fewer wetlands. While predation risks were low, encounters with brown bears (*Ursus arctos*), black bears (*Ursus americanus*), and wolves (*Canis lupus*) occur sporadically within the enclosures (Dan Thompson, pers comm.).

METHODS

Moose Handling

A total of 10 moose were immobilized during 4 routine immobilization periods at the MRC (December, April, June, and September) following the procedure outlined by Thompson et al. (2017). Each of the 10 moose was fitted with a uniquely marked (i.e., color taped) Vectronic GPS collars (GPS Plus Iridium; Vectronic Aerospace GmbH; Berlin Germany) to facilitate individual recognition by the observers. The GPS collars recorded location data on board in 30-minute intervals and all data were downloaded after removal. Each GPS collar was equipped with a dual axis acceleration sensor, generating acceleration values on both a horizontal (X-value) and vertical (Y-value) plane which were summarized over 5-min intervals (refer to Herberg et al. 2017 for details). In addition to geographic location and activity, the GPS-collars also recorded ambient temperature in 5-min intervals.

Moose Observations

To determine how the activity values relate to moose behavior, we conducted behavioral observations on 8 captive moose during 6-hour long intervals. Each animal was observed twice in four 2-week long observations period in January, April, July, and October (i.e., totaling 48 hours of observations per moose over the entire study and 384 observation hours for all animals). The 6-hour observation intervals were spread randomly throughout the day from 600 to 2200 hours, and observations were made during all weather conditions. During an observation window the observer would stand at a distance ≤10 m from a given moose, and record the exact time when a new behavior occurred using Recon/Juno data loggers (Trimble Navigation Limited Trimble, Sunnyvale, California) to the nearest second in a procedure similar to Moen et al. (1996). The behaviors that were recorded included: foraging low (snout below the bottom of stomach), foraging medium (snout above the bottom of the stomach and below the top of the shoulders), foraging high (snout above the top of the shoulders), resting, ruminating, drinking/eating snow, walking, standing, running, shaking, grooming, and interacting (i.e., boxing). A 6-hour observation interval might contain missing data in instances where visual contact was lost with the observed moose (i.e. spooked and ran). If this happened, the moose being observed was relocated using VHF telemetry and missing observations were removed from subsequent analyses. All animal handling procedures were approved by the Animal Care and Use Committee, Alaska Department of Fish and Game, and Division of Wildlife Conservation (protocol No. 09–29).

Weather and Temporal Covariates

We obtained weather conditions from the National Oceanic Atmosphere Administration (NOAA) Climate Reference Network (CRN) weather station located at the MRC (Alaska, USA, 66.7251, -150.4493; https://www.ncdc.noaa.gov/crn/qcdatasets.html). Weather data were collected in 5-minute intervals and linearly interpolated to match the exact time stamps of GPS locations and activity data, respectively. The angle of the sun was calculated to further test how it might influence moose behavior; values were < 0 when the sun was below the horizon and > 0 when the sun was above the horizon. Seasons were assigned as follows: winter (1 November-31 March), spring (1 April-30 May), summer (1 June-31 August), and fall (1 September-31 October). Solar angles changed with each season, with larger negative values occurring during winter (i.e., less daylight) and greater positive values during summer (i.e., more daylight).

Statistical Analyses

Time stamps of NOAA temperature measurements, behavioral observation, GPS locations, and activity sensor data were not always the same; consequently we linearly interpolated temperature measurements and GPS locations between consecutive time stamps to match activity sensor time stamps. Behaviors were classified into the following 3 categories due to the overlap in X- and Y-activity values of many behaviors as well as the large number of 5-minute intervals consisting of >1 behavior: resting, foraging, and moving (Table 1).

We first calculated the proportion of time spent in each behavior category for every 5-minute activity interval by summing up the total time spent in each behavior category and dividing up by the total interval time (~5 minutes). All behavioral proportions within a 5-minute activity interval summed to 1. We also incorporated step length into some of our models, as it was shown to allow for a better distinction between resting behaviors with increasing head movements and low exertion forage/traveling behaviors (Gervasi et al. 2006). Because the temporal resolution differed between GPS locations and activity sensor data, we linearly interpolated GPS locations between consecutive 30-minute GPS locations to match the time stamps of the 5-min long behavior intervals, therefore assuming linear movements between GPS locations.

We used compositional Dirichlet regression models to quantify the relationship between the proportion of time spent resting ($R_{i,j}$), foraging ($F_{i,j}$) and moving ($M_{i,j}$) for each moose (i-th) within each 5-minute interval (j-th) as a function of X- ($X_{i,j}$) and Y-values ($Y_{i,j}$) as well as step length (Maier 2014).

We examined the effects of ambient temperature, time of day (i.e., solar angle), and habitat on the proportion of time spent resting, foraging, and moving using our best predictive model that included step length. To relate habitat use to changes in behavioral states, we first determined habitat use by spatially intersecting GPS locations with a classified imagery of habitat in ArcMAP 10.2 (ESRI 2013). Habitats were derived by the Alaska Fish and Game from a combination of satellite imagery and ground verification. Habitat types consisted of the following: Aspen, birch, water, bog, black spruce, mixed, grass, grass/black spruce, mixed closed, black spruce/birch, grass/black spruce/birch. To examine the seasonal effects of habitat in relation to changes in behavioral state and time of day, behavioral predictions were binned into 5% solar angles for each habitat within each season. Means and 95% confidence intervals were calculated for each bin using a bootstrap with 1000 iterations.

RESULTS

Captive Observations

We classified behaviors during direct observations for 4,608 5-minute intervals from 8 moose spread across 4 seasons, and retained 3,501 5-minute intervals (291.75 hours) after removing observations when the collar failed or if we lost visual contact with an animal. Moose rested more during summer observation periods (Table 2), with 67% of the time moose were observed at rest, 25% as foraging, and 8% as moving. During spring, the observed moose spent more time foraging relative to the other seasons; we classified 40% of the time moose were observed foraging, 54% as resting, and 6% as moving (Table 2). The proportion of time spent moving was similar for all seasons and ranged from 6% to 8%. Of these 3,501 5-minute intervals, 1,559 consisted entirely of resting behaviors, 106 foraging behaviors, while none consisted of only moving behaviors. The majority of 5-minute intervals (*n* = 1,836) consisted of more than one target behavior category (resting, foraging, and/or moving; hereafter referred to as mixed intervals) (Table 3).

Mean X and Y values were lowest during pure resting intervals ($\bar{x}_X$ = 1.71 ± 6.21 [SD]; $\bar{x}_Y$ = 0.84 ± 5.09) and highest for mixed intervals (X-value $\bar{x}$ 39.13 ± 23.75; Y-value $\bar{x}$ 28.90 ± 24.18; Figure 2; Table 3). Average X- and Y-activity values for all behavioral categorizations (resting, foraging, and mixed) varied significantly across seasons ($ANOVA_{X}$: $F_3 = 22.13$, $p < 0.001$; $ANOVA_Y$: $F_3 = 35.53$, $p < 0.001$). X and Y values were consistently higher for all behavioral categories during spring and summer compared to fall and winter, with the highest values observed during summer

(Table 4). A post-hoc Tukey test showed that accelerometer data were significantly different among all seasons (adjusted p-value < 0.001) with the exception of winter and fall season X-values (adjusted p = 0.78). These results justified the need to build different models for spring, summer, and combined fall/winter seasons.

Captive Models

Models were built utilizing a total of 2,449 5-minute intervals from 8 moose spread across the combined fall/winter (n = 1199), spring (n = 578) and summer (n = 672) seasons. Models were evaluated using 1052 5-minute intervals withheld from model building from the same 8 moose spread across fall/winter (n = 515), spring (n = 249), and summer (n = 288). The best model for all 3 seasons predicted the proportion of time spent resting, foraging, and moving as a function of X and Y values as well as step length (refer to Herberg et al. 2017 for details). The lowest Root Mean Squared Error (RMSE) was observed for the winter/fall model (RMSE: 0.1640), followed by summer (0.1871) and spring (0.2045). Small differences in RMSE between seasonal models using activity values and step length as predictors and those using only activity values as predictors suggests that X and Y values alone can provide good predictions of proportions of behaviors for studies utilizing larger time gaps between GPS locations. However, models without step length were found to consistently over predict proportion of time spent resting during observed foraging bouts, especially during summer.

Captive Moose Predictions

During spring, summer, and fall, MRC moose were more likely to increase the proportion of time they spent resting during the middle of the day (greatest angle of the sun) and the middle of the night (lowest angle of the sun) and were more likely to be foraging and moving during crepuscular periods (Figure 3). This pattern differed for winter; moose activity (foraging and moving) peaked during crepuscular times as well as the middle of the night (Figure 3). Along with the sun's position, we observed changes in behavior in association with variation in ambient temperature. During all seasons, with the exception of winter, we observed a positive association between the mean proportions of time spent resting and higher ambient temperature (Figure 4). This association varied by season, with increases in rest occurring at higher temperatures during spring (>18°C) than summer (>16°C) and fall (10°C). We observed a slight increase in moving behavior at temperatures >25°C during summer. Moose were more active in aspen and birch stands during the summer season; as solar angle increased moose utilizing both black spruce stands and bogs displayed the highest proportions of resting behaviors (Figure 5). Moose utilizing black spruce stands were less active during all solar angles during spring compared to those utilizing bogs, aspen and birch stands. Activity patterns did not vary much between habitat type and time of day during the winter and fall seasons (Figure 5).

DISCUSSION

We established that dual-axis activity sensors programed to record activity values in 5-minute intervals can be used to predict the proportion of time spent resting, foraging, and moving in either captive or free-ranging moose. While previous studies have utilized behavioral observations of captive animals to validate collar activity sensors, most have chosen to use time intervals consisting of only purely active or inactive behaviors to build predictive models (Ungar et al. 2005; Löttker et al. 2009). Studies that did utilize time intervals encompassing more than one behavioral state typically converted intervals to the mode behavior observed within that time period (e.g., Moen et al. 1996), which often resulted in substantial increases in error when predicting intervals of mixed behaviors (Moen et al. 1996, Löttker et al. 2009). Nearly all of our observed active 5-minute time intervals contained a mix of active behaviors (foraging, walking, running, interacting, drinking) and inactive behaviors (standing, vigilance). These observations were consistent with findings in captive roe deer (*Capreolus capreolus*), where nearly all observed active intervals contained inactive behaviors (Gottardi et al. 2010) – this confirms the need for a modeling approach (e.g., the Dirichlet modeling technique we used) that incorporates a natural mix of behaviors in ruminants.

The significant differences we observed in activity values between all 4 seasons suggest there is a need to develop season-specific (i.e., spring, summer, fall/winter combined) predictive models in this system. Several factors may affect, alone or in concert, the seasonal differences we observed. Moose's body condition may affect GPS collar fit, with the loosest fit occurring during spring and transitioning to the tightest fit during late fall/early winter (Dan Thompson, pers comm.), although we did not observe significant differences in X and Y values resulting from variation in individual moose collar fit and behavior, potentially due to the low number of observation hours performed (results not shown) in a side project designed to test how the collar fit affects activity counts. In general, however, looser collar fit combined with increased foraging activity during spring and summer could explain the higher activity values observed during both resting and active 5-minute behavioral states during those seasons compared to winter and fall. Moen et al. (1996) found increased activity counts during summer due to a combination of increases in browsing, head movement needed to strip leaves, and head movement from insect harassment. Significant differences were found in both phases of a second collar-fit experiment developed in a lab; increased rotation ("movement") and looser collar fit on the collar machine resulted in increased activity values. Significant differences were found between behavioral type using trained horses, with standing behaviors exhibiting the lowest activity values and trotting exhibiting the highest values (McGraw et al. In prep). The results of this experiment corroborate with the finding of Moen et al. (1996).

Captive MRC moose appear to modify their behavior in response to changes in ambient temperature, solar angle, and habitat type. Moose are known to be physiologically sensitive to heat (Renecker and Hudson 1986, Renecker and Hudson 1989; McCann et al. 2013). Renecker and Hudson (1986, 1990) found that temperatures greater than -5°C in the winter and 14-20°C during the warm season (late spring to early fall) were associated with increased metabolic, heart, and respiratory rates, reduced food intake, and reduced body weight. McCann et al. (2013) found similar thresholds for late spring to early fall (17-24°C). These were based on 2 and 4 captive moose respectively, and highlight the difficulty of assessing thermal thresholds outside of a captive setting. Temperature-dependent changes in behavior were the least pronounced during winter for MRC moose. Street et al. (2015) found slight increases in activity values at moderate temperatures during winter. These findings corroborate with the slight increase in activity we observed as ambient temperatures increased toward 0°C. Well adapted to tolerate cold temperatures, moose are limited by both forage quantity and quality during the winter; this could explain why we observed relatively constant activity levels across much of the ambient temperature gradient during this season (Schwartz et al. 2007). During both the summer and fall we saw marked decreases in the proportion of active behaviors as temperatures increased. The mean proportion of active behaviors decreased considerably at temperatures exceeding 15°C and 5°C during summer and fall respectively, suggesting that moose during these seasons are faced with the tradeoff between resting more frequently to reduce thermal stress and seeking quality food sources and foraging. Forced to rest during times of increased ambient temperatures, moose forfeit feeding opportunities and this deficit has been shown to reduce weight and overall body condition (Renecker and Hudson 1992).

Our results suggest, that when experiencing warm temperatures during late spring (i.e., May), moose may choose to take advantage of increased forage quality and abundance at the cost of potential thermal stress. As spring advances, rapid plant growth occurs and nutritional quality peaks. This time period also corresponds with peak energetic demands on gestating and lactating female moose (Schwartz et al. 2007); Gasaway and Coady (1974) indeed found that the metabolizable energy requirement by the end of the gestation period is 6-fold compared to March. Parturition initiates an even more energy-demanding phase, 2- to 3-fold that of gestation. Energy needs therefore peak during the early summer and gradually decline as the young are weaned (Schwartz et al. 2007).

Behavioral responses of moose to thermal conditions are consistent throughout much of North American moose range. Moose occupying the boreal forest of Québec utilized conifer forest as a thermal refuge more frequently when ambient temperatures were high (Dussault et al. 2004). Likewise, moose in British Columbia were found to select for mature forest when temperatures exceeded critical limits (Schwab and Pitt 1991). We observed similar patterns at the MRC, where moose utilizing conifer stands during both spring and summer rested more than those utilizing aspen and birch stands, especially during the middle of the day when the sun and ambient temperatures were peaking. Additionally, moose in Alberta were found to bed in wet meadows during summer to reduce both respiration rates and energy expenditure (Renecker and Hudson 1990). At the MRC, we found that the captive moose that were using bogs during summer displayed high proportions of resting behaviors, which indicates that they may be using bogs as thermal refuges Future efforts should focus on incorporating more data from the Carstensen et al. (2014) study to investigate fine-scale behavioral patterns of moose in northeastern Minnesota in response to habitat and ambient temperature.

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Table 1. Description of the 3 behavior categories that we used to evaluate the performance of dual-axis accelerometer values for predicting moose behavior. Observations were made on 8 GPS-collared captive female moose at the Moose Research Center, Kenai Peninsula, Alaska during 2015.

Behavior	Classification	Description
Laying	Resting	Bedded position with legs generally tucked, head could be up or down.
Ruminating	Resting	Predominantly bedded position, with or without head movement. Infrequently while standing.
Standing	Resting	Upright quadruped position, with or without head movement (i.e. vigilance).
Drinking	Foraging	Consumption of water during the warm season (spring, summer, fall). Could be standing or lying.
Snow intake	Foraging	Consumption of snow during the winter season. Could be standing or lying.
Foraging low	Foraging	Consumption of foraged plants, with mouth below the bottom of the stomach while standing or while lying.
Foraging medium	Foraging	Consumption of foraged plants with the mouth above the bottom of the stomach but below the shoulder hump.
Foraging high	Foraging	Consumption of foraged plants with the mouth above the top of the shoulder hump.
Walking	Moving	Slow methodical movement, forward or backward.
Running	Moving	Accelerated movement, forward.
Shaking	Moving	Accelerated up-down/side-to-side head and body movement while walking, foraging, standing, or lying.
Grooming	Moving	Self-grooming with hind hooves and/or rubbing against trees.
Interaction	Moving	Social interaction with other moose, with forelegs leaving the ground (i.e. boxing).

Table 2. Proportion of time 8 captive adult moose (>2 years of age) were observed in each behavioral state during 3,501 5-minute intervals at the Moose Research Center, Kenai Peninsula, Alaska distributed across four, user-defined seasons during 2015.

Season	Number of 5-minute intervals	Rest	Forage	Moving
Winter (1 Nov-31 Mar)	872	0.56	0.38	0.07
Spring (1 Apr-30 May)	827	0.54	0.40	0.06
Summer (1 June-31 Aug)	960	0.67	0.25	0.08
Fall (1 Sep-31 Oct)	842	0.60	0.34	0.06

Table 3. Mean (±SD) X- and Y-activity values of 5-minute intervals of pure behaviors such as resting or foraging, mixed behaviors, or for all 3,501 observation intervals obtained from observing 8 adult captive female moose at the Moose Research Center, Kenai Peninsula, Alaska during 2015. None of the intervals we observed contained strictly moving behaviors.

Behavior	Number of 5-minute intervals	Mean activity X	Mean activity Y
Resting	1559	1.71 (±6.21)	0.84 (±5.09)
Foraging	106	38.94 (±13.31)	20.25 (±8.60)
Mixed	1836	39.13 (±23.75)	28.90 (±24.18)
All	3501	22.46 (±25.77)	16.15 (±22.59)

Table 4. Mean (±SD) X- and Y-activity values across four seasons of 5-minute intervals of pure behaviors such as resting or foraging, mixed behaviors, or for all 3,501 intervals obtained from observing 8 adult captive female moose at the Moose Research Center, Kenai Peninsula, Alaska during 2015. None of the intervals we observed contained strictly moving behaviors.

Behavior	Season	Number of 5-minute intervals	Mean activity X	Mean activity Y
Resting	Winter	334	0.19 (±2.02)	0.13 (±1.44)
	Spring	316	1.23 (±5.93)	1.02 (±7.51)
	Summer	521	3.94 (±8.91)	1.64 (±6.20)
	Fall	389	0.42 (±22.44)	0.24 (±1.81)
Foraging	Winter	20	33.10 (±9.71)	15.60 (±5.92)
	Spring	44	38.84 (±7.62)	22.80 (±5.82)
	Summer	5	59.17 (±18.58)	41.00 (±10.56)
	Fall	29	39.17 (±17.90)	14.97 (±4.89)
Mixed	Winter	518	31.85 (±18.13)	22.95 (±18.18)
	Spring	467	37.27 (±21.30)	27.57 (±23.19
	Summer	434	55.17 (±28.97)	45.18 (±27.54)
	Fall	424	33.77 (±18.26)	21.01 (±19.82)

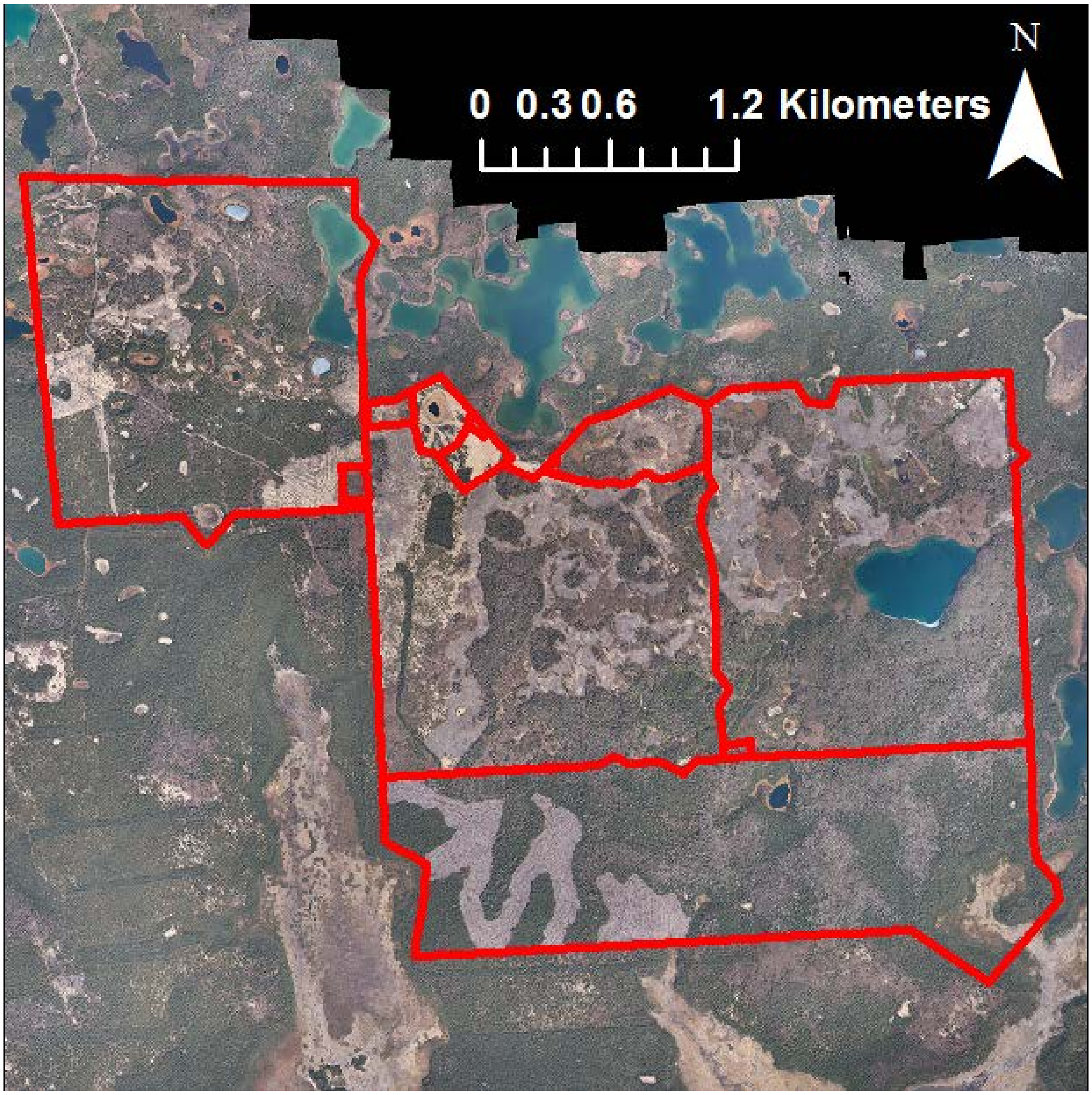

Figure 1. Map of the Moose Research Center in Game Management Unit 15A, Kenai Peninsula, Alaska.

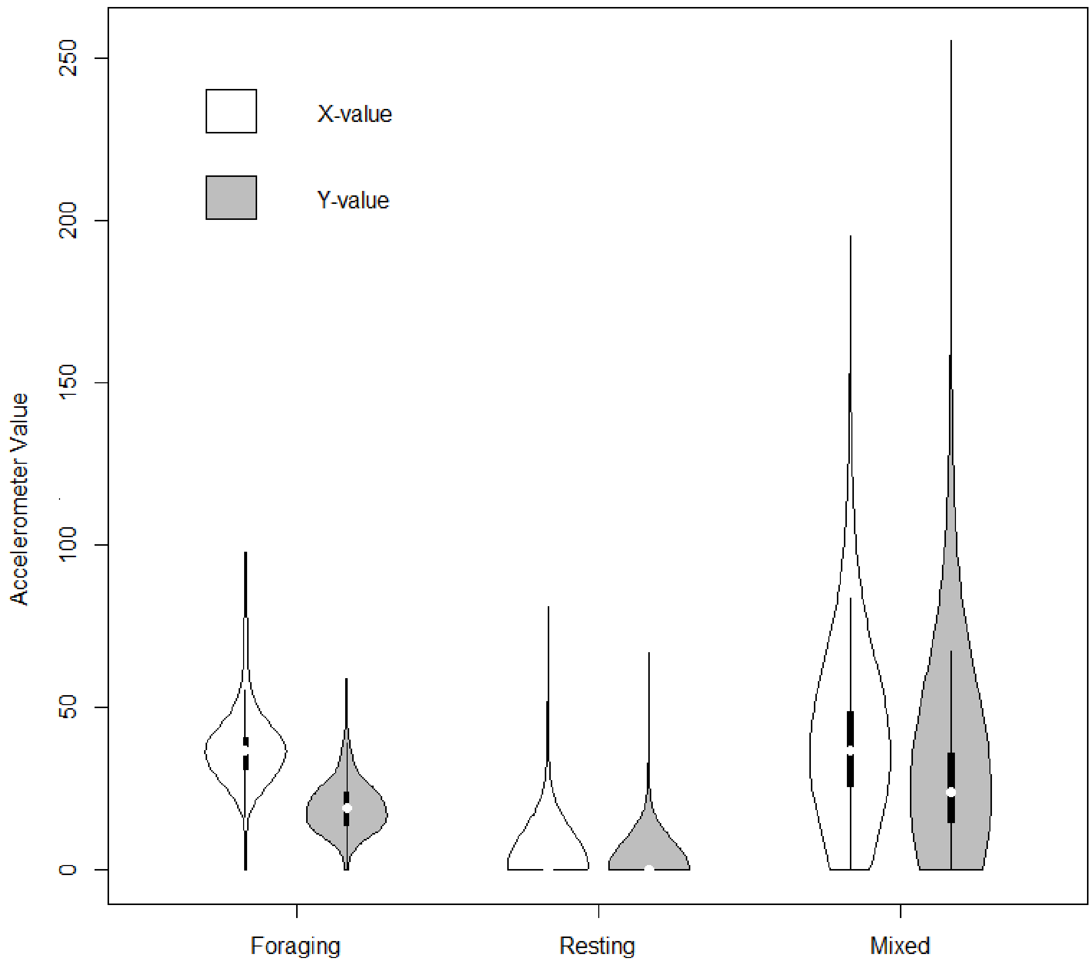

Figure 2. Visualization of X- and Y- accelerometer values from a total of 3,501 5-minute intervals across all seasons from 8 adult captive moose at the Moose Research Center, Kenai Peninsula, Alaska during 2015. 1560 intervals contained only resting behaviors, 98 only foraging behaviors, but none contained only walking/resting behaviors. The majority (1843) were mixed and contained more than 1 behavior.

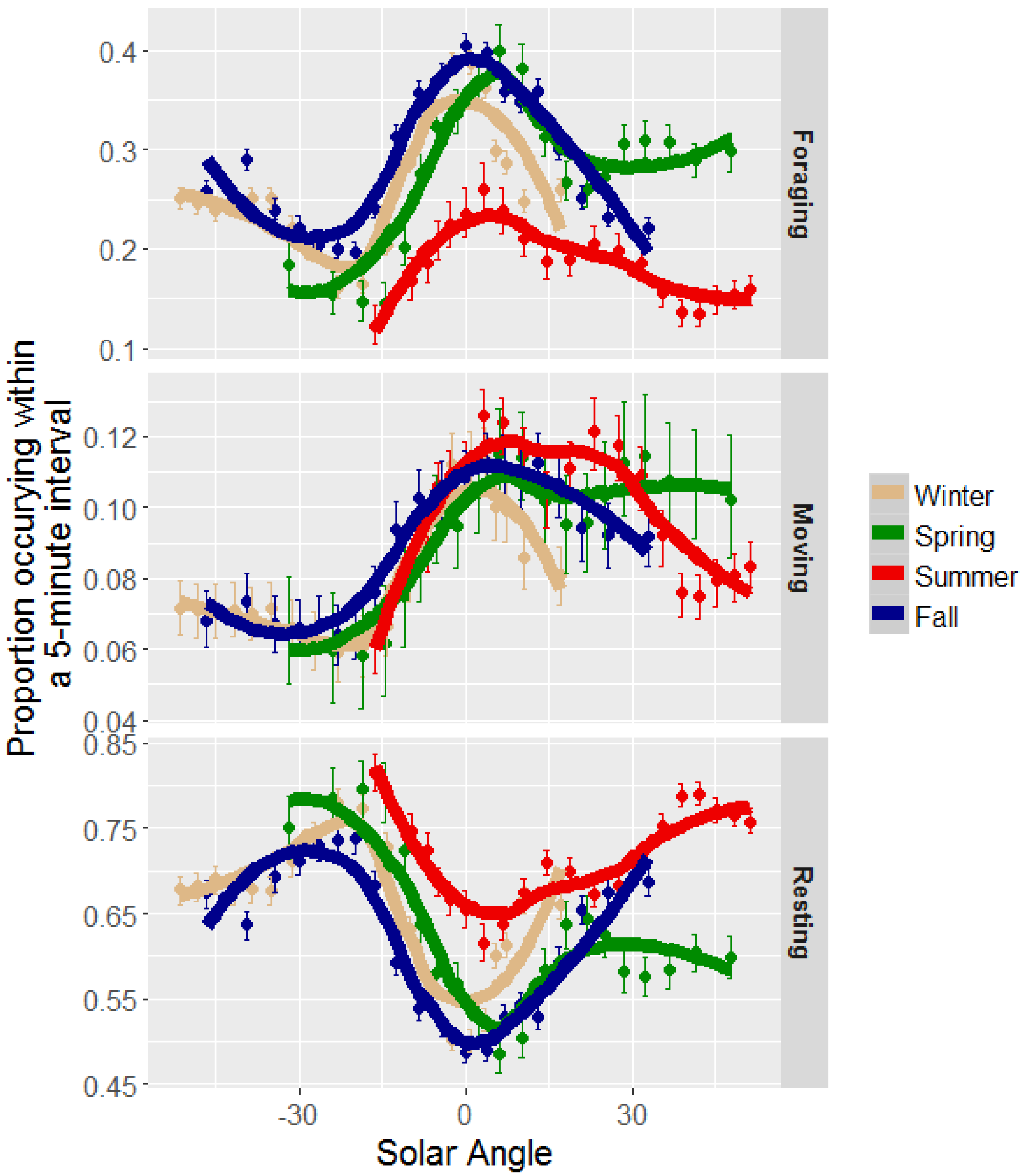

Figure 3. Mean predicted proportions of time spent foraging, moving, and resting within a 5-minute interval in response to changing solar angles for 8 captive moose at the Moose Research Center, Kenai Peninsula, Alaska during 2015. Crepuscular times are centered on zero with lowest values corresponding to the middle of the night and the highest values to the middle of the day. Predictions were binned into 5% quantiles. Means and 95% confidence intervals were calculated using bootstrapping with 1000 iterations. Trends are depicted using locally weighted smoothing curves.

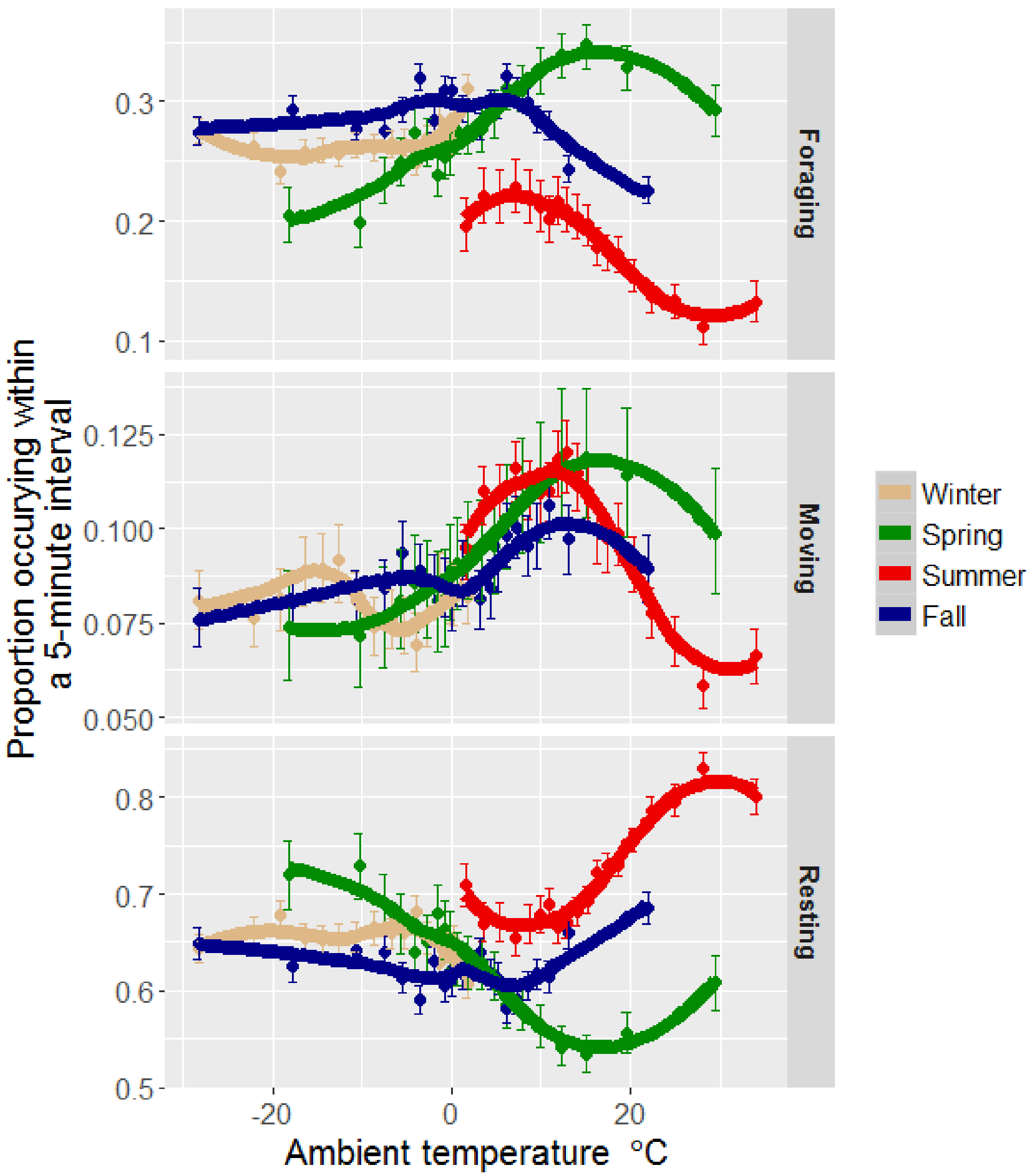

Figure 4. Mean predicted proportions of time spent foraging, moving and resting within a 5-minute interval in response to changing ambient temperature for 8 captive moose at the Moose Research Center, Kenai Peninsula, Alaska during 2015. Predictions were binned into 5% quantiles. Means and 95% confidence intervals were calculated using bootstrapping with 1000 iterations. Trends are depicted using locally weighted smoothing curves.

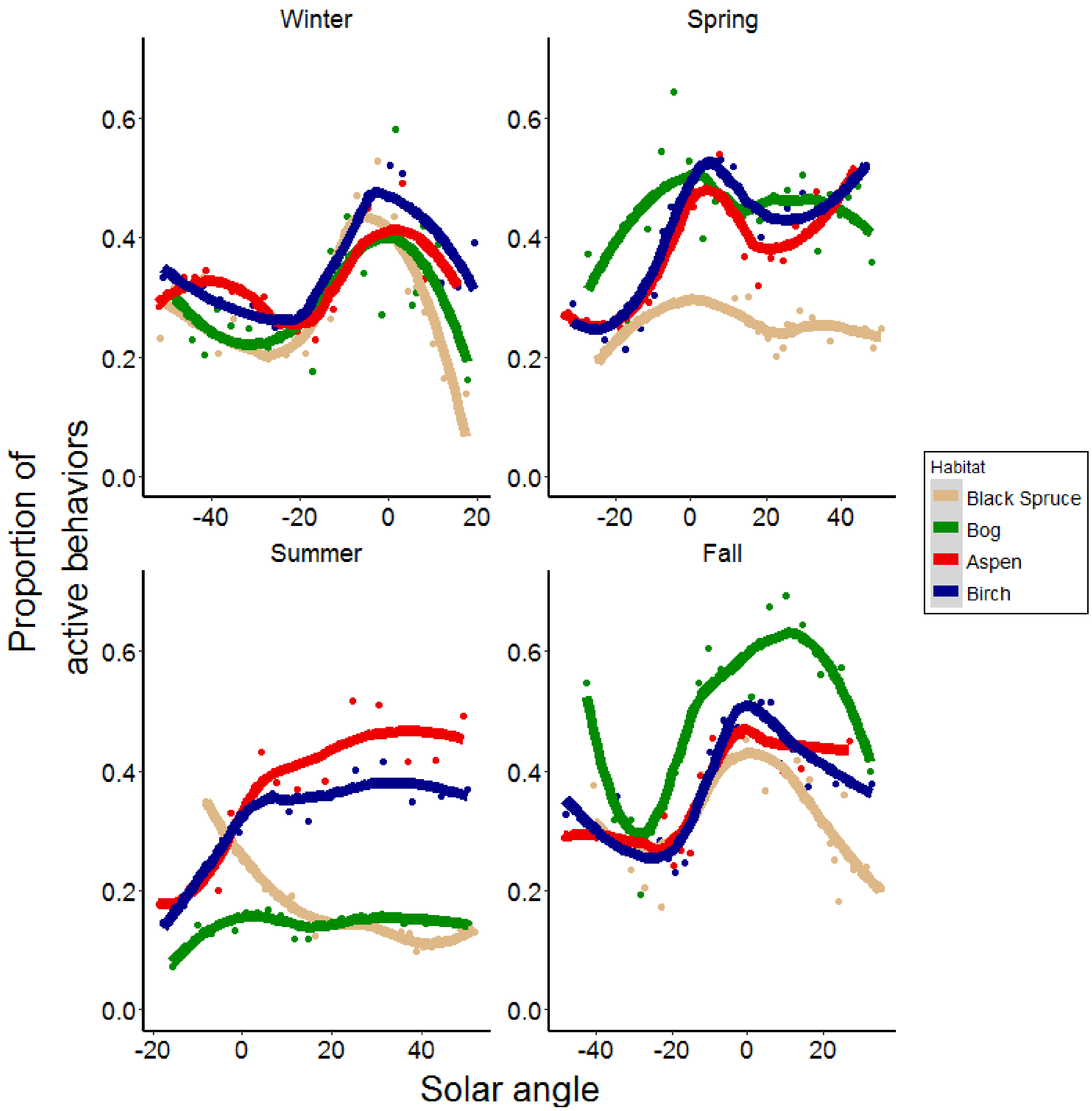

Figure 5. Mean combined predicted proportions of foraging and moving behavioral states (active) within a 5-minute intervals collected within each habitat in response to changing solar angles for 8 captive moose at the Moose Research Center, Kenai Peninsula, Alaska during 2015. Crepuscular times are centered on zero with lowest values corresponding to the middle of the night and the highest values to the middle of the day when the sun is at its highest point. Predictions were binned into 5% quantiles. Means and 95% confidence intervals were calculated using bootstrapping with 1000 iterations. Trends are depicted using locally weighted smoothing curves.