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Bed sites as thermal refuges for a cold-adapted ungulate in summer

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Ungulates that are adapted to cold climates may use bed sites as thermal refuges during summer. At the southern edge of their distribution moose *Alces alces* often encounter ambient summer temperatures above their upper critical temperature. Summer is also when moose increase food consumption and metabolism, which increases heat generation that must typically be lost at bed sites. To determine if moose use bed sites that enable heat loss when temperatures are hot, we randomly sampled bed sites of moose from across the entire range of ambient summer temperatures. We calculated kernel density estimates for each day and night using GPS locations collected each 20 min for an entire summer to identify bed sites. Kernel density estimates identified bed sites accurately. During the day, moose bedded under lowland forest canopies where substrates had high water content. At night, bed sites were in openings which are associated with greater browse availability and net heat loss. Lowland forests interspersed with openings should help moose to maintain thermal balance during summer. Because thermoregulatory behavior is linked with fitness, thermal refuges should be especially important in areas where moose population declines have been positively correlated with warming temperatures.

Ungulates that live in temperate and boreal regions face the opposing demands of increased metabolism and avoiding heat stress during summer. Forage quality and quantity is high during summer, and ungulates increase food consumption to produce milk and deposit fat and muscle in preparation for winter (Renecker and Hudson 1986b). Locomotor activity and digestion and processing of food increases the resting metabolic rate (Nilssen et al. 1984, Renecker and Hudson 1986a), which in turn increases the probability of heat stress (Kadzere et al. 2002). Thus, the likelihood for heat stress during summer increases for ungulates due to increased food intake and metabolism. Ungulates can reduce the likelihood for heat stress by employing thermoregulatory behavior. Mouflon *Ovis gmelini*, for example select thermal cover when temperatures are high during summer (Marchand et al. 2015) and alpine chamois *Rupicapra rupicapra* move to higher elevations (Mason et al. 2014).

Moose *Alces alces* are particularly susceptible to heat stress during summer because the upper critical temperature (UCT) for moose is exceptionally low (14 to 20°C during summer, Renecker and Hudson 1986a, McCann et al. 2013). Like other ungulates, moose increase food intake during summer (Renecker and Hudson 1986b, 1989a), and paradoxically, must dissipate heat generated by additional foraging activity and increased metabolism to maintain thermal balance at a time of year when conditions are least favorable for heat loss. Selecting areas to increase heat loss is critical because thermoregulatory behavior is linked to body condition (van Beest and Milner 2013), which correlates positively with reproduction and survival (Cameron et al. 1993, Sand 1996, Testa and Adams 1998, Bender et al. 2008).

Perhaps surprisingly, moose have persisted for decades at the southern edge of their range despite temperatures that are above their UCT for many days each summer (Demarchi and Bunnell 1995, Murray et al. 2012). Although moose populations have persisted, recent declines have been positively correlated with increasing temperatures (Murray et al. 2006, Lenarz et al. 2010, Dou et al. 2013, Monteith et al. 2015). With temperatures projected to increase in the future, improving our understanding of how moose dissipate heat in summer is essential, especially in the central part of North America where temperatures are expected to rise most rapidly under most climate change scenarios (Loarie et al. 2009).

Ungulates can lose heat by multiple means, including respiration, sweating, convection, and conduction to the ground and air. Wapiti *Cervus elaphus*, buffalo *Bubalus* spp., and tropical cattle *Bos indicus* can lose a significant amount of heat by evaporation of sweat (Parker and Robbins 1984, Kadzere et al. 2002, Marai and Haeeb 2010). Other species such as mule deer *Odocoileus hemionus* and sheep *Ovis aries*

lose heat primarily by respiration and by conduction (Parker and Robbins 1984, Marai et al. 2007). As in mule deer and sheep, sweating is of relatively little importance to moose. Instead, increased respiratory heat loss is one of the main mechanisms by which moose lose heat (Renecker and Hudson 1986a, McCann et al. 2013). Moose also alter behavior in response to high summer temperatures by shifting activity to night (Dussault et al. 2004), reducing daytime travel (Street et al. 2015), moving to cooler areas, and selecting shaded environments (Schwab and Pitt 1991, Demarchi and Bunnell 1995, van Beest et al. 2012, Melin et al. 2014).

Bed sites are probably important thermal refuges for moose during summer. Moose spend about half of each 24-h period walking and browsing, and the other half bedded (Renecker and Hudson 1989b, Moen et al. 1996). Intermittent periods of activity and bedding (each lasting a few hours) are distributed throughout the 24-h period. Net heat gain is likely when the ambient temperature is near or above the moose UCT and moose are walking and browsing because locomotor activity increases heat production. In contrast, net heat loss is likely when moose are bedded. Heat production resulting from locomotor activity is greatly reduced as bedded moose expend about 40% less energy than walking moose during summer (Renecker and Hudson 1989a). Bedding also increases heat loss by conduction to the ground (Moen 1973, Gatenby 1977). Although moose would also likely dissipate heat while standing still, swimming and wading, each of these activities makes up only a small proportion of the moose summer activity budget (< 5% each; Renecker and Hudson 1989b, Moen et al. 1996). It is when bedded, therefore, that moose must typically dissipate heat because locomotor activity generates heat and behaviors other than bedding that dissipate heat are relatively uncommon.

Although behavioral phases can be critical when linking patterns of space-use with biological processes (Nathan et al. 2008), studies of the effects of temperature on summer habitat selection by moose have pooled location data from active and bedded moose during analysis, and thus have not differentiated between these behavioral phases. One study included time of day as a parameter when modeling habitat selection (van Beest et al. 2012), but it is unclear whether this method elucidates patterns of bed site selection because periodicity in bedding behavior has not been reported. Thus, there is a critical gap in our understanding of how moose dissipate heat during summer that can be addressed by measuring characteristics of specific bed sites, as opposed to using locations of moose for which behavior was unknown.

To better understand how bed site use potentially increases heat dissipation by moose during hot summer periods, we sampled microsite characteristics at 155 bed sites from 25 free-ranging moose. We hypothesized that moose would use bed sites where they were most likely to dissipate heat when temperatures were hot. Additionally, we hypothesized that use of cooler sites would be greater during the day than at night, when solar radiation is absent.

Material and methods

Study area

We studied moose bed site use on and near the Superior National Forest and Voyageurs National Park in northeastern and northcentral Minnesota, USA (Fig. 1). Short warm summers and long cold winters are typical. Mean temperatures are 19°C in July and –14°C in January in Ely, Minnesota, which was located near the center of the study area (Fig. 1; National Oceanic and Atmospheric Administration 2000–2010). Vegetation was characteristic of boreal and Great Lakes forests (Heinselman 1973). Quaking aspen *Populus tremuloides* and paper birch *Betula papyrifera* were common deciduous tree species and were often mixed with white spruce *Picea glauca* and balsam fir *Abies balsamea*. Northern white cedar *Thuja occidentalis*, black spruce *Picea mariana*, tamarack *Larix laricina*, black ash *Fraxinus nigra* and red maple *Acer rubrum* were typically found in forested lowlands and were often interspersed with alder *Alnus* spp.

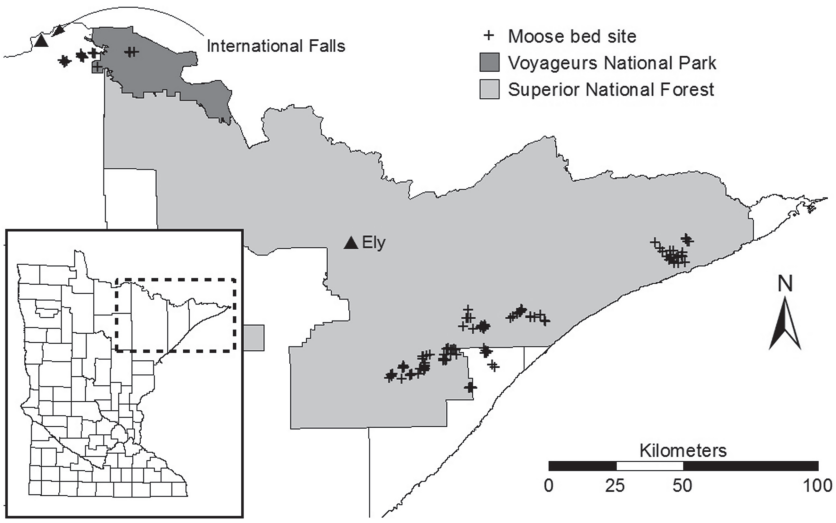

Figure 1. Study area in northern Minnesota, USA. Data were collected at 155 summer moose bed sites (Superior National Forest, USA, n = 134; Voyageurs National Park, USA, n = 21). Inset is a county map of Minnesota.

and willow *Salix* spp. Beaked hazel *Corylus cornuta* was common in open uplands and alder occurred within open, sometimes expansive bogs.

Capture and handling of moose

We captured adult moose in February and March 2011 by darting them from helicopters. We sedated moose with 1.2 ml (4.0 mg ml^{-1}) carfentanil citrate and 1.2 ml (100 mg ml^{-1}) xylazine HCl, and used 7.2 ml (50 mg ml^{-1}) naltrexone HCl and 3 ml (5 mg ml^{-1}) yohimbine HCl as an antagonist. A global positioning system (GPS) collar that obtained a location every 20 min was fitted to each immobilized moose (Sirtrack, Hawkes Bay, New Zealand, and Lotek Wireless, Newmarket, ON, Canada). Error of individual GPS locations was 7 m for a 50% circular error probable (Moen unpubl.) and location error for averaged GPS locations from stationary collars at bed sites is smaller (Moen et al. 1997). Animal capture and handling protocols met the guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011) and were approved by University of Minnesota and National Park Service Animal Care and Use committees.

Identification of bed sites for sampling

We identified bed sites used by 25 moose between 14 June 2011 and 16 September 2011 (hereafter, summer). We divided each moose location dataset (continuous locations each 20 min from throughout summer) into day and night based on sunrise and sunset (United States Naval Observatory 2012). Kernel density estimates (KDE) were then calculated for each day and night for each moose separately using the kernel density tool in ArcMap ver. 9.3 (bandwidth = 10 m). For each day and night, multiple unique polygons were created by each 75% isopleth; each polygon reflecting a peak in location density where a moose bedded. Because each polygon approximated an ellipse (reflecting location error from a stationary GPS receiver), we predicted bed sites to occur at the center of each polygon (Fig. 2). This yielded a dataset containing multiple bed sites for each moose for every day and night for the entire summer from which we sampled.

We selected bed sites from across the range of temperatures that moose experienced during summer 2011 using stratified random sampling, where strata were time period (day and night) and temperature. To develop temperature strata, we calculated mean temperatures for each day and night using hourly temperature data collected at airports in Ely, Minnesota (for moose in northeastern Minnesota; National Climate Data Center 2011a) and International Falls, Minnesota (for moose located on or near Voyageurs National Park; National Climate Data Center 2011b). International Falls airport averaged 20 km (SD = 9, n = 21) from moose bed sites we measured in Voyageurs National Park, and the Ely airport averaged 62 km (SD = 27, n = 134) from bed sites we measured in northeastern Minnesota. We used data from Ely because data were continuous and collected at a finer temporal scale than at the closer airports (where data were incomplete). Additionally, temperatures from Ely were correlated with temperatures from airports in Grand Marais, Minnesota and Silver Bay, Minnesota that were closer to the moose we studied ($R^2 > 0.83$, Moen unpubl.; average shortest distance between a bed site and either Grand Marais or Silver Bay airport = 31 km, SD = 13, n = 134), and previous research found airport temperatures to be positively correlated with temperatures recorded by moose GPS collars (Ericsson et al. 2015). We divided the distribution of temperatures into three equal parts (temperature terciles) for day and night separately. From each temperature tercile, we randomly selected three days and three nights. We then randomly chose one bed site to sample from each randomly-selected day and night. This procedure of selecting days and nights and bed sites was repeated separately for each moose. Sampled bed sites were within 1 km of an accessible road, hiking trail or shoreline for logistical reasons and sampled sites from individual moose were separated by > 100 m and > 24 h.

Evaluation of the KDE method for identifying bed sites

We verified that the kernel density estimate method for identifying bed sites from location data was accurate during summer 2012. To evaluate accuracy of the method, we used moose locations from July 2012 to October 2012 that

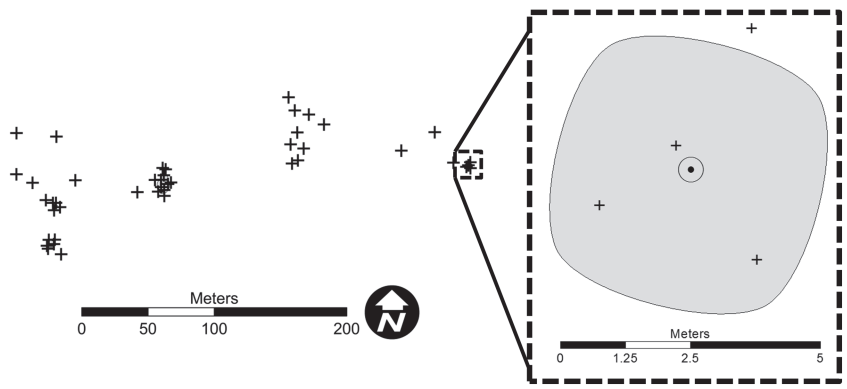

Figure 2. Example of how kernel density estimates were used to identify moose bed sites. Crosses are locations from a single moose from one summer day (sunrise to sunset). Gray polygons are 75% isopleths. The circle within the gray polygon is a centroid, where a bed site was predicted to have occurred during that day.

were less than 10 days old to predict where bed site locations would occur (using the methods described above). We went to each predicted bed site using a GPS to determine if a bed was present. Matted vegetation the size and shape of a bedded moose was evidence of a moose bed site because matted vegetation at moose bed sites lasts more than 10 days during summer (often more than 20 days; B. Olson, National Park Service, unpubl.). After determining if a bed was present at the location where a bed was predicted, we searched within 30 m of the predicted bed site. We then measured the distance from the predicted bed site to the center of all bed sites that we found.

Sampling at bed sites

We measured vegetation characteristics at bed sites used by moose during summer 2011 in the summer of 2012. This approach enabled us to sample randomly from bed sites used during the entire summer. Random sampling yields accurate, unbiased model estimates from which to make sound inferences (Ott and Longnecker 2001). Additionally, it was unlikely that annual variation affected measurements we made at bed sites because forestry measurements and shade would have been similar between years as disturbances (timber harvest, fire and windfall) had not occurred at bed sites we sampled.

At each bed site we estimated total basal area of trees and shrubs using a 10-factor basal area wedge prism and recorded the species and diameter at breast height (DBH) of individual trees and shrubs that were included in basal area calculations. Canopy closure and horizontal cover were recorded at the cardinal directions using a convex spherical densiometer and a 0.5×0.5 m cover board placed 5 m from the bed site and 0.75 m above the ground (to approximate the height of a bedded moose's head). Canopy cover provides shelter from solar radiation, and horizontal cover was potentially important as a windscreen and as protection from predators. Ground temperature was recorded each 30 min throughout summer by dataloggers that we inserted into the ground at each bed site in June 2012 and collected in September 2012 (HOBO Pendant datalogger, model UA-001-08). Ground temperature was potentially important for conducting heat to the ground (Gatenby 1977). Slope, aspect and elevation were omitted from analysis because most beds were located on flat surfaces (slopes $< 5\%$) at similar elevations.

To determine if substrate moisture differed between sites we classified as upland and lowland, we measured substrate water content (meter^3/meter^3) by inserting sensors into the ground at each bed site (water content: ProCheck ver. 6 with GS3 sensor; Decagon Devices, Pullman, WA, USA). Substrate water content was potentially important because water conducts heat, and wet substrates increase evaporative cooling when they wet the fur and skin. Water content was measured at least 24 h after rainfall to avoid the influence of recent rainfall.

Statistical analysis

For bed sites used in 2012, we used analysis of variance to test whether the accuracy of the kernel density estimate method for identifying bed sites from location data was affected by whether beds were predicted from locations collected during the day or night (GLM procedure, SAS ver. 9.3). All other analyses were for bed sites used by moose in 2011.

We determined if moose bedded under closed canopies ($> 70\%$ canopy closure) during the day more than 50% of the time using an exact binomial test. We tested whether moose bedded under greater canopy closure during the day than at night using linear mixed models, with canopy closure as the dependent variable, period (day or night) as the independent variable, and individual moose treated as random effects (MIXED procedure, SAS ver. 9.3).

We investigated whether use of environmental conditions and landcover classifications were correlated with ambient temperature using linear mixed models that we hypothesized to be biologically significant (Pinheiro et al. 2015). We modeled the ambient temperature during the time when a moose was bedded as the dependent variable (transformed by the natural log; National Climate Data Center 2011a, b) for day and night bed sites separately using independent variables describing environmental conditions (Table 1), study site (Superior National Forest and Voyageurs National Park), and sex. Two-factor additive and interaction models that included combinations of environmental conditions were also evaluated.

In separate analyses we determined if moose bedded in different landcover types at higher temperatures. We modeled ambient temperature when a moose was bedded as the dependent variable in response to landcover type classification (Pinheiro et al. 2015). We classified landcover based on whether tree species present measured at bed sites were deciduous or coniferous and were typically found in uplands or lowlands (Table 1). Two-factor additive models that included cover type classification with tree basal area and mean tree DBH were also evaluated.

We limited analysis of bed sites used during the day to those that were located in closed canopies, which increased the inference strength of our results because most bed sites that were used during the day were under closed canopies. During preliminary analyses we examined thermal inertia by replacing ambient temperature at the time of bedding with mean ambient temperature over the previous 6, 12 and 24 h (McCann et al. 2013). Thermal inertia models yielded similar results to those that used temperature measured at the time of bedding and we did not consider them further.

We used Akaike's information criterion values adjusted for small sample sizes (AIC_c) to identify models with the best relative fit ($\Delta AIC_c < 2$; Burnham and Anderson 2002). Factors in multi-term models were not collinear (tolerance < 0.40, REG procedure, SAS ver. 9.3). Full-model averaging was used to calculate parameter estimates for terms in best-fitting univariate and additive models (Lukacs et al. 2010, Symonds and Moussalli 2011, Mazerolle 2015). Because AIC_c ranks all models in a candidate set (even if none have merit) and best-fitting models can include parameters that do not improve model fit, it is necessary to evaluate best-fitting models to determine which parameters are informative (Arnold 2010, Burnham et al. 2011). Accordingly, we considered parameter estimates for terms in best-fitting univariate and additive models with 85% confidence limits that did not bound 0 as supportive of a term's

Table 1. Definitions of variables used for modeling moose bed site use during summer in northern Minnesota, USA. Models of bed site use were constructed separately using variables that characterized environmental conditions and landcover classifications.

Variable	Definition
Environmental condition	
Canopy closure	Proportion of the sky obstructed by vegetation at the bed site
Cloud cover	Proportion of the sky containing clouds when the moose was bedded. Four cloud cover classifications[a]: Clear (< 0.13 cloud cover), partly cloudy (0.13 to 0.50), mostly cloudy (0.63 to 0.88), and overcast (>0.88).
Dew point	Dew point temperature[a] when the moose was bedded
Ground temperature	Mean Aug-2012 ground temperature at the bed site. Calculated separately for day and night
Horizontal cover	Proportion of a cover board obstructed by vegetation at the bed site
Wind speed	Wind speed (m s^{-1})[a] when the moose was bedded
Landcover classification	
Forest type	Four classifications: deciduous, coniferous, mixed (deciduous and coniferous) and nonforested.
Upland-lowland species composition	Deciduous, coniferous, mixed, and nonforested classifications were lowland if lowland trees or shrubs[b] were present and were upland if lowland trees or shrubs were absent. This resulted in eight classifications: upland deciduous, upland coniferous, upland mixed, upland nonforested, lowland deciduous, lowland coniferous, lowland mixed and lowland nonforested.
Lowland coniferous forest	Two classifications in total, based on the presence or absence of lowland coniferous trees: lowland coniferous and other
Lowland forest	Two classifications in total, based on the presence or absence of lowland deciduous or coniferous trees[c]: lowland forest and other

[a]Measured at airports in Ely and International Falls, MN, USA.
[b]Lowland trees were black spruce, tamarack, and white cedar. Lowland shrub was alder.
[c]Lowland trees were black ash, black spruce, red maple, tamarack, white cedar and willow.

importance (Arnold 2010). For best-fitting models that contained interactions with wind speed, a linear regression coefficient of determination (R^2) was calculated to assess whether the model had merit (Burnham et al. 2011) by dividing data into periods of lower wind speeds (< 1.4 m s^{-1}) and higher wind speeds (> 1.4 m s^{-1}).

Results

We measured environmental conditions at 78 day bed sites and 77 night bed sites that were used by 25 different moose (18 F, 7 M). A mean of six bed sites (SD = 1, n = 155) were sampled from each moose, including three day (SD = 1, n = 78) and three night bed sites (SD = 1, n = 77). Day bed sites were used for 2.9 h (SD = 1.7 h, n = 78) and night bed sites were used for 2.2 h (SD = 1.1 h, n = 77). Mean day temperature was 22°C (SD = 5°C, n = 78) and mean night temperature was 14°C (SD = 5°C, n = 77) when moose were bedded at sites that we sampled.

Accuracy of bed site predictions

Bed sites were present at all 19 locations (9 day, 10 night) where we predicted that a bed site would occur. The mean distance between KDE-predicted bed sites and field-verified bed sites was 1.8 m (SD = 2.0, n = 19) and did not differ between day and night ($F_{1,17} = 2.3$, $p = 0.15$; day mean = 2.6 m, SD = 2.6, n = 9; night mean = 1.2 m, SD = 1.1, n = 10). Of the 19 predicted bed sites, 18 were < 5 m from a field-verified moose bed site and one was 8.4 m from a field-verified bed site. More than one adult moose bed site was located within 10 m of five predicted bed sites. These additional bed sites averaged 3.6 m (SD = 2.1, n = 5) from predicted bed site locations. Of these five additional bed sites, four were < 5 m from a predicted bed site location and one was 7 m away.

Canopy closure

Moose used bed sites with greater canopy closure during the day than at night ($F_{1,120} = 75.3$, $p < 0.0001$). Mean canopy closure was more than two times greater at day bed sites (81%; SD = 23%, n = 72) than at night bed sites (38%; SD = 38%, n = 74). Use of intermediate canopy closure (between 30% and 70%) was similar at day and night bed sites (Fig. 3).

Day bed sites

The only environmental condition we measured that moose selected for day bed sites was shade, with 58 of 72 day bed sites located under closed canopies (binomial exact test $p < 0.001$). Two of the 12 environmental conditions models that we evaluated were ranked as best-fitting

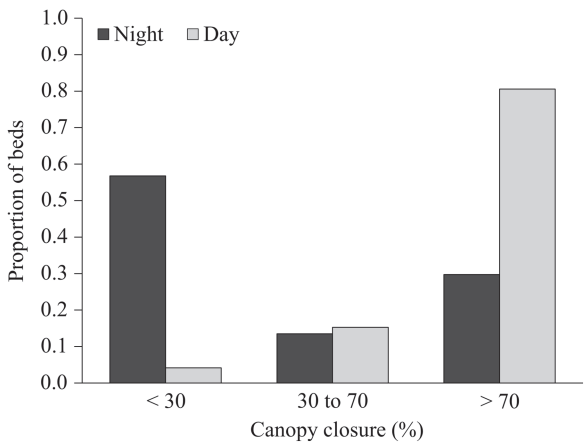

Figure 3. Distribution of canopy cover at moose bed sites. Canopy cover was measured at 78 day and 77 night moose bed sites used during summer in northern Minnesota, USA during summer 2011.

($\Delta AIC_c < 2$; Table 2). The first model contained the interaction of ground temperature and wind speed. The correlation between ambient temperature when a moose was bedded and ground temperature, however, was poor when wind speeds were low (linear regression $R^2 = 0.14$) and when wind speeds were higher ($R^2 = 0.01$), indicating this model was not supported. The second selected model contained the interaction of horizontal cover and wind speed. Correlation between ambient temperature when a moose was bedded and horizontal cover, however, was also poor (low wind $R^2 < 0.01$; higher wind $R^2 = 0.01$).

Moose bedded in lowland forests when daytime temperatures were warmer. Of the 12 cover type classification models we evaluated, four were best-fitting ($\Delta AIC_c < 2$; Table 2). Use of lowland forest and lowland coniferous forest increased with ambient temperature (Fig. 4), and 85% confidence limits for model averaged parameter estimates for lowland forest and lowland coniferous forest were greater than 0 (Table 3). Confidence limits for DBH bounded 0 (Table 3).

Day bed sites located in lowland forests had substrates with higher water content than bed sites in upland forests ($F_{1,34} = 15.54$, $p = 0.0004$). Mean substrate water content was 1.6-times greater in lowland forests than in upland forests (lowland mean = 36%, SD = 19%, n = 41; upland mean = 23%, SD = 14%, n = 36).

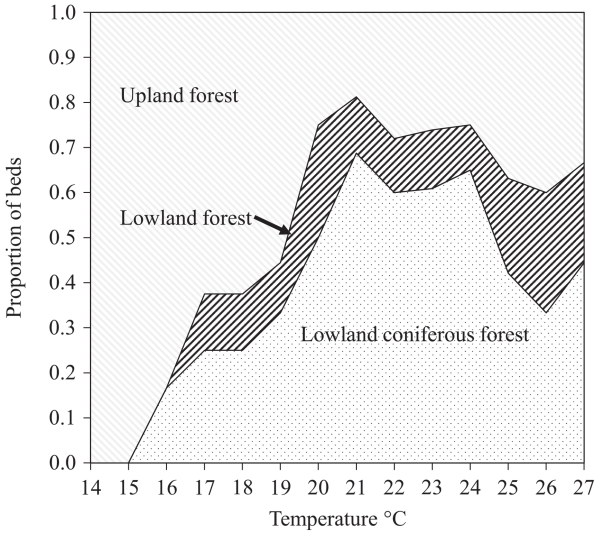

Figure 4. Relationship between ambient temperature and use of upland, lowland, and lowland coniferous forest for bed sites by moose. Upland tree species were balsam fir, jack pine *Pinus banksiana*, paper birch, quaking aspen, red pine *Pinus resinosa*, sugar maple *Acer saccharum*, white pine *Pinus strobus*, white spruce *Picea glauca* and yellow birch *Betula alleghaniensis*. Lowland tree species were black ash, red maple, and included the lowland coniferous species black spruce, tamarack, and white cedar. Proportions are from 5°C bins centered on the x-axis temperature.

Night bed sites

Use of environmental conditions was not correlated with ambient temperature at night. Of the 12 environmental conditions models that we evaluated, the interaction of horizontal cover and wind speed had the best relative fit ($\Delta AIC_c < 2$; Table 4). Correlation between ambient temperature when a moose was bedded and horizontal cover, however, was poor (low wind speed $R^2 = 0.04$; higher wind $R^2 = 0.02$).

Table 2. Model fit information for environmental condition and landcover classification models of moose day bed site use during summer in northern Minnesota, USA.

Day model	K	AIC_c	ΔAIC_c	Likelihood	Weight	Log(likelihood)
Environmental condition						
Ground temperature × Wind speed	6	–26.0	0.0	1.00	0.51	19.9
Horizontal cover × Wind speed	6	–25.2	0.8	0.67	0.34	19.5
Ground temperature × Cloud cover	6	–22.2	3.8	0.15	0.08	18.0
Horizontal cover × Cloud cover	6	–21.4	4.6	0.10	0.05	17.6
Ground temperature × Wind speed × Horizontal cover	10	–18.7	7.3	0.03	0.01	21.9
Horizontal cover	4	–15.6	10.4	0.01	0.00	12.2
Ground temperature	4	–5.6	10.5	0.01	0.00	12.2
Horizontal cover × Dew point	6	–14.2	11.9	0.00	0.00	14.0
Ground temperature × Dew point	6	–13.9	12.1	0.00	0.00	13.8
Ground temperature × Sex	6	–13.6	12.4	0.00	0.00	13.7
Horizontal cover × Sex	6	–11.6	14.5	0.00	0.00	12.7
Landcover classification						
Lowland forest	4	–20.4	0.0	1.00	0.32	14.6
Lowland forest + DBH	5	–19.3	1.0	0.59	0.19	15.3
Lowland coniferous forest	4	–19.2	1.2	0.55	0.18	14.0
Lowland coniferous forest + DBH	5	–18.6	1.8	0.40	0.13	14.9
Lowland forest + Basal area	5	–18.1	2.3	0.32	0.10	14.7
Lowland coniferous forest + Basal area	5	–16.9	3.5	0.18	0.06	14.1
Forest type + DBH	6	–13.7	6.7	0.04	0.01	13.7
Forest type	5	–13.7	6.7	0.04	0.01	12.5
Forest type + Basal area	6	–11.3	9.0	0.01	0.00	12.5
Upland-lowland species composition	8	–7.9	12.5	0.00	0.00	13.5
Upland-lowland species composition + DBH	9	–6.9	13.5	0.00	0.00	14.5
Upland-lowland species composition + Basal area	9	–5.1	15.3	0.00	0.00	13.6

Table 3. Parameter estimates for model-averaged terms in best-fitting landcover classification models of moose daytime bed site use during summer in northern Minnesota, USA. CL = confidence limit.

Day landcover parameter	β	SE	Lower 85% CL	Upper 85% CL
DBH	0.40	0.32	–0.06	0.85
Lowland coniferous forest (present)	0.10	0.05	0.03	0.18
Lowland forest (present)	0.12	0.05	0.04	0.19

Table 5. Parameter estimates for model-averaged terms in best-fitting landcover classification models of moose nighttime bed site use during summer in northern Minnesota, USA. CL = confidence limit.

Night landcover parameter	β	SE	Lower 85% CL	Upper 85% CL
DBH	0.43	0.39	–0.14	0.99
Lowland coniferous forest (present)	0.00	0.14	–0.20	0.21
Lowland forest (present)	–0.03	0.12	–0.14	0.21

Use of landcover types also was not correlated with ambient temperature at night. Of the 12 night landcover models we evaluated, five had the best relative fit ($\Delta AIC_c < 2$; Table 4). Confidence limits for model averaged parameter estimates for basal area, DBH, lowland forest, and lowland coniferous forest (terms in best-fitting models), however, bounded 0 (Table 5).

Discussion

Thermal conditions influence decisions ungulates make at different scales, ranging from selection of landcover types to selection of environmental conditions at much finer scales. Behavioral phases also influence space-use (Nathan et al. 2008) and linking behavioral phases to habitat use may be important for understanding how ungulates cope with hot temperatures (Van Moorter et al. 2009). Although bedding makes up half of the moose activity budget (Renecker and Hudson 1989b), this is the first study to examine whether moose use bed sites that help them to dissipate heat during hot summer periods.

We assessed whether temperature influenced where moose bedded by sampling bed sites from the full range of summer temperatures they experienced. GPS locations collected every 20 min across an entire summer enabled us to accurately identify bed sites by calculating KDEs. Very high frequency (VHF) telemetry location error and GPS location fix rates in previous studies made identifying bed sites unlikely. VHF location error is often hundreds of meters (Moen et al. 2011) and GPS locations were collected at long intervals relative to bedding duration in previous studies (Dussault et al. 2004, Broders et al. 2012, van Beest et al. 2012, van Beest and Milner 2013, Melin et al. 2014) which would have made patterns of locations from bedded and active moose indistinguishable and assessing influences of thermal conditions on bed site selection impossible.

Measuring bed sites in the field made it possible to assess conditions moose used because forest canopy cover and other environmental conditions often vary across short distances. Gaps in the forest canopy can be small relative to the spatial grain (sensu Turner et al. 2001) of forest inventory and satellite-derived landcover maps. Other environmental conditions such as horizontal cover also vary over

Table 4. Akaike information criterion (AIC) model fit information for environmental condition and landcover classification models of moose nighttime bed site use during summer in northern Minnesota, USA.

Night model	K	AIC_c	ΔAIC_c	Likelihood	Weight	Log(likelihood)
Environmental condition						
Horizontal cover × Wind speed	6	42.5	0.0	1.00	0.79	–14.2
Ground temperature × Wind speed × Horizontal cover	10	48.0	5.5	0.07	0.05	–10.8
Canopy closure × Wind speed	6	48.2	5.7	0.06	0.05	–17.0
Ground temperature × Wind speed	6	49.5	7.0	0.03	0.02	–17.7
Ground temperature	4	50.1	7.6	0.02	0.02	–20.6
Canopy closure × Ground temperature	6	50.5	8.0	0.02	0.01	–18.2
Canopy closure	4	50.7	8.1	0.02	0.01	–20.8
Canopy closure × Horizontal cover	6	50.7	8.1	0.02	0.01	–18.2
Horizontal cover	4	50.7	8.2	0.02	0.01	–20.9
Canopy closure × Cloud cover	6	52.0	9.4	0.01	0.00	–18.9
Horizontal cover × Sex	6	52.9	10.3	0.01	0.00	–19.3
Ground temperature × Sex	6	55.0	12.5	0.00	0.00	–20.4
Landcover classification						
Lowland forest	4	51.8	0.0	1.00	0.25	–21.4
Lowland coniferous forest	4	51.9	0.0	0.98	0.25	–21.4
Lowland forest + DBH	5	53.2	1.4	0.50	0.13	–20.8
Lowland coniferous forest + DBH	5	53.2	1.4	0.50	0.13	–20.8
Lowland forest + Basal area	5	53.8	2.0	0.37	0.09	–21.2
Lowland coniferous forest + Basal area	5	54.1	2.3	0.32	0.08	–21.3
Forest type	6	55.8	4.0	0.14	0.04	–20.8
Forest type + DBH	7	57.5	5.7	0.06	0.01	–20.3
Forest type + Basal area	7	58.2	6.3	0.04	0.01	–20.6
Upland-lowland species composition	9	60.5	8.7	0.01	0.00	–18.7
Upland-lowland species composition + DBH	10	63.0	11.2	0.00	0.00	–18.3
Upland-lowland species composition + Basal area	10	63.8	12.0	0.00	0.00	–18.7

relatively short distances, and are typically unavailable from forest inventory and satellite-derived landcover datasets.

Selection of canopy cover for bed sites on hot days by moose in this study corresponds with predictions made using optimization models (Belovsky 1981) and observations of zoo-managed moose (McCann et al. 2013). Shade reduces energy gain from solar radiation. By selecting shaded bed sites on summer days moose increase the likelihood of maintaining thermal balance and reduce the likelihood for hyperthermia (Dussault et al. 2004, McCann et al. 2013).

In addition to shade, moose appear to maintain thermal balance on summer days by bedding in forests with moist and wet substrates. Although both upland and lowland forests provided shade during summer (because leaves were present), substrate water content was greater in lowland forests than in upland forests. Because substrate water content is positively correlated with thermal conduction (Cosenza et al. 2003) bedding on moist and wet (rather than dry) substrates would result in greater dissipation of heat. Thermal conduction to the ground is an important mechanism by which ungulates dissipate heat. Sheep, for example, can conduct 30% of their heat production to the ground (Gatenby 1977). Results for moose in this study are consistent with those of another study that found roe deer *Capreolus capreolus* selected substrates with greater water content when it was hot (Mysterud 1996). Thus, moist and wet substrates under shade appear to be thermal refuges for multiple ungulate species during summer.

Foraging behavior by moose is predicted to correspond with interspersion of openings and nearby shade (provided by canopy cover) during the day, but not at night. Foraging during the day and night frequently occurs in openings, corresponding with greater forage availability (Bjørneraas et al. 2011) and greater foraging efficiency (Renecker and Hudson 1986b). We found that moose bedded in shade during the day, but increased use of openings at night. Bedding in openings at night likely helps to offset heat accumulated from increased browsing activity and the resulting increased metabolism that occurs at night because temperatures are cooler and net radiant heat loss is greater in openings than under forest canopies which trap heat (Moen 1968, Olson et al. 2014). Openings interspersed with nearby shade provide moose with both forage and shaded bed sites that enable cooling during the day. At night, shaded bed sites are unimportant for cooling and as a result moose may forage more freely in large openings that lack nearby shade, such as areas disturbed by fire and timber harvest.

Thermal refuges were identified using landcover classifications that grouped forest types associated with conditions that enabled moose to dissipate heat (shade and substrates containing greater water content). Landcover data are commonly available to researchers and managers and can be useful for identifying important habitat for many animal species (Cooper and Millspaugh 1999, McCann and Moen 2011). The accuracy with which important habitats can be identified is influenced by the spatial scale of landcover data and selection order (Johnson 1980, Turner et al. 1989). Accuracy is also influenced by how well landcover types correspond with important environmental conditions (McCann et al. 2014). For moose, our results show that this includes conditions that dissipate heat.

Lowland forests that have wet substrates appear to be thermal refuges that enable moose to dissipate heat on hot summer days. Interspersed openings are also important because moose forage and bed there at night. Managing for these conditions is especially important at the southern extent of moose range where moose population declines have been positively correlated with warming temperatures associated with climate change (Murray et al. 2006, Lenarz et al. 2010, Dou et al. 2013, Monteith et al. 2015). Because thermoregulatory behavior influences body condition (van Beest and Milner 2013), which in turn influences reproduction and survival (Cameron et al. 1993, Sand 1996, Testa and Adams 1998, Bender et al. 2008), presence of thermal refuges should improve population demographics for moose and other cold-adapted ungulates where climates warm. The degree to which thermal refuges can mitigate the adverse effects of climate change is unclear and will depend in part on the magnitude of future temperature increases.

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