MOOSE MODIFY BED SITES IN RESPONSE TO HIGH TEMPERATURES

Bryce T. Olson[1], Steve K. Windels[1], Ron A. Moen[2], and Nicholas P. McCann[3]

[1]National Park Service, Voyageurs National Park, 360 Highway 11 E, International Falls, Minnesota 56649; [2]Natural Resources Research Institute, University of Minnesota, 5013 Miller Trunk Highway, Duluth, Minnesota 55811; [3]Great Lakes Indian Fish and Wildlife Commission, P.O. Box 9, Odanah, WI 54861

ABSTRACT: Moose (*Alces alces*) employ physiological and behavioral mechanisms to enable them to dissipate excess heat when ambient temperature is above the upper critical temperature of their thermoneutral zone. In this note, we describe 2 cases where GPS radio-collared female moose modified summer bed sites as a potential thermoregulatory response to high temperatures. The first case occurred on 18 - 21 July 2011 when ambient temperatures averaged 25 °C (8 °C above the upper critical temperature of moose) and reached 32 °C and 96% relative humidity. Based on field observations of the bed site immediately after use, the moose cleared litter and duff to expose 3 m^2 of mineral soil under a closed-canopy balsam fir (*Abies balsamea*) stand. The moose spent 64% of the time bedded during a 4-day event, with ≤11 individual bedding events in the same bed site. A second case was observed on 5 July 2013 during similar weather conditions (29 °C and 70% relative humidity) when a different moose cleared a bed site and used it continuously for 10 hours.

ALCES VOL. 52: 153–160 (2016)

Key Words: *Alces alces*, bedding, bed site, behavior, moose, temperature, thermoregulation

Moose (*Alces alces*) have a low upper critical temperature estimated at 14 °C (Renecker and Hudson 1986) and 17 °C (McCann et al. 2013) in summer during calm conditions, and under windy conditions McCann et al. (2013) estimated an upper critical temperature of 24 °C. To accommodate these physiological constraints, moose can be expected to rely on behavioral plasticity. For instance, to maintain thermal balance when summer temperatures are high, moose can be expected to reduce daytime activity and increase nocturnal activity (Dussault et al. 2004). When daytime temperatures are high, moose can also be expected to select habitats that serve as thermal refuges, including areas with thick vegetation and dense canopy cover (DeMarchi and Bunnel 1995, Dussault et al. 2004, Van Beest et al. 2012, Melin et al. 2014, Street et al. 2016), and shift nocturnal habitat use to openings (McCann et al. 2016).

Moose spend approximately half of each summer day bedded when they ruminate and rest (Renecker and Hudson 1989b, Moen et al. 1997). Proximity to browse and predator avoidance are commonly considered to be the primary drivers that influence where moose locate beds (Mysterud and Østbye 1999, Van Moorter et al. 2009). However, beyond these primary factors that influence general space use, thermal conservation can drive finer scale behaviors and influence where moose locate their bed sites, as moose use shaded bed sites with wet substrates when daytime temperatures are hot (McCann et al. 2016). Moose could increase thermal conduction to the ground on hot summer days by exposing soil under the litter layer. Bedding reduces energy expenditure (relative

Corresponding author: Bryce Olson, 360 Highway, 11 E International Falls, MN 56649, Office (218) 283-6694, Fax (218) 285-7407, bryce_olson@nps.

to walking; Renecker and Hudson 1989a), and increases thermal conduction to the ground (Moen 1973, Gatenby 1977). The litter layer has lower thermal conductivity than bare soil (Hanks et al. 1961, Barkley et al. 1965), retains moisture, and stops most incoming radiation (Kelliher et al., 1986, Schaap and Bouten 1997, Ogée et al., 2001) which dampens the fluctuations of soil temperature (Johnson-Maynard et al. 2004).

Ungulates other than moose are known to modify bed sites to enable cooling. Mule deer (*Odocoileus hemionus*) dig into the soil to modify bed sites when temperatures are high (Sargeant et al. 1994) and wapiti (*Cervus elaphus*) select bedding areas with bare soil (e.g., Merrill 1987, Millspaugh et al. 1997). These behaviors, however, have not been documented for moose. In this case study, we describe modification of bed sites by moose as a potential thermoregulatory response to extreme thermal conditions in summer.

STUDY AREA

We studied moose in Voyageurs National Park (VNP; UTM 15U 508618 / 5371882) in northcentral Minnesota along the Ontario-Canada border. The climate in this region is characterized by long winters (mean January temperature = −15 °C) and short summers (mean July temperature −19 °C; NOAA 2010), with vegetative communities comprised of a mix of southern boreal and Laurentian mixed conifer-hardwood forests (Faber-Langendoen et al. 2007). Common species include quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*) in uplands, and northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and black ash (*Fraxinus nigra*) in forested lowlands. Moose density is low in VNP (<0.15 moose/km^2; Windels and Olson 2016).

METHODS

We immobilized adult female moose in mid-winter via dart gun from helicopters (Quicksilver Air Inc., Fairbanks, Alaska, USA) using 1.2 mL (4.0 mg/mL) carfentanil citrate and 1.2 mL (100 mg/mL) xylazine HCl for immobilization. We subsequently used a combination of 7.2 mL (50 mg/mL) naltrexone HCl and 3 ml (5 mg/mL) yohimbine HCl as an antagonist. A GPS radio-collar that obtained a location every 20 min was fitted to each immobilized moose (Sirtrack Limited, Hawkes Bay, New Zealand). Animal capture and handling protocols met the guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011) and were approved by U.S. Geological Survey and University of Minnesota Animal Care and Use Committees.

The first case of a modified bed site (UTM 15U 503608/5368384) was observed while checking on the status of a female moose that had moved minimally for several days (assessed from GPS locations via Argos upload). The second case occurred when a bed site was found (UTM 15U 518511/5369230) opportunistically while conducting other field work. GPS location, photos, and size measurements of each bed site area were taken and a 50 m radius area was searched for additional bed sites, browsing, and other moose sign.

We verified that the locations of the modified bed sites corresponded with GPS locations of each collared female moose. To do this, we created a 25 m radius buffer around each bed site's GPS location. This buffer equaled the 95% circular error probable for stationary tests of the collars we used (R. Moen, unpubl. data). We then examined GPS locations from all collared moose in VNP using ArcGIS 10 (ESRI 2011) to confirm that locations from other collared moose did not overlap the 25 m buffer.

Because thermal conditions were predicted to influence bed site modification, we obtained ambient air temperature, relative humidity, and solar radiation data for the period of use from the VNP meteorological station nearest the bed sites (mean 10.1 ± 1.3 km, Sullivan Bay CASTNet). Previous research found that temperatures from nearby weather stations were correlated with temperatures recorded by other GPS radio-collars on moose (Ericsson et al. 2015).

RESULTS

Case 1

An area of 2 m x 1.5 m was nearly cleared entirely of litter and duff leaving the underlying mineral soil exposed (Fig. 1), and moose hoof prints and hair were found within the bed site. Further investigation revealed multiple hoof scratch marks suggesting deliberate removal of the litter and duff layers as indicated by it being piled at the edges of the bed site. No other bed site was found within a 50 m radius around the modified bed site, and evidence of recent intensive browsing was within 50 m of the bed site. The bed site and the surrounding area was within the deciduous shrubland cover type, with >90% canopy coverage of balsam fir overstory immediately above the bed site. Soil type at the bed site was sandy loam and relatively dry at the time of observation.

Sixty-four percent of GPS locations over a 96-h period (18 - 21 July 2011) were within the 25 m radius buffer around the modified bed and accurately preceded the period when the freshly disturbed site was observed

Fig.1. Modified bed site from Case 1 showing litter and duff cleared and piled to the edges by GPS radio-collared female moose in northern Minnesota, USA. The modified bed site in Case 2 was nearly identical.

on 3 August 2011. During this period, the moose made 8 short (< 75 m) and 3 longer movements (200-400 m) to and from the bed site. The shorter movements were probably foraging events or movements to nearby water; most were within the area of intensive browsing (Fig. 2).

Mean temperature during the 96-h period was 25 °C, with a maximum daily high of 32 °C (Fig. 2). Relative humidity averaged 67%, with a maximum of 96%. Skies were mainly clear with only a single, short precipitation event during this time period.

Case 2

The second case of a modified bed site was similar to Case 1 but the cleared area was smaller (1.5 m x 1.1 m). Moose hoof prints and hair were found within the bed site and no other bed sites were found within a 50 m radius surrounding the bed site; little browsed vegetation was observed. The bed site and surrounding area were in the boreal forest cover type, with >90% canopy coverage of balsam fir above the bed site. Soil type at the bed site was sandy loam and it was relatively dry at the time of observation.

All GPS locations were in the 25 m buffer around the bed site location consecutively for 10 h on 5 July 2013. One movement of ~50 m followed by 1 location back at the bed site was recorded before the moose left the area without returning.

Mean temperature during the 10-h event was 25 °C, with a maximum daily high of 29 °C (Fig. 3). Relative humidity averaged 62%, with a maximum of 70% (Fig. 3). Skies were mainly clear and no precipitation was recorded.

DISCUSSION

The environment selected by animals influences their ability to maintain thermal homeostasis when temperatures are outside of their thermoneutral zone, and animals exhibit a wide range of behavioral responses to

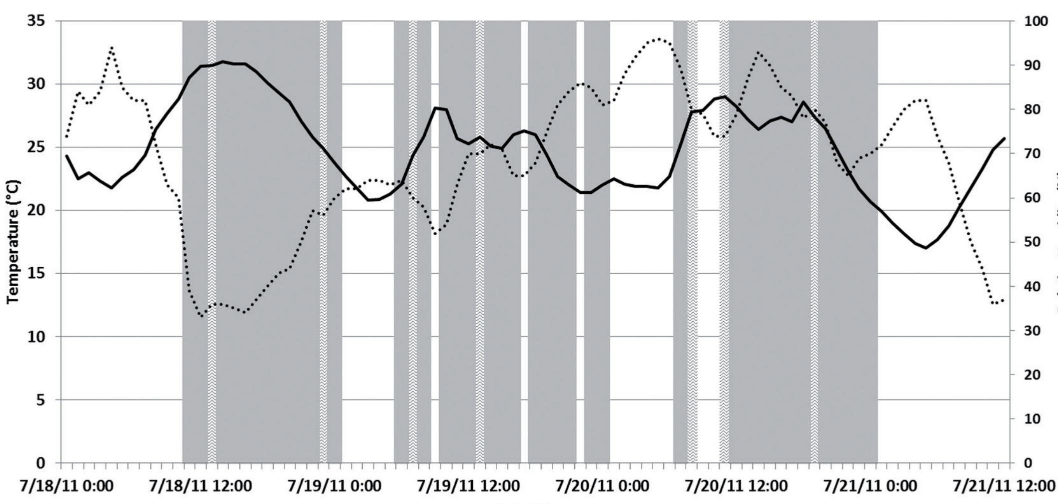

Fig. 2. Ambient air temperature (°C; solid black line) and relative humidity (%; dotted black line) during long bedding events for GPS radio-collared female moose on 18 - 21 July 2011 (Case 1). Gray bars indicate when the moose was within 25 m of the bed site and assumed to be bedded. Cross-hatched bars indicate when the moose moved from the bed site to nearby standing water. Moose locations in other areas are indicated by the white. Air temperatures were recorded at the Sullivan Bay CASTNet meteorological station near Ash River, Minnesota, USA.

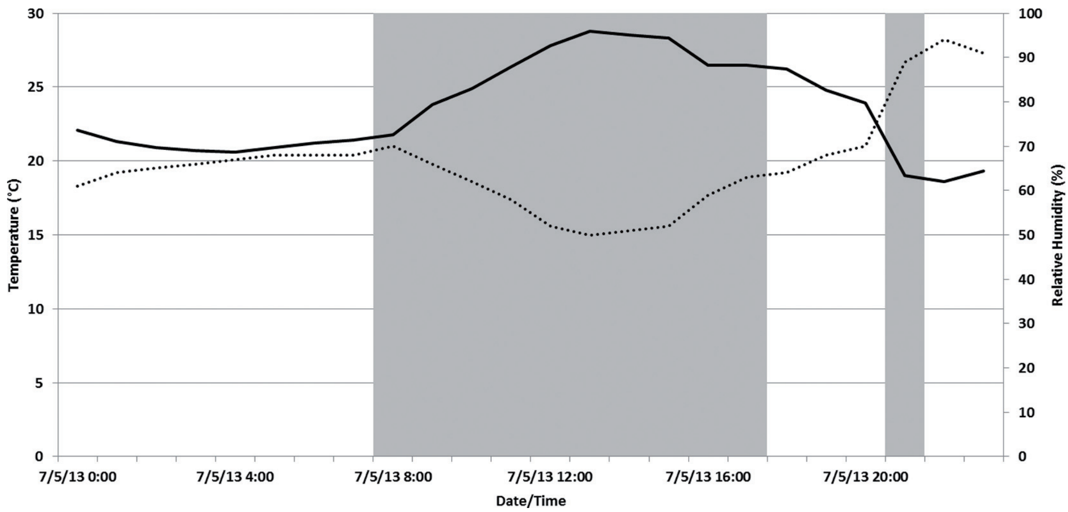

Fig. 3. Ambient air temperature (°C; solid black line) and relative humidity (%; dotted black line) during long bedding events for GPS radio-collared female moose on 5 July 2013 (Case 2). Gray bars indicate when the moose was within 25 m of the bed site and assumed to be bedded. Moose locations in other areas are indicated by white. Air temperatures were recorded at the Sullivan Bay CASTNet meteorological station near Ash River, Minnesota, USA.

balance energy gains and losses (Moen 1968). Bed site modification and selection of bed site locations in response to high temperatures has been documented in other ungulates, including mule deer and wapiti (Sargeant et al. 1994, Merrill 1987, Millspaugh et al. 1997). Moose commonly exhibit thermoregulatory behavior (DeMarchi and Bunnel 1995, Dussault et al. 2004, van Beest et al. 2012, Melin et al. 2014, Street et al. 2016) and it should not be surprising for them to exhibit these same behaviors.

Moose cleared away duff and litter to expose mineral soil under a closed canopy. Exposing soil would have improved thermal conductivity at bed sites and reduced internal heat loads during periods of extreme thermal conditions, thereby helping moose maintain thermal balance. It is highly probable that increasing thermal conductivity was important in both cases because of the extreme thermal conditions. Habitats around each bed site fit the description of thermal refuges that moose select for bed sites during hot temperatures (McCann et al. 2016).

The bed site modification behavior we describe may be most common when moose bed in drier soils as it is known that moose use bed sites with higher moisture content during times of high temperatures (McCann et al. 2016), and bed in wet soils in hot weather even when standing water exists (Renecker 1987). Energy expenditure was reduced 9% and respiration rate 29% when moose bedded in wet versus dry soils (Renecker 1987). In both cases we describe, the soils were sandy loam that was relatively dry at the time of use. Removing the insulating litter should have improved conductivity by exposing the cooler soil underneath (Hanks et al. 1961, Barkley et al. 1965, Kelliher et al. 1986, Schaap and Bouten 1997, Ogée et al. 2001). However, it is possible the soil was moist when the bed site was modified and dried out prior to our inspections.

In both cases, the hoof marks extending to the edge of the bed site strongly suggest this material was deliberately cleared while standing. During times when temperatures were above the upper critical temperature, moose in Alberta were observed bedded in shade with legs extended (Renecker and Hudson 1989a, 1990). This repeated leg extension and process of lying down and getting up could shift some vegetative material to the edges of the bed site, though the litter would likely remain in the middle of the bed site. In the cases we describe, the entire bedding area, similar in size to other moose bed sites investigated in the area (NPS unpubl. data), was cleared of litter and duff. Moose have been viewed scratching at the ground prior to bedding in the Kenai Peninsula of Alaska, though meteorological conditions and habitat characteristics were not documented (J. Crouse, pers comm).

Addison et al. (1993) recorded cow moose creating small "scratch holes" during the calving season in central Ontario. These scratch holes were attributed to territorial markings due to their positioning near calving sites in a high density moose area. The bed sites we describe were created outside the calving season and moose densities were low in our study area (Windels and Olson 2016), suggesting they reflect thermoregulatory behavior not territorial marking.

The behavior we describe appears to be uncommon in northern Minnesota as McCann et al. (2016) visited 57 bed sites within 51 days of use by GPS radio-collared moose (n = 8) and never observed similar modification of bed sites in the larger study area. Additionally, they visited another 155 bed sites in 2012 that were made the previous summer and did not observe bed site modifications. Though some evidence of modification could have been obscured during the ≥10 months (e.g., by fall litter deposition or vegetative growth the following spring) between use of a bed site and the subsequent visitation, we believe that the deliberate exposition of soil would have been evident at some sites.

While sample size limits the inferences which can be drawn from this case study, we describe a thermoregulatory behavior undocumented for moose, though not uncommon for other ungulates. Further research might better explain how this behavior varies across moose range and in response to different environmental conditions. These studies should focus on determining the potential thermal benefits of bed site modification in various habitat types, the frequency of occurrence under different climatic regimes and landscape compositions, and potential reasons for bed site fidelity.

REFERENCES

Addison, E. M., R. F. Mclaughlin, D. J. H. Fraser, and M. E. Buss. 1993. Observations of pre- and post-partum behavior of moose in central Ontario. Alces 29: 27–33.

Barkley, D. G., R. E. Blaser, and R. E. Schmidt. 1965. Effect of mulches on microclimate and turf establishment. Agronomy Journal 57: 189–192.

Demarchi, M. W., and F. L. Bunnell. 1995. Forest cover selection and activity of cow moose in summer. Acta Theriologica 40: 23–36.

Dussault, C., J. Ouellet, R. Courtois, J. Huot, L. Breton, and J. Larochelle. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. Ecoscience 11: 321–328.

Ericsson, G., H. Dettki, W. Neumann, J. M. Arnemo, and N. J. Singh. 2015. Offset between GPS collar-recorded temperature in moose and ambient weather station data. European Journal of Wildlife Research 61: 919–922.

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

Faber-Langendoen, D., N. Aseng, K. Hop, M. Lew-smith, and J. Drake. 2007. Vegetation classification, mapping, and monitoring at Voyageurs National Park, Minnesota: an application of the U.S. National Vegetation Classification. Applied Vegetation Science 10: 361–374.

Gatenby, R. M. 1977. Conduction of heat from sheep to ground. Agricultural Meteorology 18: 387–400.

Hanks, R. J., S. B. Bowers, and L. D. Boyd. 1961. Influence of soil surface conditions on net radiation, soil temperature, and evaporation. Soil Science 91: 233–239.

Johnson-Maynard, J. L., P. J. Shouse, R. C. Graham, P. Castiglione, and S. A. Quideau. 2004. Microclimate and pedogenic implications in a 50-year-old chaparral and pine biosequence. Soil Science Society of America Journal 68: 876–884.

Kelliher, F. M., T. A. Black, and D. T. Pierce. 1986. Estimating the effects of understory removal from Douglas fir forest using a two-layer canopy evaporation model. Water Resources Research 22: 1891–1899.

McCann, N. P., R. A. Moen, and T. R. Harris. 2013. Warm-season heat stress in moose (*Alces alces*). Canadian Journal of Zoology 91: 893–898.

________, ________ S. K. Windels, and T. Harris. 2016. Bed sites as thermal refuges for a cold-adapted ungulate in summer. Wildlife Biology 22: 228–237.

Melin, M., J. Matala, L. Mehtatalo, R. Tiilikainen, O. Tikkanen, M. Maltamo, J. Pusenius, and P. Packalen. 2014. Moose (*Alces alces*) reacts to summer temperatures by utilizing thermal shelters in boreal forest – an analysis based on airborne laser scanning of the canopy structure at moose locations. Global Change Biology 20: 1115–1125.

Merrill, E. H. 1987. Habitat ecology and population dynamics of Mount St. Helens elk. Ph. D. Dissertation, University of Washington, Seattle, Washington, USA.

Millspaugh, J. J., K. J. Raedeke, G. C. Brundige, and C. C. Willmott. 1997. Summer Bed Sites of Elk (*Cervus elaphus*) in the Black Hills, South Dakota: considerations for thermal cover management. The American Midland Naturalist 139: 133–140.

Moen, A. N. 1968. The critical thermal environment: a new look at an old concept. BioScience 18: 1041–1043.

__________. 1973. Wildlife Ecology: An Analytical Approach. W. H. Freeman and Company, San Francisco, California, USA.

Moen, R. A., J. Pastor, and Y. Cohen. 1997. A spatially explicit model of moose foraging and energetics. Ecology 78: 505–521.

Mysterud, A., and E. Østbye. 1999. Cover as a habitat element for temperate ungulates: effects of habitat selection and demography. Wildlife Society Bulletin 27: 385–394.

NOAA (National Oceanic and Atmospheric Administration). 2010. Climatological data for International Falls, Minnesota. National Climatic Data Center, Ashville, North Carolina, USA.

Ogée, J., E. Lamaud, Y. Brunet, P. Berbigier, and J. M. Bonnefond. 2001. A long-term study of soil heat flux under a forest canopy. Agricultural and Forest Meterology 106: 173–187.

Renecker, L. A. 1987. Bioenergetics and behavior of moose (*Alces alces*) in the aspen dominated Boral Forest. Ph. D. Thesis, University of Alberta, Edmonton, Canada.

____________, and R. J. Hudson. 1986. Seasonal energy expenditures and thermoregulatory responses of moose. Canadian Journal of Zoology 64: 322–327.

____________, and ____________. 1989a. Ecological metabolism of moose in aspen-dominated boreal forests, central Alberta. Canadian Journal of Zoology 67: 1923–1928.

____________, and ____________. 1989b. Seasonal activity budgets of moose in aspen-dominated boreal forests. Journal of Wildlife Management 53: 269–302.

Renecker, L. A, and R. J. Hudson. 1990. Behavorial and thermoregulatory responses of moose to high ambient temperatures and insect harassment in aspen-dominated forests. Alces 26: 66–72.

Schaap, M. G., and W. Bouten. 1997. Forest floor evaporation in a dense Douglas fir stand. Journal of Hydrology 193: 97–113.

Sargeant, G. A., L. E. Eberhardt, and J. M. Peek. 1994. Thermoregulation by Mule Deer (*Odocoileus hemionus*) in arid rangelands of southcentral Washington. Journal of Mammology 75: 536–544.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92: 235–253.

Street, G. M., J. Fieberg, A. R. Rodgers, M. Carstensen, R. Moen, S. A. Moore, S. K. Windels, and J. D. Forester. 2016. Habitat functional response mitigates reduced foraging opportunity: implications for animal fitness and space use. Landscape Ecology: 1–15.

Sullivan Bay CASTNet. Meteorological station data. http://ard-request.air-resource.com/data.aspx (accessed February 2015).

Van Beest, F. M., B. Van Moorter, and J. S. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Animal Behavior 84: 723–735.

Van Moorter B., J. M. Gaillard, P. D. Mcloughlin, D. Delorme, F. Klein, and M. S. Boyce. 2009. Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales. Oecologia 159: 669–678.

Windels, S. K., and B. T. Olson. 2016. Voyageurs National Park Moose Population Survey Report 2016. Natural Resource Data Series NPS/VOYA/NRDS-2016/1031. National Park Service, Fort Collins, Colorado, USA.