SPATIAL AND TEMPORAL HETEROGENEITY IN THERMAL CONDITIONS FOR WILDLIFE

Nicholas J. DeCesare[1], Richard. B. Harris[2], Jesse R. Newby[3], and Collin J. Peterson[4]

[1]Montana Fish, Wildlife and Parks, Missoula, Montana 59804, USA; [2]Montana Fish, Wildlife and Parks, Helena, Montana 59620, USA; [3]Montana Fish, Wildlife and Parks, Dillon, Montana 59725, USA; [4]Montana Fish, Wildlife and Parks, Kalispell, Montana 59901, USA.

ABSTRACT: Temperature is an important component of climatic conditions that drive animal evolution, niche space, and life history traits. We used field-deployed temperature sensors and generalized linear mixed-effects models to quantify the spatiotemporal variation of ambient temperatures in three study areas of western Montana, in support of concurrent studies of moose ecology and population dynamics. We found substantial potential for thermal refuge for moose; temperature ranges observed simultaneously among sites within study areas averaged 7.0°C during summer and 6.1°C during winter. We considered 6 site variables hypothesized to affect local temperatures (elevation, topographic position, aspect, land cover type, forest canopy cover, and the interaction of land cover and solar radiation), and all contributed to model performance. However, the direction and magnitude of effects varied in a cyclic fashion during the 24-hour diel cycle, and in many cases, exhibited reversed effects between day and night. Although spatial heterogeneity in temperature during summer was only slightly higher than during winter, our ability to explain such pattern was much better during summer (average $R^2 = 0.51–0.56$) than during winter (average $R^2 = 0.09–0.23$). We encourage researchers and managers to explore field collection and spatiotemporal modeling of temperature sensor data for cost-effect description of thermal environments for wildlife in local settings.

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Temperature is an important component of climatic conditions that drive animal evolution, niche space, and life history traits (Magnuson et al. 1979). Wildlife responses to variation in temperature can include spatial and temporal shifts in behavior (Heide-Jørgensen et al. 2020), physiological costs (Haroldson et al. 1998), and effects on growth and demography (Frishkoff et al. 2015, Pérez-Barbería et al. 2020). Although the sensitivity of ectotherms to spatial variation in microclimatic conditions is well established (Woods et al. 2015), evidence in the literature is mixed regarding the relative importance of thermal conditions for ungulates. Ungulates in temperate regions commonly exhibit behavioral responses to temperature such as shifts in habitat selection towards areas of thermal cover to mitigate warm conditions (Bowyer and Kie 2009, DelGiudice et al. 2013, Wiemers et al. 2014). These findings emphasize thermal cover as a component of ungulate habitat, and habitat management practices for species such as elk (*Cervus canadensis*) commonly include thermal cover prescriptions (Smith and Long 1987). However, Cook et al. (1998) argued the positive energetic benefits of thermal cover are outweighed by negative reduction of forage in such environments when managing habitat for elk, while Long et al. (2014) suggested the relative importance of forage and thermal conditions are context-dependent.

Among ungulates, the cold-adapted moose (*Alces alces*) has received particular attention with regards to impacts of temperature on physiology, habitat selection, and fitness. Heat can increase metabolic costs for moose at lower temperature thresholds than observed for other sympatric ungulates (Renecker and Hudson 1986). Although population performance has been negatively correlated with temperature (Lenarz et al. 2009; but see Mech and Fieberg 2014), no empirical data exist to link population performance to ambient temperature, unlike indirect impacts related to habitat change (Monteith et al. 2015, Holmes et al. 2021) and parasitism (Pekins 2020). In addition to intrinsic adaptations to thermal stress (Thompson et al. 2019, 2020), moose commonly employ thermoregulatory behavior through micro- and macro-habitat use at high summer temperatures (Schwab and Pitt 1991, Dussault et al. 2004, Broders et al. 2012, van Beest et al. 2012, van Beest & Milner 2013, Melin et al. 2014, Street et al. 2015, McCann et al. 2013, Ditmer et al. 2018, Alston et al. 2020, Borowik et al. 2020) and during winter (Burkholder et al. 2022). A notable exception was found in Ontario, where the general lack of moose behavioral response to temperature was attributed to low underlying variability in temperature across the study area (Lowe et al. 2010).

The importance of thermal conditions in driving wildlife behavior in any local system likely depends upon the heterogeneity of micro-climates (Long et al. 2014, Londe et al. 2020). Spatial variation in the thermal environment is often ignored in wildlife management (Elmore et al. 2017). However, the spatial and temporal variation of thermal conditions can be complex functions of broad-scale climate context and fine-scale heterogeneity in vegetation type and structure, topography, hydrology, season, and time of day (Lookingbill and Urban 2003, McGraw et al. 2012, Olson et al. 2014, Londe et al. 2020). Elmore et al. (2017) suggested that heterogeneity in thermal conditions be assessed prior to conducting studies of the relative importance of thermal conditions on wildlife behavior and demography. For cold-adapted species such as moose, predicting spatial and temporal variation in temperature across habitats may be particularly important at the species' range periphery. Relatively cool locations may serve as a crucial component of habitat in such settings where high temperatures may impose metabolic costs if unmitigated (McCann et al. 2013, Ditmer et al. 2018). Under these circumstances the influence of land management decisions on thermal refugia may become a relevant concern, along with forage and security cover, in managing habitat for moose or other species (Elmore et al. 2017).

We measured spatiotemporal variation in ambient temperatures during both winter and summer within three study areas of western Montana (USA) in support of concurrent studies of moose ecology and population dynamics. Our objectives were to assess the thermal conditions available to wildlife in these areas, to understand the effects of environmental covariates on temperature across time and space, and to predict thermal landscapes as a function of those covariates.

METHODS

Study Areas

We investigated factors affecting local temperatures in 3 three areas of western Montana, USA where long-term studies of moose ecology and demography were ongoing (Newby and DeCesare 2020). The Cabinet Mountains study area (48.2°N, 115.5°W) was characterized by dense forest of diverse conifer species, ranging in elevation from 660 to

2,494 m with mean January temperatures of −8.1 to −0.8°C, mean July temperatures of 7.7 to 25.0°C, and mean annual precipitation of 91.4 cm. The Big Hole study area (45.4°N, 113.5°W) was a higher elevation valley including willow- (*Salix* spp.) riparian habitat surrounded by forested mountains, ranging in elevation from 1,842 to 3,232 m with mean January temperatures of −12.0 to −2.2°C, mean July temperatures of 5.4 to 22.9°C, and mean annual precipitation of 63.8 cm. The Rocky Mountain Front study area (47.9°N, 112.7°W) included areas of riparian and fen habitat and rugged mountainous forests, ranging in elevation from 1,200 to 2,803 m with mean January temperatures of −10.2 to −0.9°C, mean July temperatures of 7.1 to 22.6°C, and mean annual precipitation of 71.4 cm.

Field Methods

To quantify relationships between biophysical variables and local air temperatures, we used temperature sensors (iButton Model DS1921G-F5; Maxim Integrated, San Jose, California) to measure ambient temperature at selected, non-random locations within each of the 3 study areas. Sensors (n = 96; 32 per study area) were deployed a minimum of 1 km apart during one winter and one summer session lasting 85 days each, as dictated by memory limitation of the sensors. We programmed sensors to take temperature readings during the same hourly schedule within each study area and season. Season dates were not identical across study areas as certain sensors initiated or ended a few days apart. Overall, winter sampling occurred during 18 November 2013–16 February 2014 in the Cabinet Mountains, 14 December 2013–9 March 2014 in the Big Hole, and 19 November 2014–13 February 2015 in the Rocky Mountain Front. Summer sampling occurred during 9 July–3 October, 2014 in the Cabinet Mountains, 3 July–27 September, 2014 in the Big Hole, and 17 July–11 October, 2014 in the Rocky Mountain Front (Fig. 1). We anchored sensors at a height of 2 m above ground to the stems of trees or shrubs where available, or to existing wooden fence structures in open areas (Lundquist and Huggett 2008), and shielded sensors from solar radiation using custom radiation shields following Holden et al. (2013).

We subjectively selected sampling sites to include shrubland and forested vegetation cover types (MNHP 2017) across a gradient in elevation that aligned with areas used by radio-collared moose in a related study (Newby and DeCesare 2020; 858–1,444 m in the Cabinet Mountains, 1,847–2,263 m in the Big Hole, and 1,330–1,764 m in the Rocky Mountain Front). Temperature was recorded at hourly intervals (i.e., 0:00, 1:00, 2:00, …) throughout the 24-hr diel cycle. To represent ambient conditions generally in each study area, we developed reference values from data collected at Remote Automatic Weather Stations (RAWS) administered by the National Interagency Fire Center.

Range in Temperature as Metric of Potential Thermal Refuge

We first used descriptive comparisons of temperature data across sites within each study area and season to evaluate the degree of spatiotemporal variation. Because temperature sensors were collecting concurrent temperature measurements during the same day and hour within each area, we used the range (maximum – minimum) in temperatures at each sensor during each day-hour as a metric of potential for thermal refuge among environmental conditions at a given time. We used scatter density plots to visualize the variation in temperature ranges within each season and estimated the average range per hour for each site and season. This established the degree of variation which we then

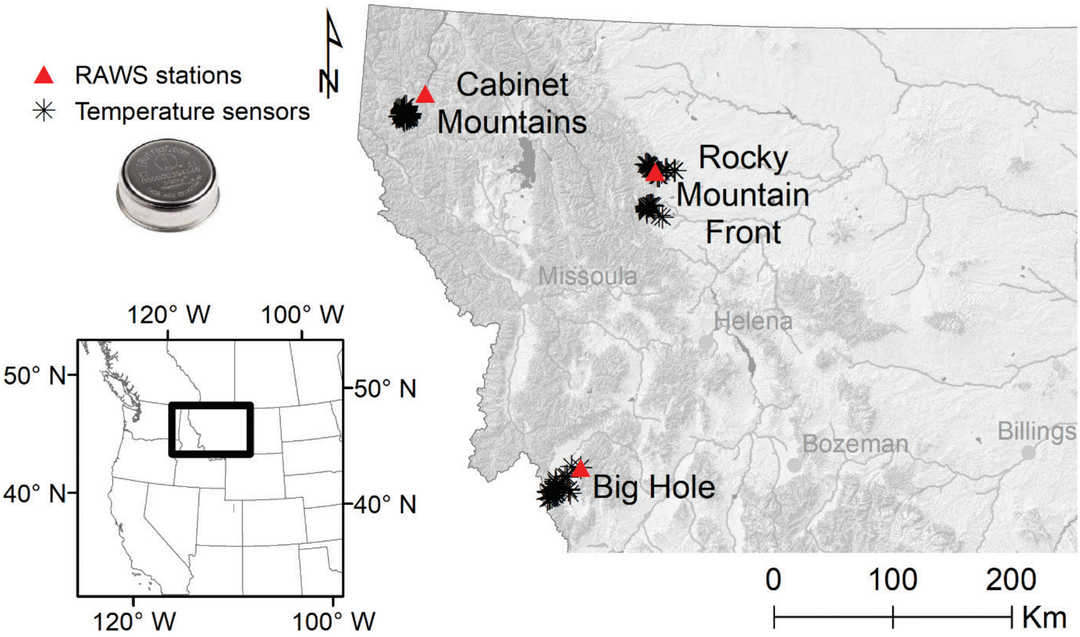

Fig. 1. Locations of study areas, temperature sensors, and Remote Automatic Weather Station (RAWS) sites for monitoring ambient temperature, western Montana, 2013–2015.

sought to explain with environmental covariates and generalized linear models.

Environmental Covariates

To quantify site characteristics affecting temperature, we first estimated metrics of topography using a digital elevation model from the USGS 3D Elevation Program (USGS 2019). From the DEM we estimated elevation, aspect, and a topographic position index (TPI). TPI generally discriminated the gradient of landforms from drainages (negative values) to ridges (positive values) and was estimated as the difference in elevation between any given pixel and the average elevation of the surrounding neighborhood, 1-km in radius (Weiss 2001). We used a trigonometric transformation of aspect (cos[aspect-45]; McCune and Keon 2002) that indexed heat load received according to variation in slope aspect. This transformation of aspect ranged from −1 to 1 along a southwest to northwest gradient.

We also quantified vegetation conditions at each site according to available raster layers for land cover type (MNHP 2017) and percent forest canopy cover (Homer et al. 2015). Lastly, we accounted for the effect of variable solar radiation during daytime using measurements of solar radiation ($W \cdot m^{-2}$) recorded at RAWS stations. In final stages of model-building we tested 2 interactions between solar radiation (recorded at a single RAWS site in each study area) and both land cover and aspect to assess whether the effects of these variables depended upon the relative solar radiation across days.

Statistical Analyses

We quantified spatiotemporal variation in temperature as the site- and hour-specific difference between ambient temperatures recorded by each iButton sensor and the temperature recorded simultaneously at RAWS stations located within each study area (Cabinet Mountains FIRM8; Big Hole

SLCM8, Rocky Mountain Front GSNM8; Fig. 1). We built models that predicted Δt (defined as $t_{\mathrm{site}} - t_{\mathrm{RAWS}}$) based on environmental covariates measured at each site. Treating Δt as the response variable in our models instead of t_{site} itself did not affect covariate patterns (because t_{RAWS} was a constant across all sites for a given day-hour), but served to link our models to widely available RAWS data and ensure that we could make predictions both in- and out-of-sample for any given location and date-time using GIS-measured variables and available RAWS data. Modeling variation in Δt also focused our analyses specifically on spatial variation in temperature by adjusting all data relative to the temporally varying measure of temperature at the RAWS sites. This effectively removed temporal (i.e., daily) variation in temperature data and left us to model spatial differences alone. We modeled effects on Δt separately by 8 separate hours of the day (0, 3, 6, 9, 12, 15, 18, 21) to better illuminate the dynamics of how site factors varied in their effects on local temperatures during the daily cycle.

Preliminary examination of data indicated that Δt readings recorded at the same time-of-day on successive days were highly autocorrelated. To minimize the effects of such serial correlation on estimates of deviance, we modeled all relationships using the function lme within the R package nlme (Pinheiro et al. 2022), treating sample site as a random variable and with autocorrelation structure modeled using corARMA within sample sites. We used maximum likelihood (rather than restricted maximum likelihood) throughout, as this has been recommended for model selection in cases where the random factors remain the same in all models within the suite but various combinations of putative explanatory variables are examined (Zuur et al. 2009).

For each combination of study area (i.e., region), season (summer vs. winter), and hour of the day, we began by evaluating univariate patterns of each environmental variable and Δt. We first centered and standardized all continuous covariates (Schielzeth 2010) and then fit univariate models for canopy, land cover type, elevation, aspect, and TPI to explore patterns in the data. We then fit global main effects models including all 5 of these same environmental covariates as hypothesized drivers of Δt for each study area, season, and hour. We were less concerned about potentially problematic effects of multicollinearity among covariates for two reasons. First, correlations among these covariates were all <0.6, and second, the underlying goals for these models were more rooted in predictions than parsimony; thus, we fit global models to all subsets of data rather than performing model selection for each study area, season, and hour. Lastly, in addition to the 5 main effects covariates, we also included the interaction of solar radiation and land cover type in all daytime models. We conducted preliminary assessment of this interaction using AIC to compare main effects models with those including the interaction, and models were improved in the majority of cases (78%, 90%, and 60% of data subsets by season and hour in the Big Hole, Cabinet Mountains, and Rocky Mountain Front study areas, respectively).

We evaluated the conditional R^2 value from each model to assess the relative amount of variation explained (Nakagawa and Schielzeth 2013) and used standardized coefficients to assess the relative importance of each covariate (Galipaud et al. 2017). Lastly, to understand the relative importance of each covariate across all times of day, we averaged the absolute values of standardized coefficients for each covariate across hour-specific models per study area and season to compare relative variable importance.

RESULTS

Ambient Temperature Data

We deployed sensors in 96 different locations, equally distributed across the 3 study areas and retrieved data from all 96 sensors during summer and 93 sensors during winter (Table 1). Restricting our interpretations to temperatures gathered at the 8 focal hours of the day analyzed here, these yielded 124,653 temperature readings for comparison with temperatures at their respective RAWS sites (Table 1). Elevations of sensors were lowest in the Cabinet Mountains study area and highest in the Big Hole study area. A higher proportion of sensors were located in forested cover types in the Cabinet Mountains than at the other two study areas; forest canopy was higher in the Cabinet Mountains (Table 1). Across all sensors and times-of-day, temperatures recorded by field sensors were, on average, 0.95–2.35°C colder than that at RAWS stations in the Cabinet Mountains and Big Hole study areas across both seasons, but more similar to that at the RAWS station on the Rocky Mountain Front (Table 1).

There was substantial potential for thermal refuge according to the temperature ranges observed among sites per study area, season, and hour (Fig. 2). On average, sites varied by 7.0°C during summer (Big Hole 6.1°C, Cabinet Mountains 7.6°C, Rocky Mountain Front 7.3°C) and by 6.1°C during winter (Big Hole 6.1°C, Cabinet Mountains 5.0°C, Rocky Mountain Front 7.4°C; Fig. 2). However, we observed considerable heterogeneity in the magnitude of temperature variation among sites on a given day and hour (Fig. 2), ranging from 0°C (e.g., identical temperatures across all sites in a given area) to maximum temperature ranges of 19, 20.5, and 22.5°C observed among sites at a single time in each study area, respectively.

Environmental Drivers of Thermal Refuge

Considered in isolation (i.e., via univariate coefficients), predictor variables not only varied in a cyclic fashion during the 24-hour diel cycle, but in many cases, exhibited reversed effects between day and night (Fig. 3). Such patterns were most pronounced during summer in the Cabinet Mountains, where conditions such as high canopy cover, forest land

Table 1. Summary of ambient temperature data, site attribute data for mean elevation, mean percent canopy closure, mean transformed aspect (TA), proportionate forest land cover, and the mean difference between temperatures measured at each site and Remote Automatic Weather Station (RAWS) sites in close proximity to each study area (Δ*t*), from 3 study areas in western Montana during summer and winter seasons, 2013–2015.

Study area	Season	Sensors (n)	Temperature readings (n)	Mean (SD) elevation, m	Mean (SD) percent canopy	Mean (SD) TA	Proportion forested	Mean (SD) Δt
Cabinet Mountains	Summer	32	21,142	1,135 (164)	71 (37)	−0.04 (0.68)	0.91	−2.14 (3.83)
	Winter	32	21,048					−0.95 (2.79)
Big Hole	Summer	32	20,459	2,061 (121)	36 (27)	0.09 (0.56)	0.59	−2.35 (2.35)
	Winter	31	19,713					−1.23 (2.54)
Rocky Mountain Front	Summer	32	21,856	1,518 (122)	32 (26)	0.10 (0.72)	0.69	0.08 (2.88)
	Winter	30	20,435					−0.43 (3.15)

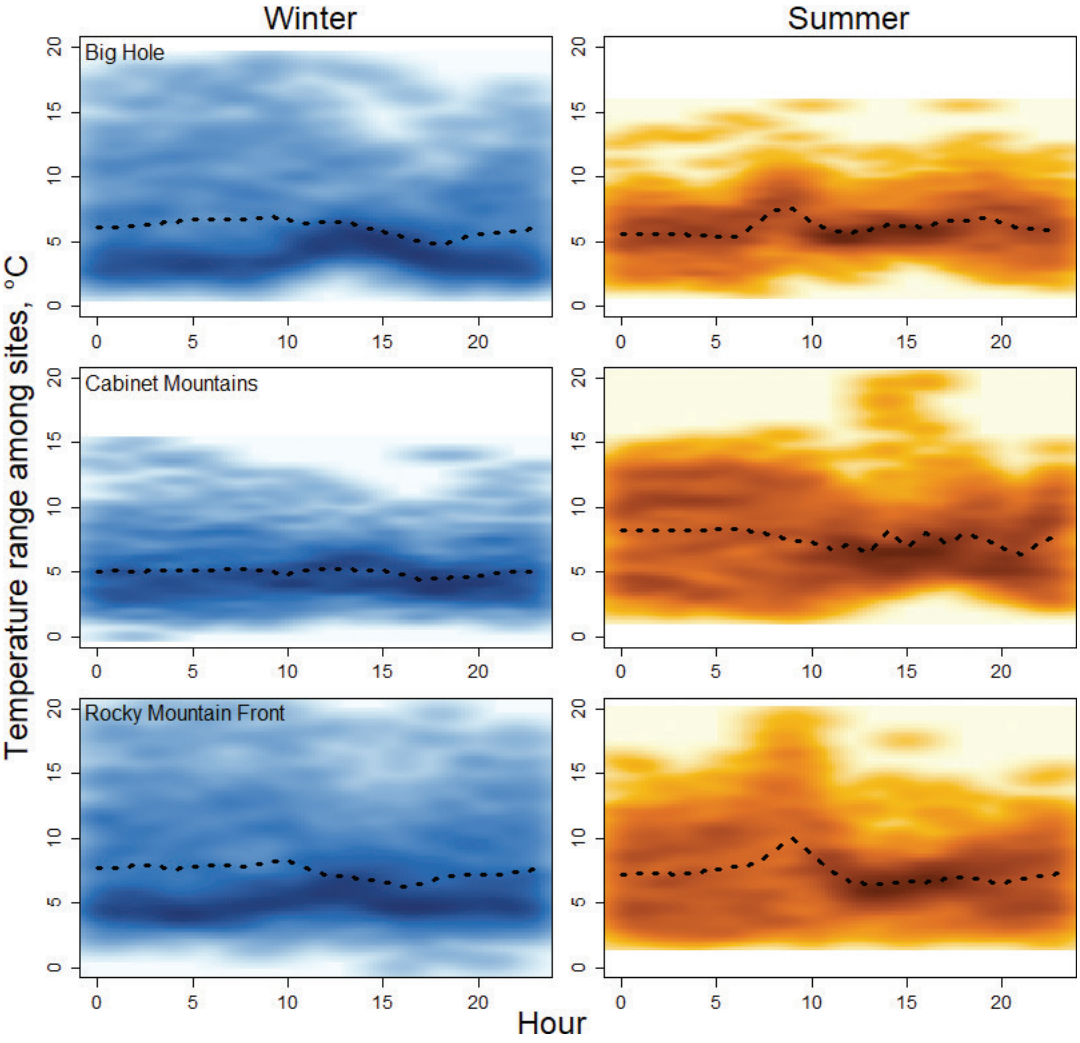

Fig. 2. Scatter density plot and average (dashed line) of the maximum range in ambient temperature measured concurrently across days at hourly intervals among sensors within 3 study area 2 seasons, western Montana, 2013–2015.

cover type, high elevation, northerly aspects, and convex topographic positions (i.e., ridges) tended to yield cooler temperatures during the day, but warmer temperatures at night (Fig. 3). Univariate results also showed stronger ability to explain spatiotemporal variation in temperature with our covariates during summer than winter across all study areas (Fig. 3).

When pooling covariates into multivariable models, all six variables (5 main effect terms and an interaction between land cover and solar radiation) made relatively similar contributions to model performance. We used average absolute values of standardized coefficients to evaluate relative importance of covariates and found forest land cover and elevation to be among the most consistently high, though canopy, aspect, and TPI were also comparable in some seasons and study areas (Fig. 4). Conditional R^2 values showed considerably higher ability to explain variation in the data with models for summer temperature (average R^2 = 0.51, 0.55, 0.56 among study areas) compared to those

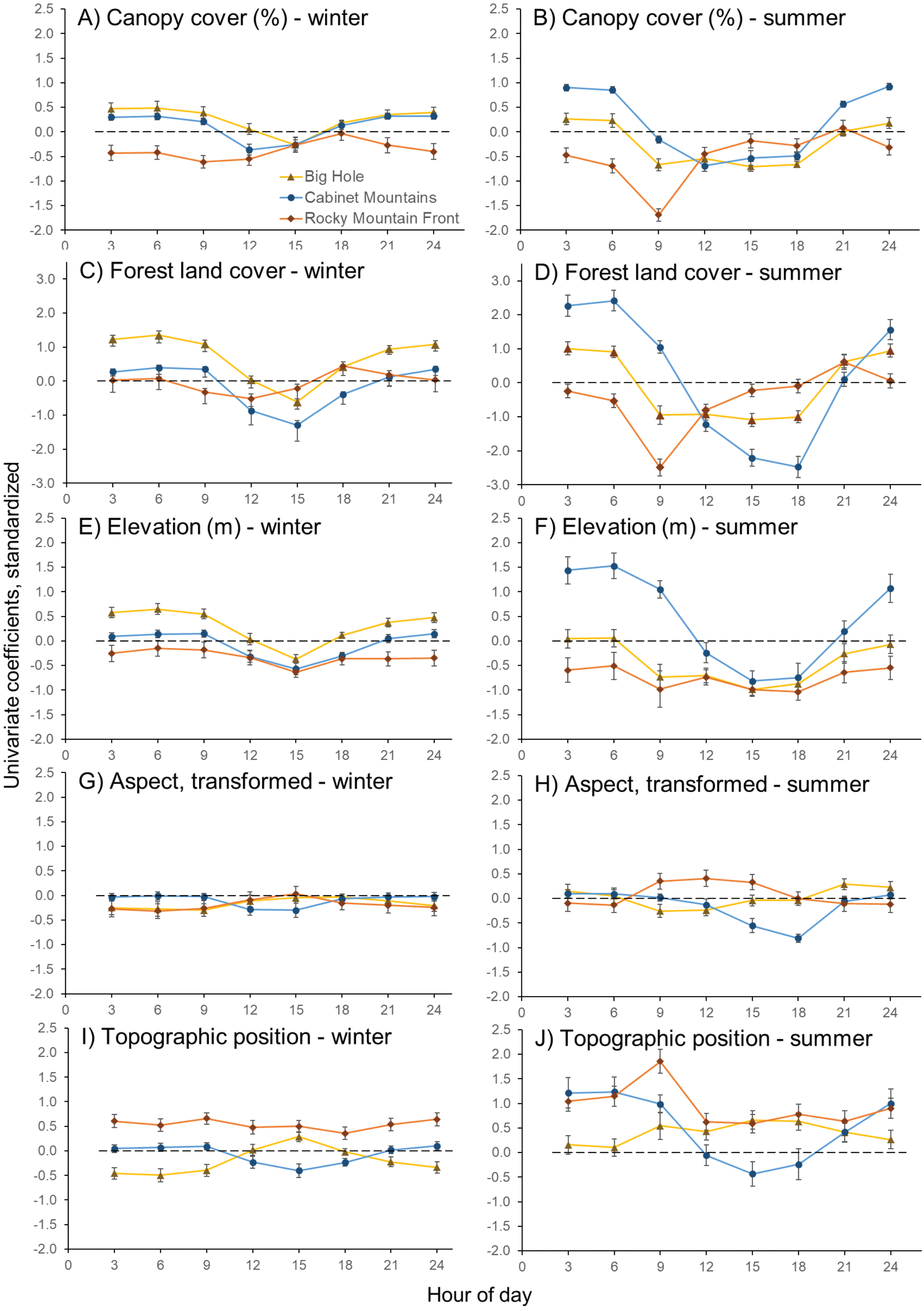

Fig. 3. Univariate coefficients and standard errors for the effects of spatial covariates and season on ambient temperature variation by time of day in the Big Hole, Cabinet Mountains, and Rocky Mountain Front study areas of western Montana, 2013–2015.

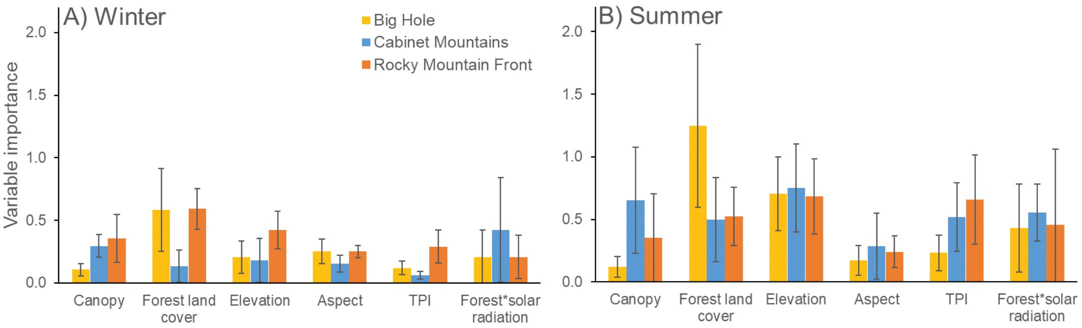

Fig. 4. Average importance of 6 variables (canopy, forest land cover, elevation aspect, topographic position index [TPI], interaction of forest land cover forest and solar radiation), in explaining spatial variation in ambient temperature in 3 study areas and 2 seasons, western Montana, 2013–2015.

estimated for winter (average R^2 = 0.09, 0.23, 0.14 among study areas). Lastly, global models facilitated the spatial prediction of ambient temperature across each study area, which also revealed differences in thermal environments between seasons and times (Fig. 5, Tables 2 and 3).

DISCUSSION

In contrast to McGraw et al. (2012) who found no differences > 2°C in radiant temperature using black globe sensors in Minnesota (minimal elevation range), we found average differences in ambient air temperatures of 6–7°C at all 3 study areas during both seasons. Under the most extreme conditions, differences between locations potentially available to moose approached 20°C, depending on study area, season, and time-of-day. Surprisingly, spatial heterogeneity in temperatures was somewhat consistent across both time of day and baseline temperature (N. DeCesare, unpublished data). The refuge effect of relatively cool sites appears consistently available; however, animal responses to temperatures, and their dependence on thermal refugia, may be accentuated during particularly extreme conditions (Pigeon et al. 2016, Robertson et al. 2022). Furthermore, drivers of spatial pattern in these differences were not static, and covariates associated with cool conditions varied widely by study area, season, and time of day (Fig. 3). Moose selection of sites as thermal refugia may therefore be conditioned temporally and spatially according to shifting patterns of heterogeneity that dictate where and when cooler conditions are available.

Combinations of biophysical variables generating cooler microclimates typically reversed between early-morning and late-afternoon time periods. Similar to studies elsewhere, we found that both forested vegetation types and increased canopy closure within forested vegetation provided cooling (relative to grass-shrub types) during midday but retained warmth at night (Olson et al. 2014, Li et al. 2015). Elevation-temperature relationships were more complex, with decreases in temperature at high elevation in some study areas and seasons, but inversion patterns of cooler temperature at low elevation in some situations (e.g., summer nighttime temperatures in Cabinet Mountains). Such summer inversion patterns have been observed previously in mountain study areas, where radiatively cooled air can accumulate in drainage bottoms during night (Holden et al. 2011). Diurnal cycles of moose movement and habitat use consistent with some of these time-varying patterns of

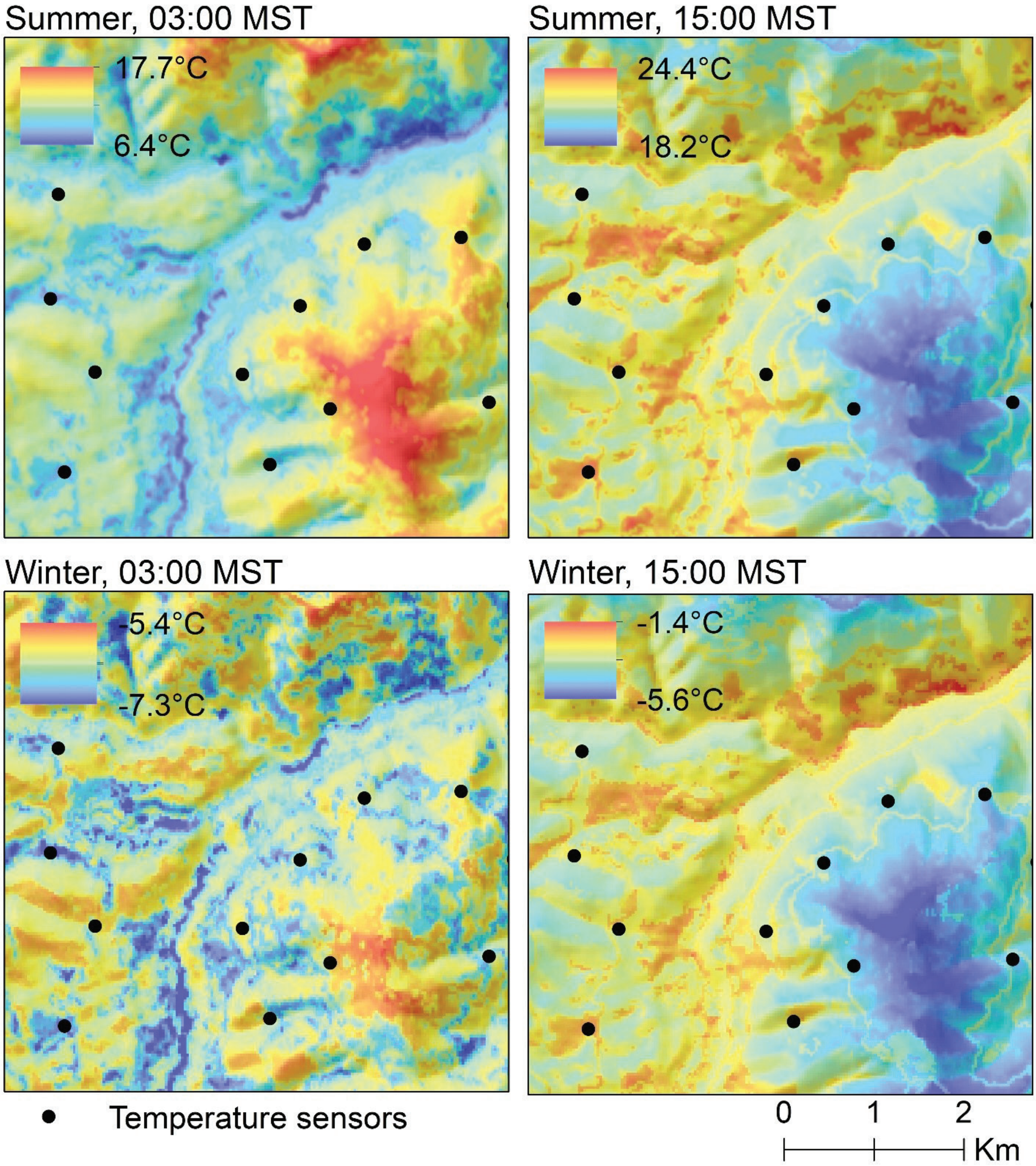

Fig. 5. Predicted ambient temperature from global generalized linear models in an example portion of the Cabinet Mountains study area during two times and seasons and relative to the average recorded temperature at Remote Automatic Weather Station (RAWS) sites during the study period, 2013–2015.

temperature have been noted by Dussault et al. (2004), Borowik et al. (2020), and Burkholder et al. (2022). Where moose have been shown to increase nighttime activity in response to warm ambient temperatures (Montgomery et al. 2019), spatial variation in temperature conditions may induce behavioral effects during both daytime and nighttime.

While spatial heterogeneity in temperature during summer was only slightly higher compared to that during winter (Fig. 2), our

Table 2. Global model coefficients (and standard errors) predicting Δt during summer, according to spatial variation in centered and standardized covariates in three study areas of western Montana, 2013–2015.

Study area	Hour	intercept	Canopy	Forest land cover	Elevation	Aspect	TPI	Forest* solar radiation
Big Hole	0	−4 (0.32)	0.08 (0.23)	2.01 (0.44)	−0.55 (0.29)	−0.06 (0.16)	0.35 (0.22)	
	3	−3.7 (0.34)	0.16 (0.25)	1.78 (0.47)	−0.45 (0.31)	−0.13 (0.18)	0.33 (0.24)	
	6	−3.32 (0.32)	0.17 (0.23)	1.6 (0.44)	−0.42 (0.29)	−0.2 (0.17)	0.28 (0.22)	
	9	−0.86 (0.57)	−0.26 (0.42)	0.64 (0.78)	−0.55 (0.52)	−0.36 (0.3)	0.32 (0.39)	−0.09 (0.04)
	12	−1.57 (0.32)	0.05 (0.23)	0.41 (0.43)	−0.86 (0.29)	−0.33 (0.16)	0.04 (0.22)	−0.29 (0.04)
	15	−2.88 (0.29)	−0.02 (0.21)	0.85 (0.4)	−1.28 (0.27)	−0.13 (0.15)	−0.03 (0.2)	−0.38 (0.05)
	18	−4.21 (0.31)	−0.15 (0.23)	0.74 (0.43)	−0.92 (0.29)	−0.13 (0.16)	0.14 (0.22)	−0.37 (0.04)
	21	−4.66 (0.34)	−0.06 (0.25)	1.95 (0.47)	−0.61 (0.31)	0.03 (0.18)	0.37 (0.24)	−1.02 (0.05)
Cabinet Mountains	0	0.02 (0.77)	1.14 (0.23)	−0.5 (0.82)	0.57 (0.33)	−0.21 (0.23)	0.79 (0.31)	
	3	0.67 (0.76)	1.07 (0.23)	−0.24 (0.81)	0.98 (0.32)	−0.15 (0.22)	0.69 (0.31)	
	6	0.79 (0.69)	1 (0.21)	−0.17 (0.73)	1.14 (0.29)	−0.12 (0.2)	0.59 (0.28)	0.3 (0.05)
	9	0.28 (0.59)	−0.09 (0.18)	−0.16 (0.62)	0.75 (0.25)	0.09 (0.17)	0.45 (0.24)	−0.38 (0.05)
	12	−3.55 (0.58)	−0.68 (0.18)	−0.46 (0.62)	−0.21 (0.25)	0.06 (0.17)	0.02 (0.24)	−0.65 (0.04)
	15	−4.96 (0.59)	−0.32 (0.18)	−0.78 (0.62)	−0.93 (0.25)	−0.51 (0.17)	0.22 (0.24)	−0.82 (0.03)
	18	−4.74 (0.81)	−0.11 (0.24)	−1.15 (0.86)	−1.09 (0.34)	−0.83 (0.24)	0.59 (0.33)	−0.79 (0.04)
	21	−2.26 (0.58)	0.79 (0.17)	−0.52 (0.61)	−0.31 (0.25)	−0.3 (0.17)	0.79 (0.23)	−0.4 (0.05)
Rocky Mountain Front	0	0.75 (0.34)	0.04 (0.3)	0.66 (0.51)	−0.45 (0.24)	−0.26 (0.23)	0.9 (0.26)	
	3	0.71 (0.33)	−0.04 (0.29)	0.5 (0.5)	−0.47 (0.23)	−0.26 (0.22)	0.96 (0.25)	
	6	0.17 (0.36)	−0.22 (0.31)	0.4 (0.54)	−0.36 (0.25)	−0.24 (0.24)	0.98 (0.27)	0.24 (0.07)
	9	−1.65 (0.3)	−1.14 (0.26)	−0.2 (0.45)	−0.67 (0.21)	0.14 (0.2)	0.93 (0.23)	−1.64 (0.06)
	12	−0.98 (0.23)	−0.47 (0.2)	0.22 (0.34)	−0.64 (0.16)	0.19 (0.15)	0.17 (0.17)	−0.43 (0.05)
	15	−0.53 (0.17)	−0.31 (0.15)	0.65 (0.26)	−1.02 (0.12)	−0.03 (0.12)	0.19 (0.13)	−0.03 (0.04)
	18	−0.65 (0.19)	−0.29 (0.17)	0.7 (0.28)	−1.23 (0.13)	−0.46 (0.13)	0.35 (0.14)	−0.36 (0.04)
	21	0.66 (0.3)	0.32 (0.26)	0.84 (0.44)	−0.62 (0.21)	−0.34 (0.2)	0.78 (0.23)	−0.03 (0.06)

Table 3. Global model coefficients (and standard errors) predicting Δ*t* during winter, according to spatial variation in centered and standardized covariates in three study areas of western Montana, 2013–2015.

Study area	Hour	intercept	Canopy	Forest land cover	Elevation	Aspect	TPI	Forest* solar radiation
Big Hole	0	−1.56 (0.16)	0.12 (0.12)	0.81 (0.23)	0.18 (0.15)	−0.3 (0.08)	0.11 (0.11)	
	3	−1.55 (0.16)	0.15 (0.12)	0.81 (0.23)	0.19 (0.15)	−0.32 (0.09)	0.02 (0.12)	
	6	−1.75 (0.19)	0.06 (0.14)	0.9 (0.26)	0.33 (0.18)	−0.34 (0.1)	0.07 (0.13)	
	9	−1.5 (0.16)	0.02 (0.12)	0.7 (0.22)	0.41 (0.15)	−0.38 (0.08)	0.18 (0.11)	−0.01 (0.07)
	12	−1.77 (0.24)	0.14 (0.18)	−0.05 (0.34)	0.06 (0.23)	−0.2 (0.13)	0.17 (0.17)	−0.27 (0.07)
	15	−1.62 (0.2)	0.07 (0.15)	−0.13 (0.28)	−0.3 (0.18)	−0.11 (0.1)	0.11 (0.14)	−0.07 (0.07)
	18	−1.38 (0.1)	0.16 (0.07)	0.47 (0.14)	−0.06 (0.09)	−0.14 (0.05)	0.15 (0.07)	−0.49 (0.05)
	21	−1.53 (0.15)	0.11 (0.11)	0.79 (0.21)	0.12 (0.14)	−0.22 (0.08)	0.15 (0.1)	
Cabinet Mountains	0	−0.29 (0.22)	0.38 (0.07)	−0.07 (0.23)	0.07 (0.09)	−0.13 (0.06)	0.11 (0.09)	
	3	−0.18 (0.23)	0.35 (0.07)	−0.06 (0.24)	0.05 (0.1)	−0.13 (0.07)	0.07 (0.09)	
	6	−0.15 (0.24)	0.35 (0.07)	−0.02 (0.25)	0.11 (0.1)	−0.1 (0.07)	0.05 (0.1)	
	9	−0.17 (0.25)	0.25 (0.07)	0.01 (0.26)	0.11 (0.1)	−0.09 (0.07)	0.05 (0.1)	−0.08 (0.05)
	12	−1.7 (0.31)	−0.3 (0.09)	−0.19 (0.33)	−0.26 (0.13)	−0.22 (0.09)	−0.08 (0.13)	−0.43 (0.05)
	15	−2.38 (0.32)	−0.15 (0.1)	−0.39 (0.34)	−0.53 (0.14)	−0.29 (0.09)	−0.03 (0.13)	−1.01 (0.05)
	18	−1.25 (0.21)	0.18 (0.06)	−0.1 (0.22)	−0.32 (0.09)	−0.15 (0.06)	0.02 (0.08)	−0.18 (0.05)
	21	−0.51 (0.21)	0.39 (0.06)	−0.21 (0.22)	0.01 (0.09)	−0.14 (0.06)	0.08 (0.08)	
Rocky Mountain Front	0	−0.79 (0.19)	−0.32 (0.16)	0.69 (0.27)	−0.43 (0.12)	−0.3 (0.12)	0.42 (0.14)	
	3	−0.41 (0.2)	−0.37 (0.17)	0.7 (0.29)	−0.34 (0.13)	−0.28 (0.13)	0.39 (0.15)	
	6	−0.64 (0.19)	−0.41 (0.17)	0.72 (0.28)	−0.26 (0.12)	−0.28 (0.12)	0.31 (0.14)	
	9	−0.91 (0.17)	−0.52 (0.14)	0.5 (0.24)	−0.25 (0.11)	−0.23 (0.1)	0.34 (0.12)	−0.06 (0.09)
	12	−1.49 (0.19)	−0.67 (0.16)	0.34 (0.27)	−0.49 (0.12)	−0.16 (0.12)	−0.02 (0.14)	−0.33 (0.08)
	15	−0.52 (0.12)	−0.29 (0.1)	0.37 (0.17)	−0.73 (0.08)	−0.2 (0.07)	0.16 (0.09)	−0.38 (0.06)
	18	−0.54 (0.16)	−0.03 (0.14)	0.69 (0.23)	−0.45 (0.1)	−0.28 (0.1)	0.31 (0.12)	−0.06 (0.07)
	21	−0.98 (0.18)	−0.23 (0.15)	0.72 (0.25)	−0.44 (0.11)	−0.28 (0.11)	0.37 (0.13)	

ability to explain such pattern was much better during summer (average $R^2 = 0.51–0.56$) than winter (average $R^2 = 0.09–0.23$). To the contrary, another study directed at predicting monthly maximum and minimum temperatures over space using covariates similar to ours found equivalent model fit during summer and winter (Estevo et al. 2022). There are likely other unmeasured drivers of spatial variation in temperature during winter for which we were not able to account. Studies of moose behavioral responses to heat have emphasized summer conditions (e.g., Melin et al. 2014), though relatively warm temperatures can also induce physiological costs during winter (Renecker and Hudson 1986). We don't fully understand animals' ability to anticipate or detect heterogeneity in the thermal environment, but it's possible that such ability may also vary between seasons.

Measures of ambient temperature are not equivalent to the operative or effective temperature (Bakken 1981) that better describes the thermal conditions experienced by an animal by accounting for the additional and potentially more impactful effects of solar radiation and wind (Mitchell et al. 2018). Heterogeneity in operative temperature in our study areas may be higher than ambient temperature alone (Dzialowski 2005, Elmore et al. 2017). Furthermore, we did not sample additional variation in realized temperatures in accordance with the ground, water, or snowpack which may mitigate thermal conditions for wildlife (McCann et al. 2013, Thompson et al. 2021).

We used a relatively modest sample size of temperature sensors and were able to find a variety of complex relationships between temperature and topographic and vegetation conditions. While spatiotemporal temperature data are already available at coarse scales from various remote-sensing or interpolated data sets, multiple studies have shown that models using locally-derived empirical temperatures outperform general models (Macek et al. 2019, Estevo et al. 2022). We encourage researchers and managers to explore field collection and spatiotemporal modeling of temperature sensor data for cost-effect and baseline description and prediction of thermal environments for wildlife (Fig. 5). The physiological effects of thermal environments are multi-faceted and complex, and improving our understanding and management of thermal environments is an important challenge for future conservation (Mitchell et al. 2018).

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