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Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate

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RH: Thermoregulatory habitat use and selection

ABSTRACT

While the behavioural response of animals to unfavourable climatic conditions has received increased attention recently, most habitat selection studies nonetheless ignore effects of ambient temperature. Thermoregulatory behaviour in endotherms should be most notable in species susceptible to heat stress. We evaluated whether a heat-sensitive northern ungulate, the moose (*Alces alces*), showed thermoregulatory behaviour in response to ambient temperature in two populations in southern Norway. We quantified the seasonal habitat use of GPS-collared adult females, as well as fine-scale habitat selection patterns, in relation to time of day and critical temperature thresholds thought to induce heat stress. We also assessed whether temperature driven changes in spatial behaviour led to a trade-off between thermal cover and forage availability. Frequent exposure to temperatures above critical thresholds occurred in both summer and winter and in both study areas. Moose responded by seeking thermal shelter in mature coniferous forest and avoiding open habitat types, leading to a trade-off between forage and cover availability in summer but not winter. Differences in habitat choice in response to temperature were most pronounced at twilight. We found that fine-scale habitat selection analyses, using step selection functions, more effectively revealed thermoregulatory behaviour in both seasons and populations than habitat use. This is because habitat selection analyses are better able to identify limiting factors operating at different spatiotemporal scales than habitat use. Future studies on thermoregulatory animal behaviour should focus on the effect of abiotic factors, such as climate, on habitat-fitness relationships, which may be critical to understanding population responses to a changing climate.

Keywords*:* climate change, deer, endotherms, habitat selection, SSF, thermoregulation, trade-off.

INTRODUCTION

Direct climatic effects on species' distribution and population dynamics are apparent in both ectotherms and endotherms (Walther et al. 2002; Parmesan 2006). The importance of temperature on the ecology and behaviour of cold-blooded species (ectotherms) has long been recognised and is studied extensively (Campbell et al. 1974; Baker 1978; Bryant et al. 2002; Hodgson et al. 2011). In contrast, the potential direct effect of temperature on changes in spatial behaviour of warm-blooded species (endotherms) such as large herbivores has only been acknowledged in recent years (Parker & Gillingham 1990; Merrill 1991; Conradt et al. 2000; Natori & Porter 2007; Aublet et al. 2009; Bowyer & Kie 2009). Indeed, Alpine Ibex (*Capra ibex*) make short-term altitudinal migrations to escape warm ambient temperatures during summer (Aublet et al. 2009), black-tailed deer (*Odocoileus hemionus columbianus*) actively select mature forest stands with dense canopy cover over open vegetation during warm days (Bowyer & Kie 2009), and Bourgoin et al. (2011) showed that ambient temperature and wind speed directly affect summer activity patterns of female mouflon (*Ovis gmelini musimon*). Quantifying such thermoregulatory behaviour is a necessary first step to effectively evaluate climate induced effects on population dynamics of large herbivores (Grosbois et al. 2008; Mysterud & Sæther 2011). For example, it has been shown that Svalbard reindeer (*Rangifer tarandus plathyrynchus*) respond to thaw-freeze events by long-distance displacements in order to find accessible grazing pasture elsewhere (Stien et al. 2010) and that the frequency of such icing events has a strong negative effect on Svalbard reindeer population growth rates (Hansen et al. 2011).

Behavioural adjustments in habitat use often involve trade-offs between positive and negative factors (Sih 1980; Hamel & Côté 2008). A much discussed trade-off in habitat selection of large ruminants is maximising energy intake (i.e. food acquisition) whilst minimising exposure to predation risk or unfavourable climatic conditions (i.e. food-cover trade-off: Schmitz 1991; Mysterud & Østbye 1999; Hebblewhite & Merrill 2009). High canopy cover often provides an advantage through reduced exposure to harsh climatic conditions or predation, whereas low canopy cover often gives greater forage availability (Schmitz 1991), although in some cases, habitat types that provide shelter may also contain high quality forage and a forage-cover trade-off might not be observed (Pierce et al. 2004). In addition, within one species the strength of the forage-cover trade-off is likely to vary between individuals and temporal scales (McNamara & Houston 1996).

The behavioural response of moose (*Alces alces*) to ambient temperatures has been investigated extensively in North America (Renecker & Hudson 1990; Schwab & Pitt 1991; Demarchi & Bunnell 1995; Dussault et al. 2004; Lowe et al. 2010). By contrast, evaluations of thermoregulatory behaviour of European moose are currently absent, yet may be a contributing factor to the recent observations of reduced demographic performance and individual fitness of populations living in southern Norway (Solberg et al. 2006; Wam et al. 2010; Milner et al. 2012). Because of their large body size and effective pelage insulation, moose are extremely well adapted to cold environments. During winter, they can tolerate temperatures down to -32°C without a change in their metabolic rate (Renecker & Hudson 1986), indicating that cold stress due to hypothermia is therefore not an important limiting factor for moose, as it is for other ungulates (Schmitz 1991; Mysterud & Østbye 1999). However, under warm conditions, moose may suffer from heat stress during both summer and winter (Renecker & Hudson 1986). Upper critical temperature thresholds for moose under captive conditions are believed to be 14 °C (increased respiration rates) and 20 °C (open-mouth panting) in summer and -5 °C and 0 °C in winter (Renecker & Hudson 1986). Much of the evidence shows that North American moose change their habitat use in relation to ambient temperature but mainly during summer (Schwab & Pitt 1991; Demarchi & Bunnell 1995; Dussault et al. 2004). However, Lowe et al. (2010) did not detect a behavioural response of moose to high ambient temperatures in summer or winter, which questions the notion that heat stress is limiting the southern distribution range of moose in North America (Murray et al. 2006; Lenarz et al. 2009).

Here we evaluate the effect of ambient temperature on habitat use and selection of GPS-collared female moose in two populations in southern Norway. Furthermore, we compare the effectiveness of these two space-use metrics to address thermoregulatory behaviour. Optimal foraging theory (OFT) predicts that when environmental conditions are favourable, animals should choose habitats based on forage abundance, and moreover, concentrate their foraging activities as long as the energetic gain exceeds the loss (MacArthur & Pianka 1966). As such, we expect high use and selection for foraging habitat (e.g. young, successional open-canopied forest) in both summer and winter, but only when ambient temperature is below levels that induce heat stress in moose (Expectation 1: E1). However, if temperature is an important limiting environmental factor, we expect increased use and selection of thermal cover (e.g. mature dense-canopied forest) during periods of high ambient temperature (E2). Furthermore, if temperature mediates behavioural adjustments in habitat use (from foraging habitat under optimal thermal conditions [E1] to shelter habitat under stressful ambient temperatures [E2]) we expect this to lead to a forage-cover trade-off.(E3).

METHODS

Study areas

Our study areas (Fig. 1) were located in Siljan and Skien municipalities, Telemark county in southern Norway, (59° N, 9° E) and in Stor-Elvdal municipality, Hedmark County, in south-eastern Norway (61° N, 11° E). Euclidean distance between the centres of the two areas was 250 km. The Telemark study area (733 km^2) was in the boreonemoral zone and ranged in elevation from 20 to 800 m with the forest line at approximately 750 m. The Hedmark study area (1 370 km^2) was in the boreal zone and ranged in elevation from 250 to 1100 m, with the tree line at approximately 800-900 m. Both areas were covered with commercially managed coniferous forest dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) but some mixed deciduous stands of birch species (*Betula pubescens* and *B. pendula*), rowan (*Sorbus aucuparia*), willow (*Salix* spp.) and aspen (*Populus tremula*) occurred throughout both areas. Sub-alpine birch woodland occurred above the upper limit of commercial forest in both areas. The climate differed between the study areas, being colder with longer snow cover in the more continental Hedmark area (Table 1). Winter moose densities in both areas were estimated to be approximately 1.3 individuals per km^2 (Milner et al. 2012). Red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) occurred at much lower densities in both areas. Large predators were essentially absent in both study areas with hunting being the single most important cause of moose mortality.

Moose and temperature data

A total of 74 adult female moose, each accompanied by a calf, were captured in January 2007 – 2010. Captured adult females were fitted with GPS collars with a VHF radio transmitter (Tellus Remote GSM, Followit AB, Lindesberg, Sweden), programmed with a 1-h relocation schedule.

The GPS data were screened for positional outliers using moose movement characteristics (Bjørneraas et al. 2010). With this approach, we removed 251 erroneous locations (<0.2% of the full GPS data set). We estimated the location error of the collars using field tests in the autumn (van Beest et al. 2010a). The mean location error of the collars was 29.9 m (range: 8–49 m) which was less than the resolution of our habitat maps (50 m x 50 m). The average GPS-collar fix rate, while on the moose, was 94% (range: 72–100%) during winter (i.e. January 1st till April 15th) and 92% (range: 71–99%) during summer (i.e. June 1st till September 15th). Both GPS fix rate and location error were well below critical thresholds to accurately estimate habitat use and selection (Johnson & Gillingham 2008). All GPS collars were equipped with a temperature sensor and during each location attempt the temperature was recorded and stored in the collar memory. Details of how we field tested the accuracy of the temperature sensors are given in Appendix 1. Field trials revealed that collar temperature was closely correlated with ambient temperature, and less with radiant heat load (a combination of air temperature, solar radiation and wind speed). Consequently, our GPS collars underestimated the actual heat load as experienced by moose, thereby providing a conservative estimate of the subsequent response to thermal conditions.

Ethical Note

All moose were captured, handled and collared using established techniques (Arnemo et al. 2003) with permission from the national management authority, the Directorate for Nature Management, and evaluated and approved by the Norwegian Agency of Animal Welfare. Animal capture and handling was conducted by professionals following a capture protocol developed specifically for moose. All animals were observed until full recovery was evident. To minimize stress, following times of animals by helicopter was kept to a minimum and time between first observation and recovery was typically under 1 hour. Within the project we made 252 captures and experienced 2 directly capture-related mortalities (1 euthanized due to a broken leg and 1 asphyxiated by vomit), a mortality rate of 0.8% which falls within the 2% mortality limit considered acceptable in Scandinavia (Arnemo et al. 2006). No other animals showed severe stress with physiological side-effects. The weight of GPS collars was 1035g, less than 1 % of the body weight of moose. Collars were not believed to impede or increase costs of locomotion (Eriksen et al. 2011). Collars were retrieved by re-capturing (18), locating fallen collars (8), locating animals that died of natural causes (3) or by shooting during the hunting season (44) as part of the annual quota for adult female moose set by the local wildlife board.

Habitat maps and thermal cover

Habitat maps were derived from a combination of digital forest stand maps and satellite land cover maps with a resolution of 50 m x 50 m (Appendix 2). We considered the following 6 habitat classes: mature coniferous forest, open mixed forest, young pine forest, young spruce forest, deciduous forest, and other (all non-forest habitats including moorland, heath, bog, agricultural land and open water).

To identify which habitat types provided the best thermal cover in our study areas, we used the temperature data collected by the GPS collars while on the moose. We modelled changes in ambient temperature for each habitat type throughout the day using generalized additive mixed effect models (GAMM) in the library mgcv implemented in R (R Development Core Team 2012). We expected ambient temperature to change non-linearly over time and GAMMs provided a suitable framework as explanatory variables with expected non-linear effects could be fitted as parametric or non-parametric smoothing terms and, moreover, additional variables could be included as random effects. The response variable was temperature and the explanatory variables were habitat type and hour of the day, fitted as a smoothing function. The smoothing function was fitted for each habitat type separately (i.e. as a habitat x time interaction) to allow temperature to vary non-linearly over time and space. We used cyclic regression splines, with the optimal smooth curve estimated by the generalized cross-validation procedure (Wood 2006). Moose ID was fitted as a random intercept to account for repeated measurements from the same individual. To account for temporal dependency among observations, we used a continuous correlation structure (corARMA), which provided the best fit based on AIC (Pinheiro & Bates 2000).

Habitat use and habitat selection

To assess the influence of ambient temperature on moose space use, we quantified habitat use and habitat selection relative to seasonal thermoregulation thresholds (E1 and E2). Habitat use and selection of moose typically vary seasonally (van Beest et al. 2010b) but also daily (Dussault et al. 2004; Bjørneraas et al. 2011). To incorporate potential circadian patterns into our analyses, we categorised all GPS locations by time of day according to prevailing light conditions (light, twilight, and dark). Light conditions for each study area and study period were obtained from the U.S. Naval Observatory (http://aa.usno.navy.mili). Within each season and time of day, moose locations were partitioned into 3 temperature classes based on respiratory responses reported by Renecker & Hudson (1986; Table 1): 1) Low ambient temperature (collar temperature < -5°C in winter and < 14°C in summer), 2) moderate ambient temperature (≥ -5°C < 0°C in winter and ≥

14°C < 20°C in summer) and 3) high ambient temperature (≥ 0°C in winter and ≥ 20°C in summer).

For each individual, seasonal habitat use was estimated for each light condition and temperature class separately by calculating the proportion of GPS locations in the different habitat types. Differences in use of habitat classes were subsequently tested using analysis of variance (ANOVA). Proportion of locations in each habitat was logit transformed (Warton & Hui 2011). Post hoc paired Tukey Honest Significant Differences (HSD) tests were performed to determine where differences between temperature classes occurred. All analyses were performed in the statistical software R (R Development Core Team 2012).

Habitat selection was calculated by measuring the relationship between use and availability. We estimated moose habitat selection as a function of ambient temperature using resource selection functions (RSFs; Manly et al. 2002). Because ambient temperature directly affects movement of moose at short temporal scales (van Beest et al. 2011), we quantified temperature-mediated RSFs at the scale of an individual's movement trajectory using a matched case-control design (also known as Step Selection Functions; SSF: Fortin et al. 2005a; Forester et al. 2009). With this approach, each observed (GPS) location (scored 1) is linked to a set of random (available) locations (scored 0) dependent on where the individual was at that time. In our case, each observed location was associated with 5 random locations sampled from around the observed location using the observed step length and turning angle distributions from each individual during a given season. Mean (SD) step lengths as observed in Telemark were 63.6 m (13.0 m) and 86.1 m (16.5 m) for winter and summer respectively. In Hedmark these were 71.9 m (18.2 m) and 99.7 m (22.8 m). The RSFs were solved using conditional logistic regression from the R package survival. To account for possible individual effects and autocorrelation in the data we calculated robust standard errors (sensu Forester et al. 2009). Using this approach, we first analysed the residuals of the conditional logistic regression using a linear mixed model with moose ID as a random intercept. This procedure showed that autocorrelation in step length disappeared beyond lag 10 (hours) for all animals. We then used the autocorrelation function to re-calculate the covariance matrix and robust standard errors.

The selection coefficients estimated by the conditional logistic regression are the log odds ratio for a habitat type being chosen relative to a reference habitat type ($\beta = 0$). As such, selection for the reference habitat occurs when the other habitat types have $\beta < 0$. The reference category in our RSF models was set to deciduous forest. To detect differences in selection within and between habitat types across temperature classes and light conditions, we calculated 95 % confidence intervals, which were based on robust standard errors (as explained above). The explanatory variables in the RSFs were habitat type, temperature class, light condition and their interactions. The number of individuals included in the winter RSFs were N = 31 and 39 for Telemark and Hedmark respectively and N = 27 and 35 in the summer RSFs. To evaluate predictive success of the population level RSFs we used the *k*-fold cross-validation procedure, evaluated with Spearman-rank correlation (r_s), proposed by Boyce et al. (2002).

Forage and cover availability

To evaluate whether temperature-driven behavioural adjustments in habitat use led to changes in the forage and cover availability experienced (E3), we restricted the GPS data of collared moose to the Telemark study area only (N = 31) as we had no landscape-scale data on forage and cover availability in Hedmark. We quantified forage availability using seasonal forage availability maps (50 m x 50 m), based on field estimates of available biomass of the six most common browse species eaten by moose in southern Norway; full details are given in van Beest et al.(2010b). For each moose location, we extracted the total amount of forage biomass from the forage availability maps (i.e. the sum of the six most common browse species) and calculated the mean forage available for each temperature class, light condition and moose separately.

We used seasonal canopy closure, measured with a spherical densitometer, as an index of cover availability (Mysterud & Østbye 1999). Details on how canopy closure was measured, analysed and mapped across the study area are given in Appendix 3 and Table A1. For each moose location, we extracted the predicted value for seasonal canopy closure and then calculated the mean for each temperature class. Within each season, we tested for differences in both forage availability and canopy closure between light condition and temperature classes using ANOVA, followed by post hoc paired Tukey HSD tests if differences between groups occurred.

RESULTS

Thermal cover

Mean temperature in both study areas and seasons fluctuated non-linearly during the day (Fig.1: edf ≥ 7.78, F ≥ 100, $P < 0.001$ for all habitat types; Appendix 4, Table A2). Mean temperature was generally higher in open habitat (e.g. young pine and spruce stands) compared to mature coniferous stands (mean difference = 4 °C in winter, $F = 13.61$, $P < 0.001$, and 2 °C in summer, $F = 7.58$, $P < 0.001$), suggesting that mature coniferous stands provide the best cover from high temperatures in both areas and seasons.

During winter, mean temperature exceeded the lower critical threshold (-5 °C) throughout the 24 hour period in all habitat types and in both study areas, except mature coniferous forest in

Hedmark. In Telemark, mean temperatures in open habitats and deciduous forest were above the upper critical threshold (0 °C) for a large part of the day (between 8:00 and 17:00). Mature coniferous forest stands were the coolest habitat type in both areas but did exceed the upper (0 °C) critical temperature threshold for part of the day (between 10:00 and 15:00) in Telemark but never in Hedmark. In Hedmark, mean temperature rarely rose above the 0 °C critical threshold except in young forest stands.

During summer, temperature exceeded the lower critical threshold (14 °C) in all habitat types but only during the day (between 7:00 and 18:00 in Telemark and between 8:00 and 17:00 in Hedmark). Mean temperature never rose above the upper (20 °C) critical threshold in any of the habitat types or areas. Again, mature coniferous forest stands were always the coolest in both areas.

Thermoregulatory habitat use and selection

During winter, habitat use of moose did not change in relation to critical temperature thresholds and light conditions in either study area (Fig.2; $F_{4,282} = 0.155$; $P = 0.960$ in Telemark and $F_{4,345} = 0.078$; $P = 0.989$ in Hedmark). During summer, moose showed a behavioural response to ambient temperature in Telemark during light (Fig. 3: $F_{2,81} = 3.61$; $P = 0.031$) and twilight ($F_{2,81} = 3.21$; $P = 0.0455$) but not in Hedmark ($F_{4,309} = 1.529$; $P = 0.194$). In Telemark, moose used mature coniferous forest more at high temperatures than at low temperatures during light and twilight (Tukey HSD, $P < 0.01$) and young spruce stands less at high temperatures than at low temperatures during both light and twilight (Tukey HSD: $P = 0.03$).

In contrast to the habitat use results, the winter RSFs revealed changes in habitat selection patterns as a function of ambient temperature in both study areas (Fig. 4). In Telemark, selection for mature coniferous stands increased with temperature, with a significant difference between low and high temperature classes (i.e. non-overlapping 95% confidence intervals between temperature classes) but only during twilight. Conversely, selection of young spruce stands and, to a lesser extent young pine stands, tended to be higher under low than moderate temperatures during both light and twilight but surprisingly, did not differ significantly from selection at high temperatures irrespective of light condition. In Hedmark, selection for mature coniferous stands did not differ between temperature classes or light conditions. Selection for young spruce and young pine stands was higher at low than moderate temperatures during twilight and darkness, but not significantly higher than at high temperatures during twilight. The amount of variation explained (R^2) by the winter RSF models was 0.23 for Telemark (max possible in conditional logistic regression is 0.45) and 0.19 for Hedmark. The models had good predictive performance, with significant r_s across five cross-validation sets (0.76 ± 0·011 (SD), $P < 0{\cdot}001$ for Telemark and 0.82 ± 0·010, $P < 0{\cdot}001$ for Hedmark).

During summer, habitat selection patterns of moose changed clearly in relation to critical temperature thresholds in both study areas (Fig. 5). During all light conditions moose increased selection for mature coniferous stands and reduced selection for open habitat types as temperature increased. Differences in habitat selection between temperature classes were most pronounced at twilight and, in Telemark, during the hours of darkness. The R^2 for the summer RSF models was 0.27 for Telemark and 0.26 for Hedmark. The models also had good predictive performance, with significant r_s across five cross-validation sets (0.83 ± 0·018, $P < 0{\cdot}001$ for Telemark and 0.80 ± 0·013, $P < 0{\cdot}001$ for Hedmark).

Forage-cover availability trade-off

Considering only the Telemark area, forage availability and canopy closure at moose locations were similar across temperature classes and light conditions during winter (Fig. 6: forage availability: $F_{4,265} = 0.156$, $P = 0.96$; canopy closure: $F_{2,265} = 0.287$; $P = 0.886$). By contrast, during summer, moose locations differed in forage availability in relation to critical temperature thresholds during light ($F_{2,78} = 33.576$; $P < 0.001$) and twilight ($F_{2,69} = 7.737$; $P < 0.001$), such that moose used areas with lower forage availability during periods of high ambient temperature compared to periods of low ambient temperature (Tukey HSD, $P < 0.05$ in all cases). Canopy closure also changed in relation to critical temperature thresholds during light ($F_{2,78} = 79.224$; $P < 0.001$) and twilight ($F_{2,69} = 24.731$; $P < 0.001$) as moose used areas with higher canopy closure when ambient temperature was high compared to periods of low ambient temperature (Tukey HSD, $P < 0.01$ in all cases).

DISCUSSION

Temperature is considered a crucial abiotic factor directly influencing animal spatial behaviour and population dynamics (Hansen et al. 2011). This is likely to become increasingly apparent as the climate warms (Mysterud & Sæther 2011). Nonetheless, most studies of endothermic species ignore the effects of climate on habitat choice, despite growing evidence of the importance of temperature and also precipitation and wind speed effects on spatial behaviour (Aublet et al. 2009; Bowyer & Kie 2009; Bourgoin et al. 2011). We have shown how both habitat use and especially fine-scale habitat selection of adult female moose living in southern Norway changed as summer temperature increased. When ambient temperature was below critical thresholds, moose typically selected for foraging habitat (young, successional open-canopied forest) as predicted by OFT, but when temperature was above critical thresholds moose increased selection for thermal cover (mature, dense-canopied forest) as expected by E1 and E2. Moreover, and as expected (E3), the behavioural adjustment leads to a trade-off between forage availability and canopy cover. During winter, however, we found little support for the prediction that temperature was an important factor influencing moose behaviour (E2). Moose did not change habitat use (Fig. 2) and only made minor changes to habitat selection (Fig. 4) relative to critical temperature thresholds, despite ambient temperatures being frequently above the thresholds. Overall, these findings are in agreement with studies of North American moose as well as of other ungulates (Bourgoin et al. 2008; Aublet et al. 2009), which have shown that that temperature mediated behaviour occurs mostly in summer and not in winter (but see Schwab & Pitt 1991). Our results also showed that differences in thermoregulatory behaviour were revealed depending on the space use metric considered (i.e. habitat use versus habitat selection).

In line with E1 and E2, when ambient temperature was above critical thresholds during summer, moose generally decreased their use and selection of open successional forest (foraging habitat) whilst increasing their use and selection of shelter habitat such as mature coniferous forests. As a result, moose traded forage availability off against cover but only during daylight and twilight. Although forage quantity was reduced when using mature forest compared to open foraging habitat, changes in forage quality may have been minor, as habitat types that provide shelter may also contain high quality forage for large herbivores (Pierce et al. 2004). Indeed, closed canopy habitats have a high fitness value for moose during warm summers (Hjeljord et al. 1990; Bo & Hjeljord 1991; Hjeljord & Histol 1999)due to a direct effect of abundant thermal cover in mature forests coupled with an indirect effect of canopy shade on the nutritional quality of forage by delaying the growth rate and maturation of the vegetation (i.e. the forage maturation hypothesis; Hjeljord et al. 1990; Hebblewhite et al. 2008). The relationship between reduced use and selection of foraging habitat and increased use and selection of shelter habitat with increasing temperature was most pronounced during twilight when moose typically increase their foraging activity(Belovsky 1981; Van Ballenberghe & Miquelle 1990; Bjørneraas et al. 2011). Moreover, this relationship was most evident in the more southerly study area where temperatures were above critical levels for a larger proportion of the time (Table 1). The lack of a clear temperature-mediated habitat use pattern in the northern study area could suggest that heat stress was of less concern for moose in that area.

During winter, despite the frequent occurrence of temperatures above critical thresholds likely to induce heat stress in moose (Table1), we did not observe a behavioural response to ambient temperature in terms of changes in habitat use and found only a minor response when using a habitat selection framework. Neither did we observe a population-level forage-cover trade-off during any of the light conditions. The absence of changes in habitat choice with increasing temperature during winter may be due to other limiting factors such as snow cover. Movement in deep snow is known to increase energy expenditure across a range of species (Schmidt 1993; Grignolio et al. 2004; Fortin et al. 2005b) and has a direct negative effect on daily home range size of moose (van Beest et al. 2011) and red deer (Rivrud et al. 2010). It is possible that moving between habitats following an increase in ambient temperature during winter is more costly, at least in the short term (e.g. several hours), than remaining stationary and bedding down on the spot. Indeed, alternative behaviours such as bedding down on cool substrates (e.g. snow) can reduce heat load in ungulates even in open habitat types (Cain et al. 2006). Such postural adjustments, either to reduce or increase heat loss, have been shown very effective in thermoregulation across a wide range of species such as lamoids (de Lamo et al. 1998), lizards (Bauwens et al. 1996), and vultures (Ward et al. 2008). In addition, our data suggests that mean temperatures were consistently above the lower critical temperature threshold (-5°C) in all habitat types in both study areas during winter (Fig.1), suggesting that behavioural adjustments in habitat use would be an ineffective thermoregulation strategy. Alternatively, previously reported critical temperature thresholds for moose (sensu Renecker & Hudson 1986) may be inaccurate (see also Lowe et al. 2010). A re-evaluation of heat stress thresholds of moose seems appropriate, especially under winter conditions as multiple studies on thermoregulatory behaviour have observed strong patterns in summer and not in winter.

Importantly, we detected more pronounced thermoregulatory behaviour in both seasons, but especially in summer, when using a habitat selection rather than habitat use framework. The discrepancy in results highlights a fundamental distinction between habitat use and habitat selection analyses. As RSFs are based on both used and available locations (Manly et al. 2002), habitat use is standardized by what is available and better reflects how habitats are perceived by an individual (Rosenzweig 1981), which may differ across spatial and temporal scales (Wiens 1989). In our study the available locations were sampled in relatively close proximity to the used locations, using distance moved between locations as a criterion (SSF; Fortin et al. 2005a). Therefore, our comparison of used and available locations reflects fine-scale habitat selection of moose. This seemed appropriate as temperature effects on spatial behaviour of large herbivores are typically most pronounced at fine spatial and temporal scales(Loe et al. 2007; Aublet et al. 2009; van Beest et al. 2011), and may explain the lack of behavioural adjustments to temperature found in a previous large scale habitat selection analysis of moose (e.g. Lowe et al. 2010). However, as environmental conditions change over long temporal scales, climatic indices such as temperature can ultimately influence habitat selection patterns at very coarse spatial scales (e.g. home range establishment) as is already apparent by the northward range shifts of various species (Walther et al. 2002; Parmesan 2006), which is also expected for moose in North America (Murray et al. 2006; Lenarz et al. 2009). Moreover, direct links between fitness and habitat selection patterns are increasingly being uncovered (McLoughlin et al. 2006; Van Moorter et al. 2009; Hodson et al. 2010). Habitat use is less likely to reveal potential habitat-fitness correlations as the intrinsic value, or quality, of habitats is not solely based upon their use but instead on its relation with availability and population density (McLoughlin et al. 2008; Gaillard et al. 2010). In ectotherms, fitness is strongly temperature dependent: increasing temperature typically causes a rise in fitness (e.g. intrinsic growth rate) up to an optimum, followed by a rapid decline in fitness as body temperature increases above critical thresholds while in unfavourable habitat (Amarasekare & Savage 2012). So far, temperature has not been considered a potential mediator of habitat-fitness relationships in endotherms such as large herbivores. Yet, as the climate warms, the impact of temperature on animal space use and potentially fitness will likely increase (Mysterud & Sæther 2011). This should be most notable in heat-sensitive species, especially at the southern limit of their distributional range. To assess temperature induced changes in space use and potential habitat-fitness effects, we recommend a fine scaled (spatial and temporal) habitat selection approach as applied in our study.

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Table 1. Summary statistics of temperature recordings from the GPS collars used in the two study areas (N = 31 in Telemark and N = 39 in Hedmark) in southern Norway during winter (January 1st - April 15th) and summer (June 1st - September 15th). Percentage of moose GPS locations are given for 3 ambient temperature classes thought to induce heat stress in moose.

	Telemark	**Hedmark**
Winter		
Mean hourly temperature (°C)	0.84	-3.97
Min; max hourly temperature (°C)	-21.0; +23.0	-33.0; +22.0
% GPS locations < -5°C (low)	15.1	42.8
% GPS locations ≥ -5°C < 0°C (moderate)	28.7	32.5
% GPS locations ≥ 0°C (high)	56.1	24.6
Summer		
Mean hourly temperature (°C)	14.59	13.21
Min; max hourly temperature (°C)	-3.0; +39.0	-4.0; 38.0
% GPS locations < 14°C (low)	52.3	61.2
% GPS locations ≥ 14°C < 20°C (moderate)	34.7	29.7
% GPS locations ≥ 20°C (high)	12.9	9.1

Figure captions

Figure 1. Mean temperatures (°C) among habitat types throughout the day in both summer and winter in Telemark (a) and Hedmark (b) in southern Norway. Dotted lines indicate seasonal specific lower (grey) and upper (black) temperature thresholds inducing heat stress in moose. Note that habitat type “Other” and confidence intervals are not displayed to optimize graph interpretability (see Appendix 4 for full details).

Figure 2. Habitat use of moose during winter in two areas in southern Norway (N = 31 and 39 in Telemark and Hedmark respectively) relative to seasonal temperature classes and light conditions. Error bars represent 95% confidence intervals.

Figure 3. Habitat use of moose during summer in two areas in southern Norway (N = 27 and 35 in Telemark and Hedmark respectively) relative to seasonal temperature classes and light conditions. Error bars represent 95% confidence intervals. Letters indicate a significant difference in use between temperature classes.

Figure 4. Habitat selection estimates of moose during winter in southern Norway (N = 31 and 39 in Telemark and Hedmark respectively) relative to seasonal temperature classes and light conditions. Error bars represent 95% confidence intervals (CI) based on robust standard errors. All estimates are in comparison with the reference category: deciduous forest stands. Habitat classes marked with * have non-overlapping 95% CI between low and high temperature classes, indicating a significant difference in selection.

Figure 5. Habitat selection estimates of moose during summer in southern Norway (N = 27 and 35 in Telemark and Hedmark respectively) relative to seasonal temperature classes and light conditions. Error bars represent 95% confidence intervals (CI) based on robust standard errors. All estimates are in comparison with the reference category: deciduous forest stands. Habitat classes marked with * have non-overlapping 95% CI between low and high temperature classes, indicating a significant difference in selection. A red x indicates that selection coefficients could not be calculated for that particular habitat type due to insufficient available locations in that temperature class and light condition.

Figure 6. Forage availability and canopy closure in relation to seasonal temperature classes and light conditions at locations used by GPS-collared moose in Telemark, southern Norway (N = 31 and 27 in winter and summer respectively). Dots indicate the population-level mean and error bars are 95% confidence intervals. Letters indicate a significant difference in forage and cover availability between temperature classes.

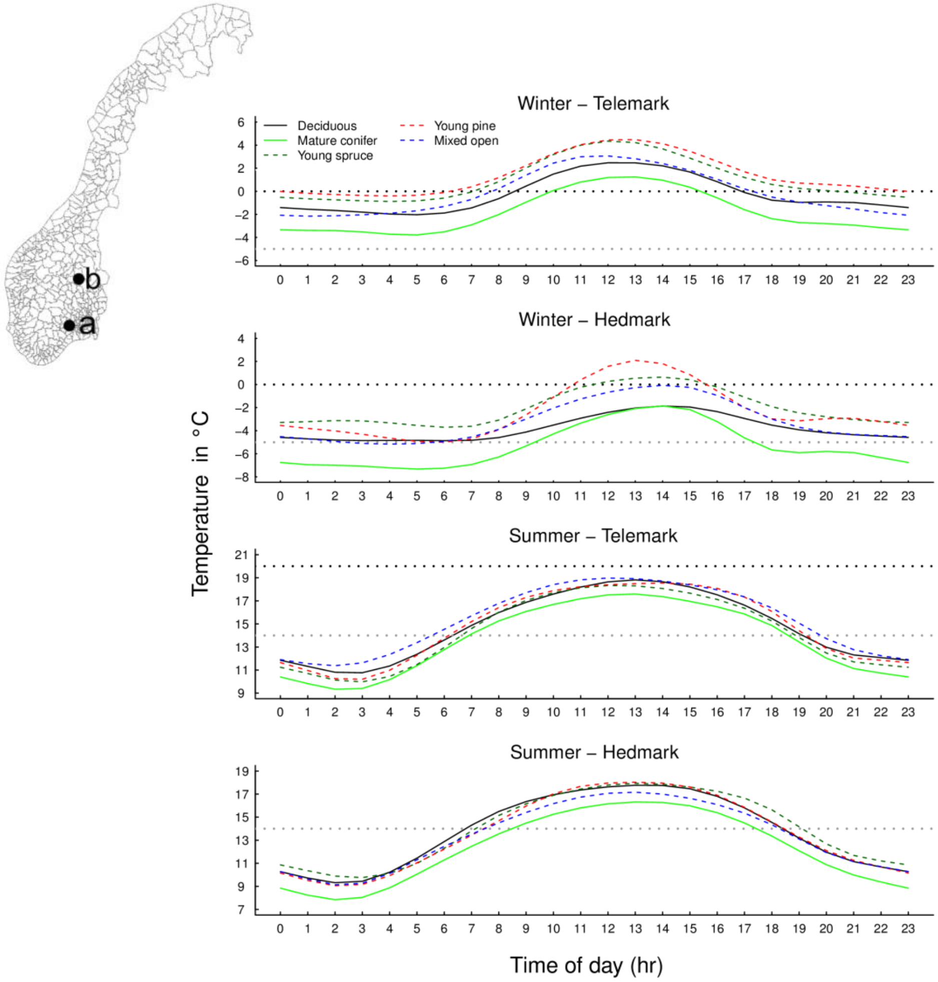

b
a
Winter – Telemark
Deciduous
Mature conifer
Young spruce
Young pine
Mixed open
Winter – Hedmark
Summer – Telemark
Summer – Hedmark
Temperature in °C
Time of day (hr)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23

Fig. 1

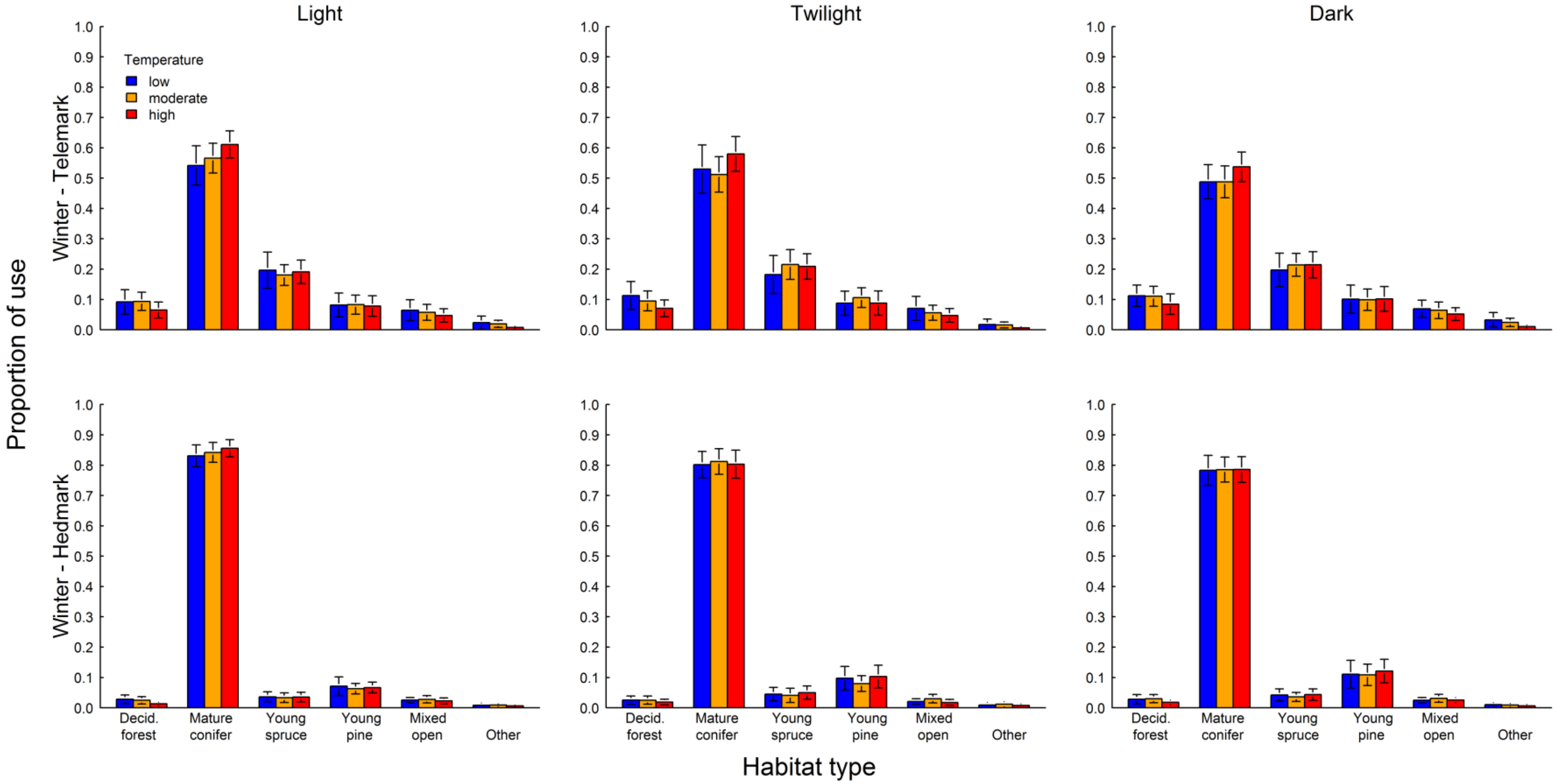

Light
Twilight
Dark
Temperature
low
moderate
high
Proportion of use
Winter - Telemark
Winter - Hedmark
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Decid. forest
Mature conifer
Young spruce
Young pine
Mixed open
Other
Habitat type

Fig. 2

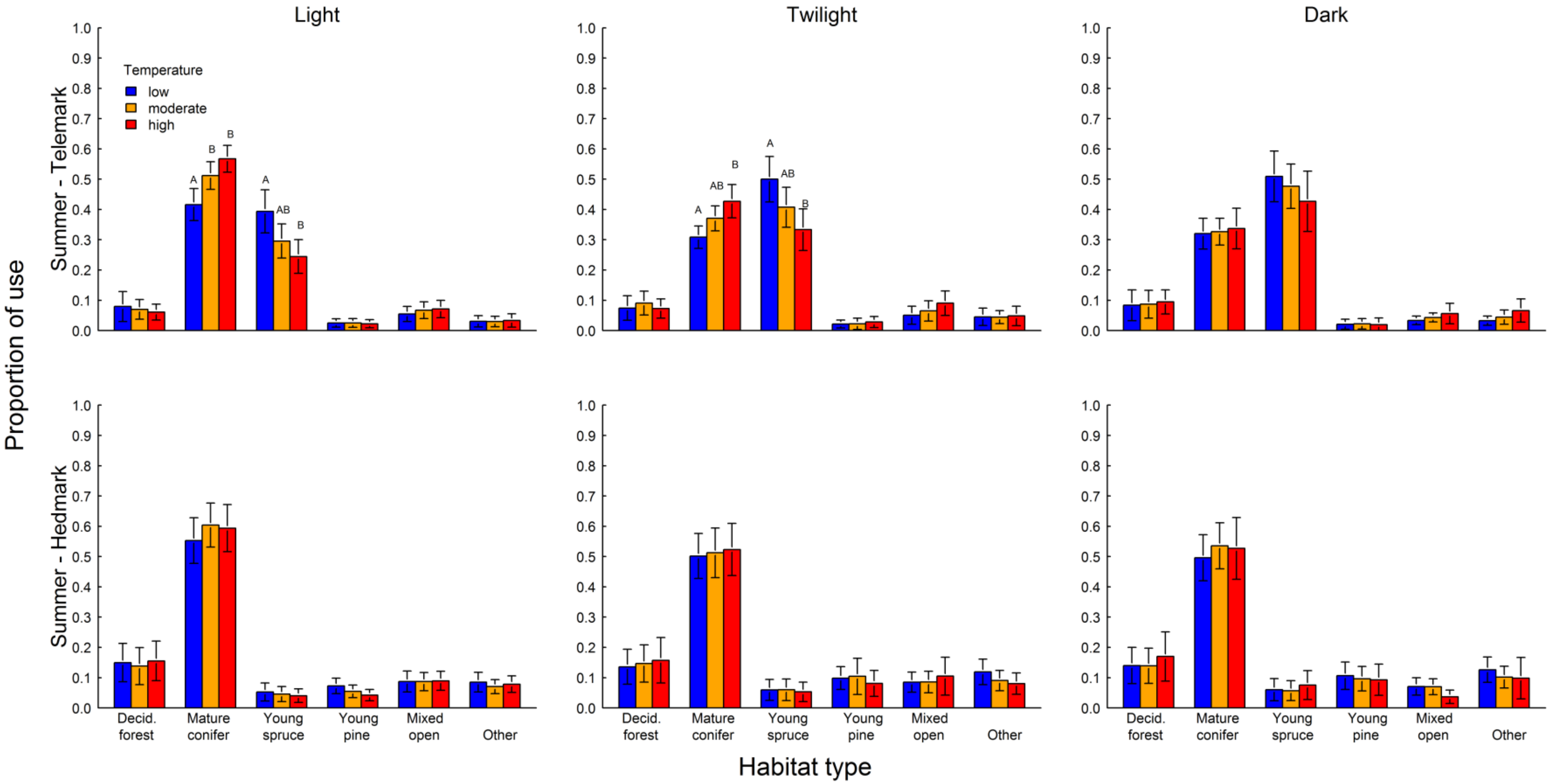
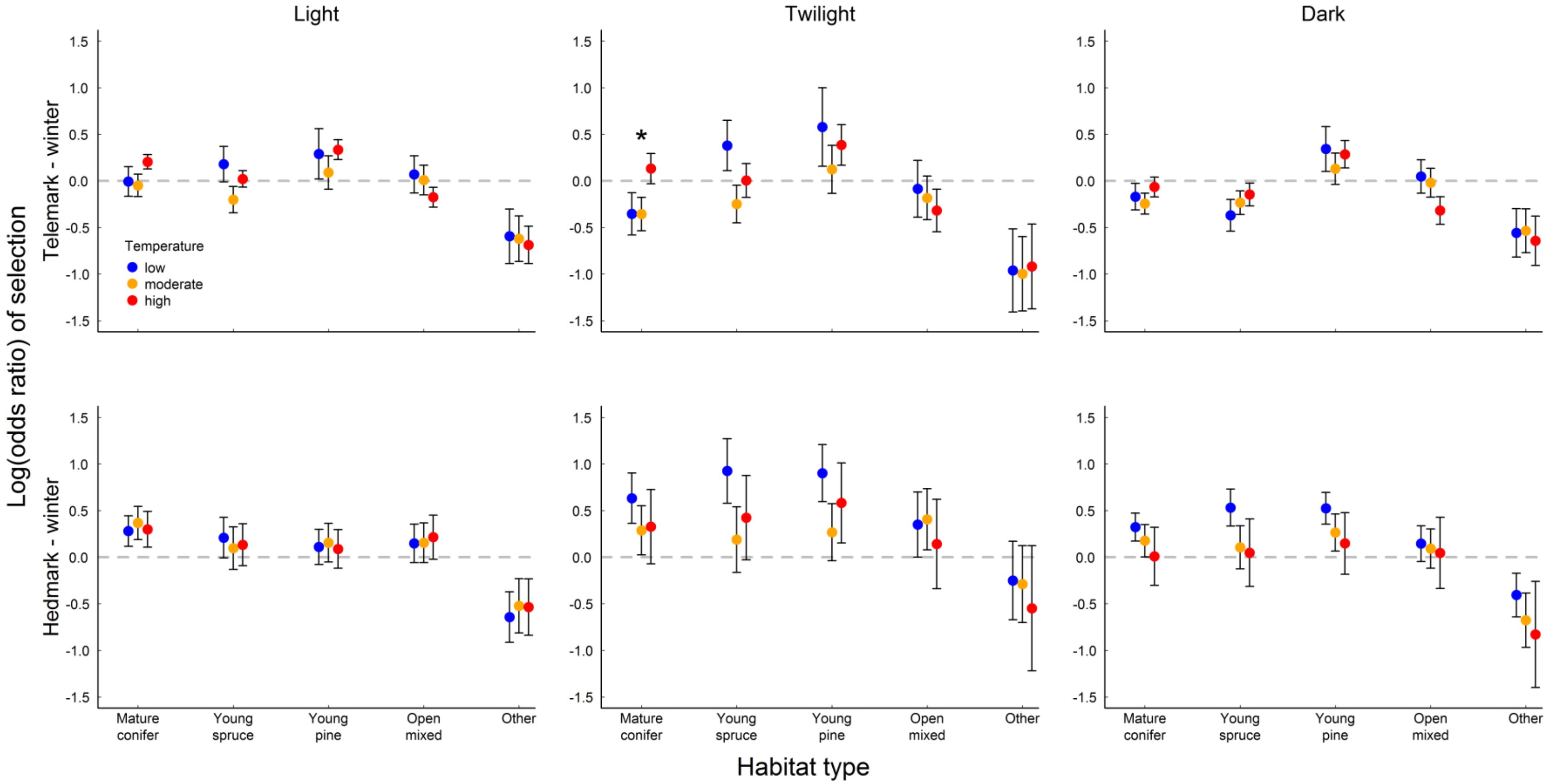

Light
Twilight
Dark
Proportion of use
Summer - Telemark
Summer - Hedmark
Temperature
🟦 low
🟧 moderate
🟥 high
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
A
B
B
A
AB
B
A
AB
B
A
AB
B
Decid. forest
Mature conifer
Young spruce
Young pine
Mixed open
Other
Habitat type

Fig. 3



Light
Twilight
Dark
Log(odds ratio) of selection
Telemark - winter
Hedmark - winter
Temperature
low
moderate
high
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
*
Mature conifer
Young spruce
Young pine
Open mixed
Other
Habitat type

Fig. 4

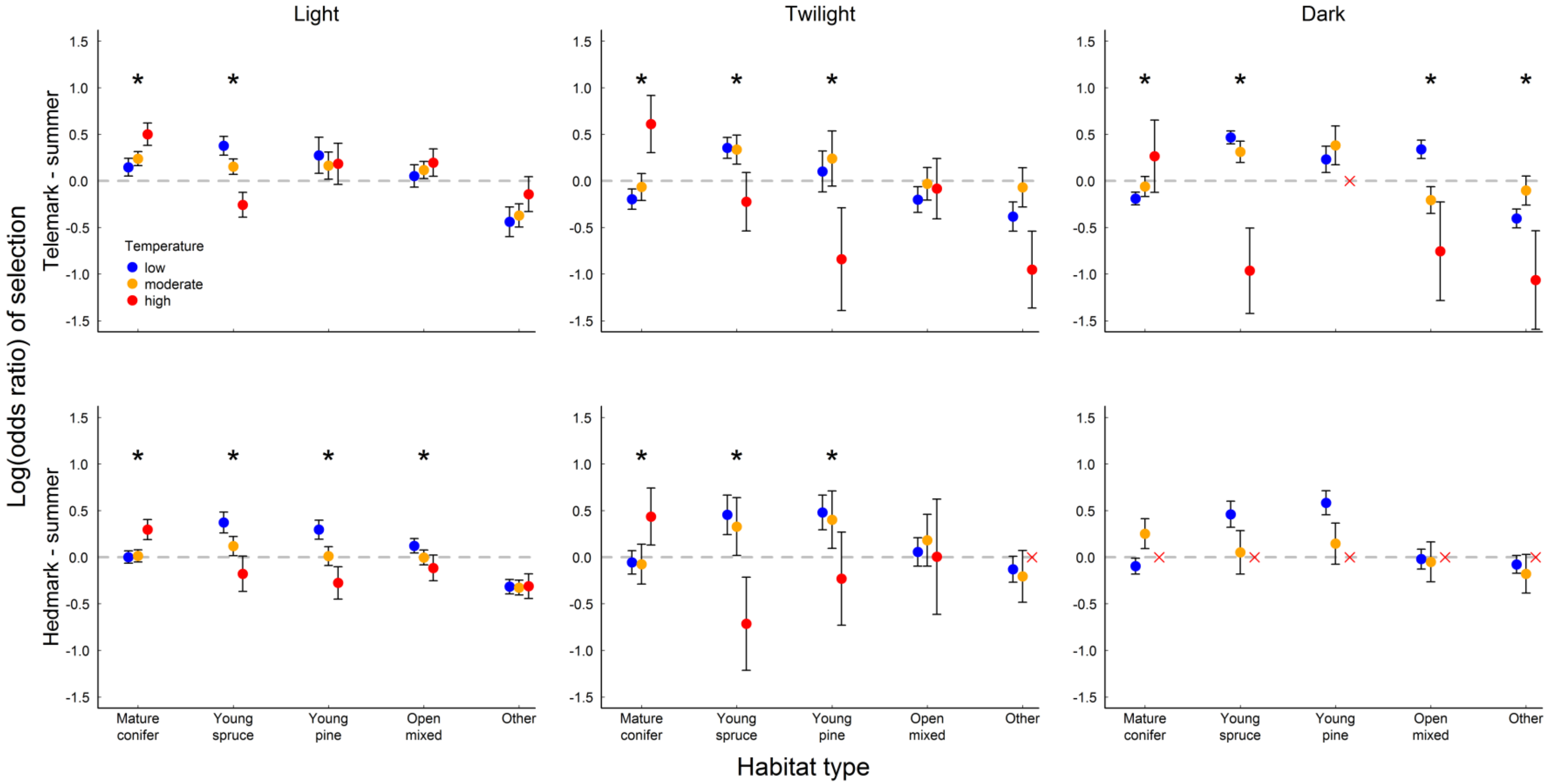

Light
Twilight
Dark
Log(odds ratio) of selection
Telemark - summer
Hedmark - summer
Temperature
low
moderate
high
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
*
Mature conifer
Young spruce
Young pine
Open mixed
Other
Habitat type

Fig. 5

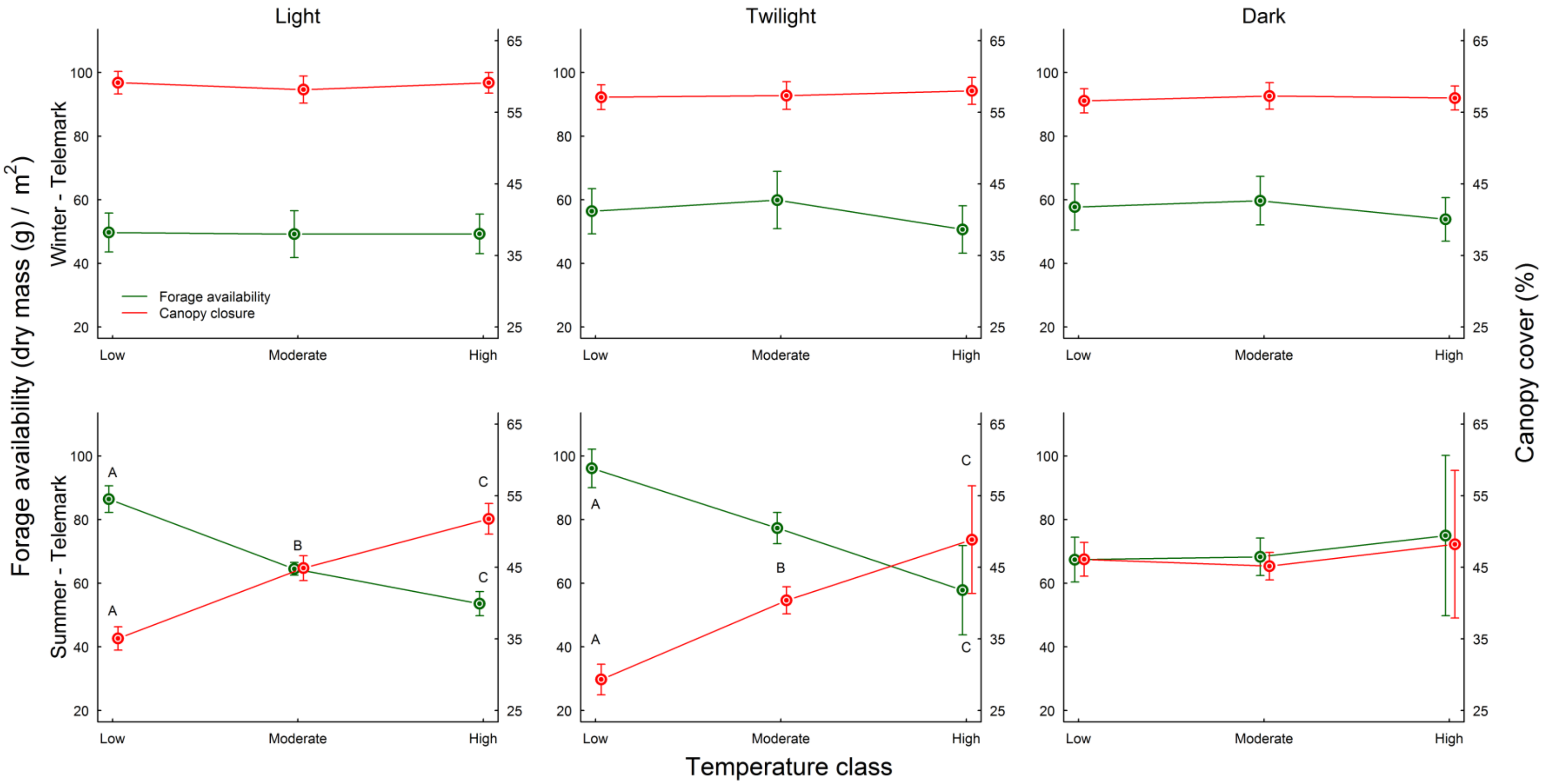

Light
Twilight
Dark
Forage availability (dry mass (g) / m^2)
Winter - Telemark
Summer - Telemark
Canopy cover (%)
Forage availability
Canopy closure
100
80
60
40
20
65
55
45
35
25
Low
Moderate
High
A
B
C
Temperature class

Fig. 6

APPENDIX 1

Temperature data

Previous studies have shown that temperature recordings from GPS collars are more useful than data from weather stations when studying fine-scale behavioral response of animals to thermal conditions (Markham & Altmann 2008; Bourgoin et al. 2009). Our GPS collars were equipped with a temperature sensor and during each location attempt the temperature was recorded and stored in the collar memory. Collar temperature was highly correlated ($r_s = 0.97$, N = 4 collars) with temperatures recorded by loggers (Diligence EV, Comark, UK) in various habitat types during field trials in summer 2008 (Nöthlich 2009). Collar temperature was also highly correlated with the temperature in a cooling cell ($r_s = 0.98$) and freezer ($r_s = 0.96$) where ambient temperatures were controlled at +1.5 and -21 °C respectively. In addition, the field trials revealed that collar temperature was more closely correlated to ambient temperature ($r_s = 0.97$), as recorded by the loggers, than conditions recorded by a black globe device ($r_s = 0.85$). Black globe temperature integrates air temperature, solar radiation and wind speed (Bakken 1992) and is frequently used to estimate radiant heat load experienced by ungulates (Hebert et al. 2008; Bowyer & Kie 2009). Consequently, our GPS collars underestimated the actual radiant heat load, thereby providing a conservative estimate of the subsequent response of moose to thermal conditions.

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APPENDIX 2

Habitat maps

Habitat maps were derived from a combination of digital forest stand maps and satellite land cover maps with a resolution of 50m x 50m (Bjørneraas et al. 2011). In Hedmark, maps of forest stand age and tree species composition were made for the areas of commercially-managed forest using satellite data from the Norwegian Forest and Landscape Institute (Gjertsen 2007). In Telemark these satellite data were unavailable for a large part of the study area so we used ground-truthed forestry maps (see van Beest et al. 2010) which accounted for 77% of GPS locations in the area. A satellite data vegetation map produced by the Northern Research Institute (NORUT; Johansen et al. 2009) was used to classify all remaining areas used by moose in both study areas. Land cover was classified into the following 6 habitat classes: mature forest (dense canopy coniferous forest and conifer-dominated stands of felling classes 3-5 of the Norwegian National Forest Inventory), open mixed forest (mixed coniferous or mixed coniferous / deciduous stands ≤40 years old and open canopy mixed or coniferous stands of unknown age), young pine forest (Scots pine stands ≤40 years old, felling classes 1-2), young spruce forest (Norway spruce stands ≤40 years old, felling classes 1-2), deciduous forest (deciduous stands of all ages, including sub-alpine birch woodland), and other (all non-forest habitats including moorland, heath, bog, agricultural land and open water).

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APPENDIX 3

Canopy cover measurement and analysis

We used seasonal canopy closure as an index for cover availability, estimated with a spherical densiometer (Mysterud & Østbye 1999), as the mean of the proportion of canopy closure in each cardinal direction. Canopy closure was measured in a total of 945 plots across 189 forest stands during both summer and winter, with plots at least 25 m apart and >15 m from forest stand edges. To predict seasonal canopy closure across the study area, we used linear mixed models in the R library 'nlme' (Pinheiro et al. 2011). Arcsine square-root-transformed canopy closure was fitted as the response variable. Spatial covariates included cutting class, dominant tree species, stand productivity (2 class factor; high and low), altitude (m), slope (°), and aspect and all possible interactions. Covariates were screened for collinearity using $r < 0.5$. Forest stand ID was included as a random factor to account for dependence between plots within forest stands and we used the Akaike Information Criterion (AIC) to evaluate whether the inclusion of a random effect was indeed necessary (Pinheiro & Bates 2000). We also tried fitting spatial and temporal correlation structures to incorporate any residual dependence among observations (Pinheiro and Bates 2000) but these did not improve model fit based on AIC. To find the most parsimonious models predicting seasonal canopy closure across the study area, we used backward selection with F tests using $P = 0.05$ as the threshold for inclusion of predictor variables and their interactions (Murtaugh 2009). To evaluate the predictive performance of the models we randomly withheld 20% of the data and compared observed with predicted canopy closure values. With $r_s = 0.694$ (winter) and $r_s = 0.737$ (summer) we judged the models to be effective. The final models are presented in Table D1. We used the fixed effects of the models to map canopy closure throughout the study area using RASTER calculator in ArcGIS v.9.2 (2006

ESRI, Redlands, CA, USA). For each moose location, we extracted the predicted value for seasonal canopy closure and then calculated the mean for each heat stress class. Within each season, we tested for differences in canopy closure between heat stress classes using multivariate analysis of variance with moose ID as the statistical unit as explained above.

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Pinheiro, J. C. & Bates, D. M. 2000. *Mixed-effects models in S and S-Plus: statistics and computing.* New York, USA: Springer Verlag.

Pinheiro, J. C., Bates, D. M., DebRoy, S. & Sarkar, D. 2011. *nlme: linear and non-linear mixed effects models.* R package version 3.1-102, R Foundation for Statistical Computing, Vienna, Austria.

Table A1. Summary of the mixed-effects regression models predicting canopy closure during winter (January 1st - April 15th) and summer (June 1st - September 15th) across the Telemark study area in southern Norway. All variables retained in the final model were significant at $P \leq 0.05$.

Fixed effects	***Summer***		***Winter***	
	β	**SE**	**β**	**SE**
(Intercept)	0.497	0.060	0.150	0.011
Cutting class [a]				
2	0.326	0.076	0.444	0.123
3	0.733	0.070	0.652	0.065
4	0.776	0.066	0.532	0.057
5	0.951	0.064	0.646	0.068

Dominant tree species [b]				
Scots pine	-0.098	0.075	0.159	0.034
Norway spruce	-0.164	0.099	0.168	0.041
Slope (°)	-0.004	0.001	0.005	0.001
Altitude (m)	< 0.001	< 0.001	< 0.001	< 0.001
Cutting class x Dominant tree species [a,b]				
2 x Scots pine	-0.176	0.117	0.244	0.142
3 x Scots pine	-0.191	0.093	0.235	0.078
4 x Scots pine	-0.111	0.096	0.366	0.073
5 x Scots pine	-0.323	0.094	0.202	0.086
2 x Norway spruce	0.280	0.134	0.302	0.143
3 x Norway spruce	0.008	0.117	0.397	0.080
4 x Norway spruce	0.175	0.116	0.561	0.072
5 x Norway spruce	0.104	0.112	0.407	0.081
Random effect	SD		SD	
Forest stand ID	0.102		0.137	

[a] Reference category = 1 (clear cut)

[b] Reference category = Deciduous forest stands

APPENDIX 4

Table A2. Parameter estimates of seasonal-, and area-specific GAMM models predicting circadian changes in ambient temperature across habitat types. The models form the analytical basis for Fig. 1.

Study area	**Season**	**Parametric coefficients**	**Estimate**	**S.E.**	***t*-value**	***p*-value**
Telemark	Winter	Deciduous forest	-0.505	0.439	-1.15	0.251
		Mature coniferous forest	-1.133	1.076	-1.05	0.293
		Young spruce	0.593	0.445	1.33	0.182
		Young pine	0.313	0.551	0.57	0.570
		Mixed open	0.187	0.658	0.29	0.776
		Other	0.152	0.325	0.47	0.640
		Smooth terms	**edf**	***F*-value**	***p*-value**	
		s(hour = Deciduous forest)	6.76	63.94	< 0.001	
		s(hour = Mature coniferous forest)	6.44	563.18	< 0.001	
		s(hour = Young spruce)	6.44	208.60	< 0.001	
		s(hour = Young pine)	6.42	78.39	< 0.001	
		s(hour = Mixed open)	6.35	57.09	< 0.001	
		s(hour = Other)	6.29	10.96	< 0.001	

		Random Intercept	**N**	**Std.Dev.**	**Residual**	
		Collar ID	31	1.254	4.988	

Study area	**Season**	**Parametric coefficients**	**Estimate**	**S.E.**	***t*-value**	***p*-value**
Hedmark	Winter	Deciduous forest	-3.712	0.651	-5.70	< 0.001
		Mature coniferous forest	-0.797	0.386	-1.81	0.070
		Young spruce	-0.128	0.912	-0.14	0.889
		Young pine	-0.465	0.667	-0.70	0.486
		Mixed open	-0.699	0.928	-0.86	0.391
		Other	0.773	1.431	0.54	0.589
		Smooth terms	**edf**	***F*-value**	***p*-value**	
		s(hour = Deciduous forest)	6.38	33.34	< 0.001	
		s(hour = Mature coniferous forest)	6.44	693.47	< 0.001	
		s(hour = Young spruce)	6.04	17.74	< 0.001	
		s(hour = Young pine)	6.29	7.96	< 0.001	
		s(hour = Mixed open)	6.44	91.00	< 0.001	
		s(hour = Other)	5.90	8.57	< 0.001	
		Random Intercept	**N**	**Std.Dev.**	**Residual**	
		Collar ID	39	1.407	6.209	

Study area	**Season**	**Parametric coefficients**	**Estimate**	**S.E.**	***t*-value**	***p*-value**
Telemark	Summer	Deciduous forest	7.217	0.412	17.52	< 0.001
		Mature coniferous forest	-0.449	0.932	-0.48	0.630
		Young spruce	0.297	0.300	0.99	0.321
		Young pine	1.692	0.307	5.52	< 0.001
		Mixed open	2.735	0.606	4.52	< 0.001
		Other	1.682	0.720	2.34	0.019
		Smooth terms	**edf**	***F*-value**	***p*-value**	
		s(hour = Deciduous forest)	6.44	1586.40	< 0.001	
		s(hour = Mature coniferous forest)	6.44	151.90	< 0.001	
		s(hour = Young spruce)	6.44	249.20	< 0.001	
		s(hour = Young pine)	6.78	322.10	< 0.001	
		s(hour = Mixed open)	6.44	2029.90	< 0.001	
		s(hour = Other)	6.43	213.60	< 0.001	
		Random Intercept	**N**	**Std.Dev.**	**Residual**	
		Collar ID	27	0.736	3.983	

Study area	**Season**	**Parametric coefficients**	**Estimate**	**S.E.**	***t*-value**	***p*-value**
Hedmark	Summer	Deciduous forest	6.616	0.291	22.70	< 0.001
		Mature coniferous forest	-0.619	0.442	-1.40	0.161

Young spruce	1.276	0.543	2.35	0.019
Young pine	1.680	0.457	3.68	< 0.001
Mixed open	1.015	0.486	2.09	0.037
Other	1.784	0.232	7.70	< 0.001
Smooth terms	**edf**	***F*-value**	***p*-value**	
s(hour = Deciduous forest)	6.44	244.20	< 0.001	
s(hour = Mature coniferous forest)	6.43	437.90	< 0.001	
s(hour = Young spruce)	6.44	343.30	< 0.001	
s(hour = Young pine)	6.78	766.20	< 0.001	
s(hour = Mixed open)	6.44	2750.60	< 0.001	
s(hour = Other)	6.44	624.20	< 0.001	
Random Intercept	**N**	**Std.Dev.**	**Residual**	
Collar ID	35	1.234	2.343	