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

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The behavioural response of animals to unfavourable climatic conditions has received increased attention recently. While many studies have examined the behavioural responses of endotherms to cold temperatures, thermoregulatory behaviour may also occur in response 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-associated changes in spatial behaviour led to a shift in the availability of thermal cover and forage at the chosen location. 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 decrease in local forage availability in summer but not in 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 did habitat use. This is because habitat selection analyses are better able to identify limiting factors operating at different spatiotemporal scales than is habitat use. Our results clearly show that ambient temperature affected fine-scale behavioural decisions of moose with consequences for forage accessibility, especially during summer. As the climate changes, the limiting effect of ambient temperature (cold and high) on animal behaviour is likely to increase, potentially influencing individual fitness and population dynamics.

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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 recognized and is studied extensively (Campbell et al. 1974; 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). For example, 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) found that ambient temperature and wind speed affect summer activity patterns of female mouflon, Ovis gmelini musimon. Quantifying such thermoregulatory behaviour is a necessary first step to evaluate climate-induced effects on population dynamics of large herbivores effectively (Grosbois et al. 2008; Mysterud & Østbye 2011). For example, Svalbard reindeer, Rangifer tarandus platyrhynchus, respond to thaw–freeze events by long-distance displacements in order to find accessible grazing pasture elsewhere (Stien et al. 2010), and 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 trade-off in habitat selection of large ruminants is maximizing energy intake (i.e. food acquisition) whilst minimizing exposure to predation risk or unfavourable climatic conditions (i.e. food–cover trade-off; Schmitz 1991; Mysterud & Østbye 1999;
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). In some cases, however, 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, the strength of the forage–cover trade-off is likely to vary between individuals and at different 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 of individuals within populations living in southern Norway (Wam et al. 2010; J. M. Milner, T. Storaas, F. M. van Beest & G. Lien, unpublished data). The influence 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), suggesting that cold stress due to hypothermia is not an important limiting factor for moose under natural conditions, 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. Much of the evidence shows that North American moose change their habitat use in relation to ambient temperature, 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 habitat 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 predicts that when environmental conditions are favourable, animals should choose habitats based on forage abundance, and moreover, continue 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. 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. Furthermore, if temperature mediates behavioural adjustments in habitat use (from foraging habitat under optimal thermal conditions to shelter habitat under stressful ambient temperatures), we expect this to lead to a shift in the balance between forage and cover availability.

**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 southeastern Norway (61°N, 11°E). Euclidean distance between the centres of the two areas was 250 km. The Telemark study area (733 km²) 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 (1370 km²) 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. Subalpine 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 km² (J. M. Milner, T. Storaas, F. M. van Beest & G. Lien, unpublished data). 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**

We captured a total of 74 adult female moose, each accompanied by a calf, 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 × 50 m). The average GPS-collar fix rate, while on the moose, was 94% (range 72–100%) during winter (i.e. 1 January–15 April) and 92% (range 71–99%) during summer (i.e. 1 June–15 September). Both GPS fix rate and location error were well below critical thresholds to estimate habitat use and selection accurately (Johnson & Gillingham 2008). All GPS collars were equipped with a temperature sensor that recorded and stored the temperature during each location attempt. Details of how we field-tested the accuracy of the temperature sensors are given in the Supplementary Data S1. Field trials revealed that collar temperature was closely correlated with ambient temperature and less correlated 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 by professional wildlife veterinarians using published techniques (Anemó 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. 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 h. Within the project we made 252 captures and experienced two capture-related mortalities (one was euthanized.
because of a broken leg and one was 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 1035 g, 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 recapturing (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 × 50 m (Supplementary Data S2). We considered the following six habitat classes: mature coniferous forest, open mixed forest,
young pine forest, young spruce forest, deciduous forest, and other (all nonforest 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 nonlinearly over time. GAMMs provide a suitable framework to analyse such patterns as these models allow for nonlinear relationships between the response variable and multiple explanatory variables (Wood 2006). This is done by fitting explanatory variables with expected nonlinear effects as parametric or nonparametric smoothing terms. Moreover, additional variables can be included as random effects to account for unbalanced data (Pinheiro & Bates 2000; Wood 2006). The response variable in our models 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 × time interaction) to allow temperature to vary nonlinearly over time and space. We used cyclic regression splines, with the optimal smooth curve estimated by a 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. 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 categorized all GPS locations by time of day according to prevailing light conditions (light, twilight, dark). Light conditions for each study area and study period were obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil). Within each season and time of day, moose locations were partitioned into three temperature classes based on respiratory responses reported by Renecker & Hudson (1986; Table 1); (1) Low ambient temperature (collar temperature: winter: \( \leq -5 \) °C; summer: \( <-14 \) °C); (2) moderate ambient temperature (winter: \( \geq -5 \) °C, \( <0 \) °C; summer: \( \geq 14 \) °C, \( <20 \) °C); (3) high ambient temperature (winter: \( \geq 0 \) °C; summer: \( \geq 20 \) °C).

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 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. We also considered altitude and aspect as explanatory variables in the habitat use analyses, but preliminary results indicated no differences in use of altitude (winter: \( F_{2,29} = 1.79, P = 0.171 \); summer: \( F_{2,81} = 0.014, P = 0.985 \)) or aspect (winter: \( F_{2,93} = 0.11, P = 0.895 \); summer: \( F_{2,81} = 0.240, P = 0.787 \)) between temperature classes. We therefore excluded these variables from further analyses. Although moose can tolerate temperatures down to \(-32 \) °C or lower without a change in their metabolic rate, their behaviour may nevertheless be affected by cold ambient temperature. Therefore, we also evaluated whether low ambient temperatures affected habitat use in either season. All analyses were performed in the statistical software R (R Development Core Team 2012).

Habitat selection was estimated 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 (Boye 2006). In our case, each observed location was associated with five 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 ± 13.0 m and 86.1 ± 16.5 m for winter and summer, respectively. In Hedmark, these were 71.9 ± 18.2 m and 99.7 ± 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 recalculate 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 31 and 39 for Telemark and Hedmark, respectively, and 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).

### Table 1

<table>
<thead>
<tr>
<th></th>
<th>Telemark</th>
<th>Hedmark</th>
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<tbody>
<tr>
<td><strong>Winter</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean hourly temperature (°C)</td>
<td>0.84</td>
<td>-3.97</td>
</tr>
<tr>
<td>% GPS locations &lt; -5 °C (low)</td>
<td>-21.0; +23.0</td>
<td>-33.0; +22.0</td>
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<tr>
<td>% GPS locations &gt; -5 °C &lt; 0 °C (moderate)</td>
<td>15.1</td>
<td>42.8</td>
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<tr>
<td>% GPS locations &gt; 0 °C (high)</td>
<td>28.7</td>
<td>32.5</td>
</tr>
<tr>
<td><strong>Summer</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean hourly temperature (°C)</td>
<td>14.59</td>
<td>13.21</td>
</tr>
<tr>
<td>% GPS locations &lt; -14 °C (low)</td>
<td>-3.0; +39.0</td>
<td>-4.0; 38.0</td>
</tr>
<tr>
<td>% GPS locations &gt; -14 °C &lt; 20 °C (moderate)</td>
<td>52.3</td>
<td>61.2</td>
</tr>
<tr>
<td>% GPS locations &gt; 20 °C (high)</td>
<td>34.7</td>
<td>29.7</td>
</tr>
<tr>
<td>14°C; summer: ( \geq 14 ) °C, ( &lt;20 ) °C; (3) high ambient temperature (winter: ( \geq 0 ) °C; summer: ( \geq 20 ) °C)</td>
<td>12.9</td>
<td>9.1</td>
</tr>
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</table>

Percentage of moose GPS locations are given for three ambient temperature classes.
Forage and Cover Availability

To evaluate whether temperature-mediated behavioural adjustments in habitat use led to changes in the forage and cover availability experienced, we restricted the GPS data of collared moose to the Telemark study area (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 × 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 Supplementary Data S4, Table S1. 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 conditions and temperature classes using ANOVA, followed by post hoc paired Tukey HSD tests.

RESULTS

Thermal Cover

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 and 2 °C in summer), suggesting that mature coniferous stands provided the best cover from high temperatures in both areas and seasons (Fig. 1, Supplementary Table S2).

During winter, mean temperature exceeded the lower critical threshold (−5 °C) throughout the 24 h 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 0800 and 1700 hours). 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 1000 and 1500 hours) 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 0700 and 1800 hours in Telemark and between 0800 and 1700 hours 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

Cold ambient conditions did not influence moose habitat use in either study area or season (see Supplementary Data S3). During winter, habitat use of moose did not change in relation to high critical temperature thresholds or light conditions in either study area (Telemark: F4,282 = 0.155, P = 0.966; Hedmark: F4,245 = 0.078, P = 0.989; Fig. 2). During summer, moose showed a behavioural response to ambient temperature during light (F2,81 = 3.61, P = 0.031; Fig. 3) and twilight (F2,81 = 3.21, P = 0.0455) in Telemark but not in Hedmark (F4,309 = 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 used 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. nonoverlapping 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 temperatures than under 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 temperatures than at moderate temperatures during twilight and darkness, but not significantly higher than at high temperatures during twilight. The amount of variation explained (R²) by the winter RSF models was 0.27 for Telemark and 0.26 for Hedmark. The models had good predictive performance, with significant rs across five cross-validation sets (mean ± SD: Telemark: 0.76 ± 0.011, P < 0.001; Hedmark: 0.83 ± 0.010, P < 0.001).

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 R² for the summer RSF models was 0.27 for Telemark and 0.26 for Hedmark. The models also had good predictive performance, with significant rs across five cross-validation sets (Telemark: 0.83 ± 0.018, P < 0.001; Hedmark: 0.80 ± 0.013, P < 0.001).

Changes in Forage–Cover Availability

Considering only the Telemark area, forage availability and canopy closure at moose locations were similar across temperature classes and light conditions during winter (forage availability: F4,265 = 0.156, P = 0.96; canopy closure: F4,265 = 0.287, P = 0.88; Fig. 6). By contrast, during summer, moose locations differed in forage availability in relation to critical temperature thresholds during light (F2,78 = 33.576, P < 0.001) and twilight (F2,69 = 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 (F2,78 = 79.224, P < 0.001) and twilight (F2,69 = 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). Nevertheless, most studies of large herbivores ignore the effects of climate on
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. Different letters above bars 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. *Indicates nonoverlapping 95% CI between low and high temperature classes and a significant difference in habitat 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. *Indicates nonoverlapping 95% CI between low and high temperature classes and a significant difference in habitat selection. An ‘×’ indicates that selection coefficients could not be calculated for that particular habitat type because of 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. Different letters indicate a significant difference in forage and cover availability between temperature classes.
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 foraging habitats (young, successional open-canopied forest) as predicted by optimal foraging theory, but when the temperature rose above critical thresholds, moose increased their selection for thermal cover (mature, dense-canopied forest). Consequently, behavioural adjustments lead to a decrease in forage availability and an increase in canopy cover at used locations, suggesting that moose traded forage for cover when ambient temperature increased. During winter, however, we found little evidence to suggest that temperature was an important factor influencing moose behaviour. 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 those of other ungulates (Bourgoin et al. 2008; Aublet et al. 2009), which have shown that the thermoregulatory demand for increased cover is most evident in moose during summer and not in winter (but see Schwab & Pitt 1991). Our results also show that differences in thermoregulatory behaviour are revealed depending on the space-use metric considered (i.e. habitat use versus habitat selection).

Although at high ambient temperatures during summer, moose selected locations with increased canopy cover and reduced forage quantity compared with open foraging habitat, changes in forage quantity may have been minor. 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, in part, to 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 (Table 1), 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; Grignoli 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 show 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 thermostable adjustments in habitat use would be an ineffective thermoregulatory strategy. Alternatively, previously reported critical temperature thresholds for moose (sensu Reneker & 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 thermostable regulatory behaviour have observed strong patterns in summer but not in winter.

Importantly, we detected more pronounced thermostable regulatory behaviour in both seasons, but especially in summer, when using a habitat selection framework rather than a habitat use framework. The discrepancy in results highlights a fundamental distinction between habitat use and habitat selection analyses. Habitat use analyses are highly relevant when objectives are to improve or evaluate management or conservation action of a species in a specific area. Although habitat selection analyses are also frequently used for such applied purposes, their value for management may be low if selected habitats are rare. In contrast, habitat selection analyses, such as RSFs, are well suited to identify limiting factors influencing animal behaviour, which may operate at different spatiotemporal scales (Boye et al. 2002; Boyce 2006). 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). 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; Boyce 2006). 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). Indeed, sampling of resource availability should be matched to the most appropriate spatial and temporal scale (Bowyer & Kie 2006). Sampling resource availability at coarser scales or the inclusion of additional variables may yield different outcomes (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). This is also expected for moose in North America (Murray et al. 2006; Lenarz et al. 2009).

Our results clearly showed that ambient temperature during summer affects fine-scale behavioural decisions of moose, which led to a reduction in forage availability at used locations as temperature increased. The importance of ambient temperature as a limiting factor on foraging behaviour seems clear (Aublet et al. 2009; this study) but its effects on individual fitness and population dynamics remain largely unexplored. In ectotherms, individual fitness is strongly temperature and habitat dependent (Amasekare & Savage 2012), but such relationships have not been considered for endotherms despite the fact that direct links between fitness and habitat selection patterns are increasingly being uncovered (McLoughlin et al. 2006; Van Moor ter et al. 2009; Hodson et al. 2010). Our study suggests that temperature-induced
changes in space use may limit foraging opportunities with a clear potential for temperature-mediated habitat—fitness effects.

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Supplementary Material

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References


Bowyer, R. T. & Kie, J. G. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity and Distributions, 12, 244–257


