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RESEARCH ARTICLE

Habitat functional response mitigates reduced foraging opportunity: implications for animal fitness and space use

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Abstract

Context Animals selectively use landscapes to meet their energetic needs, and trade-offs in habitat use may depend on availability and environmental conditions. For example, habitat selection at high temperatures may favor thermal cover at the cost of reduced foraging efficiency under consistently warm conditions.

Objective Our objective was to examine habitat selection and space use in distinct populations of moose (*Alces alces*). Hypothesizing that endotherm fitness is constrained by heat dissipation efficiency, we predicted that southerly populations would exhibit greater selection for thermal cover and reduced selection for foraging habitat.

Methods We estimated individual step selection functions with shrinkage for 134 adult female moose in Minnesota, USA, and 64 in Ontario, Canada, to assess habitat selection with variation in temperature, time of day, and habitat availability. We averaged model coefficients within each site to quantify selection strength for habitats differing in forage availability and thermal cover.

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Results Moose in Ontario favored deciduous and mixedwood forest, indicating selection for foraging habitat across both diel and temperature. Habitat selection patterns of moose in Minnesota were more dynamic and indicated time- and temperature-dependent trade-offs between use of foraging habitat and thermal cover.

Conclusions We detected a scale-dependent functional response in habitat selection driven by the trade-off between selection for foraging habitat and thermal cover. Landscape composition and internal state interact to produce complex patterns of space use, and animals exposed to increasingly high temperatures may mitigate fitness losses from reduced foraging efficiency by increasing selection for foraging habitat in sub-prime foraging landscapes.

Introduction

Animal fitness is constrained by energetic considerations—that is, organisms must take in enough energy to maintain internal conditions, grow, and reproduce. This observation implies an economy of energy central to animal ecology, where the rate of energy output is balanced by the rate of energy input. In this supply-expenditure framework, ecologists frequently consider the supply component in the form of resource acquisition, processing, and energy storage. This has led to the idea that metabolic rates scale with body size and temperature, and that energy and resources are fundamentally and functionally relatable (i.e., the metabolic theory of ecology; Brown et al. 2004). The underlying assumption of such studies is that energy supply is the primary constraint on individual fitness; organisms attempt to meet an energy budget wherein they must acquire enough resources (or have enough in storage) to maintain homeostatic conditions while still producing and supporting offspring. Other studies have highlighted the importance of energy expenditure in balancing the metabolic equation. For example, an organism's maximum energetic expenditure may be limited by the combined metabolic rates of its component tissues (Hammond and Diamond 1997) or by its ability to dissipate heat (Speakman and Król

2010), and expenditure may sometimes supersede supply considerations, particularly under energy rich conditions. These two perspectives differ in which side of the energy equation is given priority—supply or expenditure—but both extol the importance of different components of a complex and dynamic system of energetic trade-offs.

If energy budget is a primary driver of animal fitness, it naturally follows that animals select habitat based on energetic considerations. Much research on energy acquisition has centered on foraging efficiency (e.g., Charnov 1976; Ritchie 1990; Illius et al. 1995), and how foraging considerations influence selective use of associated landscapes (e.g., Fryxell et al. 2008; Owen-Smith et al. 2010; Mitchell and Powell 2012). Comparatively little research has focused on energetic expenditure as a driver of space use and habitat selection and how it may influence fitness, particularly in endotherms (but see Aublet et al. 2009; Speakman and Król 2010; Van Beest et al. 2012). From this perspective, animals may exhibit preferences for habitats that reduce expenditure, for example by facilitating movement (Avgar et al. 2013) or by providing thermal cover (Van Beest et al. 2012; Street et al. 2015). Preference for habitats providing foraging opportunities or thermal cover should vary across the diurnal cycle and is likely dependent on animal state (e.g., hunger, thermal stress) and environmental context (Fryxell et al. 2008; Avgar et al. 2013). That environmental and landscape conditions are not constant over space can further alter both the supply and expenditure components of the energy equation, often simultaneously, thus a full examination of the relative importance of energy supply versus expenditure requires data across broad spatiotemporal extents and bioclimatic gradients to capture variation in habitat use across a variety of conditions and contexts.

Our objective was to investigate the influence of temperature and time of day on patterns of habitat selection and movement in an endothermic animal, the moose (*Alces alces*). Moose are generalist browsers that exhibit a strong preference for deciduous vegetation types (Belovsky 1981). They are also cold-adapted and exhibit physiological responses associated with heat stress at temperatures as low as 14 °C in the summer and −5 °C in the winter (Renecker and Hudson 1986). As such, the interaction between deciduous forage availability and temperature is often considered a primary driver of the southern limit of

moose population ranges. For example, Street et al. (2015) described changes in habitat selection by moose toward habitats providing thermal cover with increasing temperature at mid-day, suggesting that temperature regulation plays a role in moose behavior and space use at temperatures approaching moose thermal optima. However, this study was limited to a single population of moose and to locations at mid-day only. Such limitation is acceptable to the extent that habitat selection may be mediated by individual internal state (e.g., temperature) but is insufficient to fully characterize the relationship between temperature and behavior if that relationship is not consistent across space or time of day (Avgar et al. 2013). Alternatively, moose populations may be regulated at the southern extent of their range by factors including parasite loads (Murray et al. 2006) and predation (Mech and Fieberg 2014). Evaluating the potential for temperature to influence moose space use across landscapes would provide additional information about the realized niche of this species while simultaneously advancing our understanding of the interplay between biotic and abiotic conditions in shaping patterns of animal space use.

We estimated models of habitat selection and movement of individual moose across two study sites (northern Minnesota, USA, and northwest Ontario, Canada) representing ecologically distinct populations occupying landscapes of different composition. Given the hypothesis that endotherm fitness is constrained by efficiency of heat dissipation (Speakman and Król 2010), we predicted that (1) selection for land cover types by moose would vary with temperature and time of day, consistent with prior observations; and (2) moose in landscapes characterized by a higher abundance of thermal cover would select less strongly for these habitat types than moose in landscapes with limited shelter (or, more generally, that estimated selection for different landscape components is unique to a particular combination of habitat availability and environmental conditions).

Methods

Study area

This comparative study was conducted at two sites: one in northeast Minnesota at 47°50′N, 92°8′W; and

the other in northwest Ontario at 49°15′N, 92°45′W (Fig. 1).

The southern site is located in Minnesota's Northern Superior Uplands forest region northwest of Lake Superior (Hanson and Hargrave 1996). The northern site is located northwest of Ontario's Quetico Provincial Park on the Quetico-Great Lakes-St. Lawrence/boreal forest boundary (Rowe 1972). Both sites are a matrix of forested stands and wetlands (e.g., bogs, lakes). Dominant tree species are consistent between sites and include white spruce (*Picea glauca*), black spruce (*Picea mariana*), and jack pine (*Pinus banksiana*). Balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*) are interspersed throughout both sites. Both sites are primarily disturbed by forest fire and are subject to timber harvest. Moose co-occur throughout both study sites with white-tailed deer (*Odocoileus virginianus*) and are primarily predated upon by gray wolves (*Canis lupus*) and black bears (*Ursus americanus*).

Data

In Minnesota throughout January and February from 2010 to 2015, technicians captured 170 adult female moose by netgunning or aerial darting from a helicopter using carfentanil (4.5 or 6.0 mg) or thifentanil (16 mg) and xylazine (100 or 150 mg) as immobilizing agents, and naltrexone (245–575 mg) and tolazoline (400 mg) as reversal agents. Moose were fitted with Iridium Global Positioning System (GPS) radiocollars (VECTRONIC Aerospace GmbH, Berlin, Germany; and Sirtrack Ltd., Hawkes Bay, New Zealand). Animal handling followed American Society of Mammalogists wild animal care guidelines (Sikes, Gannon & the Animal Care and Use Committee of the American Society of Mammalogists 2011). Collars recorded animal locations at 4.25, 2, and 1.065-h intervals, depending on region and study schedules. We subsampled data collected at higher sampling rates to achieve a consistent 4.25-h fix rate ±0.25 h. See Carstensen et al. (2014) for more details.

In Ontario from 1995 to 2001, technicians captured 122 adult female moose by netgunning from a helicopter throughout the northern study site and deployed NAVSTAR GPS radiocollars (LOTEK Engineering Inc., Newmarket, Ontario) on each.

Fig. 1 Map of study sites. *Insert* indicates general location of study sites relative to Ontario and Minnesota. *Triangles* represent NOAA or Environment Canada weather stations
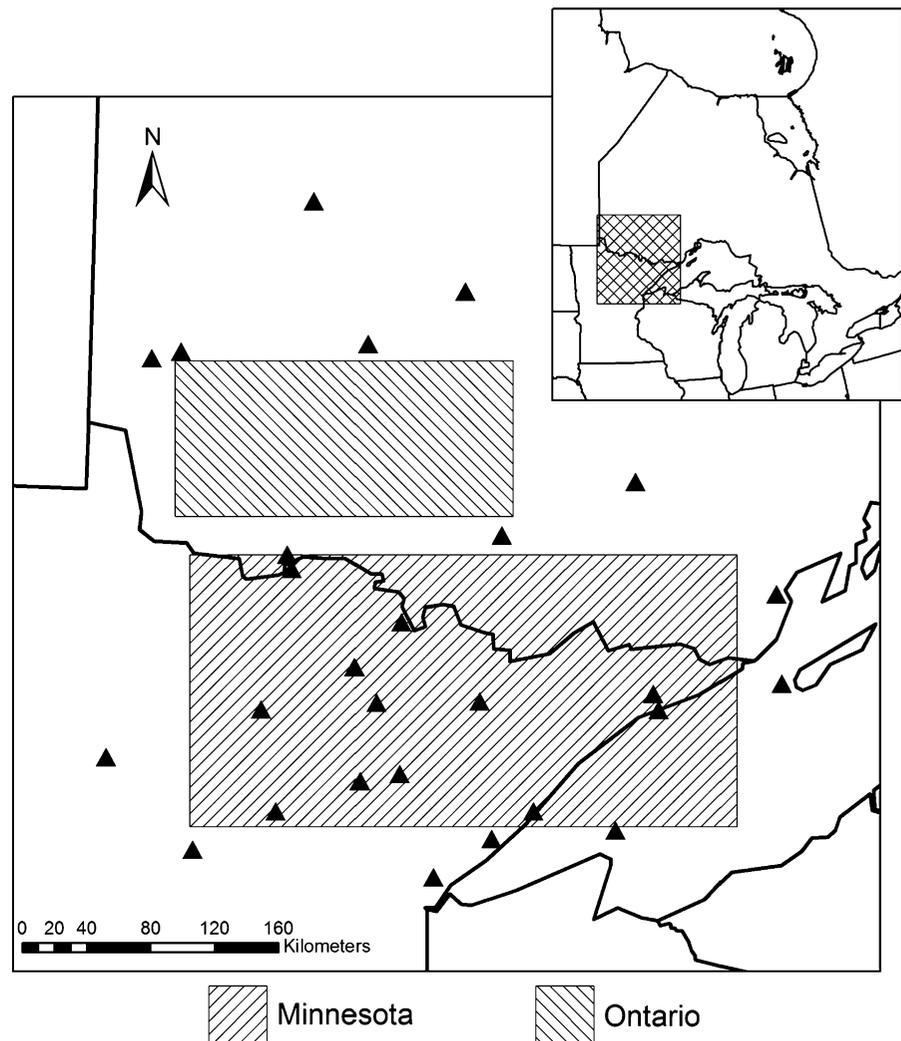
Capture and collaring procedures followed Canadian Council on Animal Care Guidelines and were approved by the Ontario Ministry of Natural Resources and Forestry Animal Care Committee. Collars recorded animal location at approximately 4-h intervals throughout the year, with frequent gaps between 4-h fixes. We resampled these data to achieve a consistent 4-h fix rate ± 0.25 h. For more details, see Rodgers et al. (1996) and Street et al. (2015). Captures in Minnesota took place from January 22 to February 9, and in Ontario from January 24 to February 22, in each year in the respective datasets.

We included only 3-dimensional, differentially corrected fixes with horizontal dilution of precision (HDOP) <10, providing a location accuracy of 3–7 m

(Rempel and Rodgers 1997). We removed all fixes within 24 h of collar deployment or following animal mortality as reported by the collar and verified by field technicians. We limited our analysis to summer (June 1–September 30) to achieve in-season constancy in habitat covariates such as flowering phenology (Street et al. 2015). After resampling, 8077 fixes (range per individual = 1–442, mean = 79) remained for 98 individuals in Ontario, and 112,057 fixes (range per individual = 13–1983, mean = 837) remained for 134 individuals in Minnesota. We excluded animals with fewer than 10 fixes (34 animals), giving a total of 120,134 fixes from 198 adult female moose for this analysis.

We created an aggregate land cover classification system using the Ontario Provincial Land Cover 2000

(OLC; Anonymous 2004), available from Land Information Ontario (LIO; https://www.javacoeapp.lrc.gov.on.ca/geonetwork/srv/en/main.home), and the U.S. National Land Cover Database 2011 (NLCD; Jin et al. 2013), available from the Multi-Resolution Land Characteristics Consortium (MRLC; http://www.mrlc.gov/nlcd2011.php), at 25 and 30 m² resolutions, respectively. We aggregated OLC and NLCD land cover classifications into common classifications based on similarities in class descriptions (Table A1 in supplementary materials). Land cover datasets may differ in their definitions of cover types; the primary difference between our OLC and NLCD datasets is how forest types are classified. For example, OLC named forest stands (i.e., deciduous, coniferous) are considered dense forest, and non-dense forests are lumped into a "sparse forest" category that may be either predominately deciduous or coniferous, but no distinction is made based on dominant vegetation type (Anonymous 2004). NLCD forest types are classified based on >20 % coverage by trees and a 75 % threshold in coverage by conifer or deciduous trees, and the NLCD has no analogous sparse cover classification (Jin et al. 2013), prohibiting the use of the OLC sparse category here. As such, the Ontario dataset may have a lower abundance of deciduous habitat than might be represented on the landscape based on the prevalence of sparse deciduous forests. To examine whether aggregated land cover classes were informative, we conducted cross validation of models of habitat selection (see "Analysis" section, below). Additionally, habitats can generally be ranked in terms of foraging quality based on the availability of deciduous foliage (Peek et al. 1976; Belovsky 1981), but the use of remotely sensed land cover data clearly prohibits an explicit evaluation of habitat quality.

Although GPS collars recorded temperature (°C), these data are biased by numerous factors such as position on the animal, pelage, activity level, heat loss via radiation, etc. (Van Beest et al. 2012). Consequently, we associated used and available locations with ambient temperature data as recorded by the NOAA or Environment Canada weather station closest to a given fix in space and time. Ambient temperatures used in this fashion are highly correlated with collar data and better represent the conditions experienced by an individual that may influence habitat selection (Street et al. 2015). Used locations were on average 17.76 km (Minnesota range

0.41–72.46; Ontario range 25.57–127.90) from the nearest weather station and 0.13 h (Minnesota range 0–2.86; Ontario range 0.01–0.98) from the closest recorded weather observation in time.

Analysis

We estimated models of habitat selection using step-selection functions (SSFs; Thurfjell et al. 2014). SSFs use a case–control design wherein the occurrence of a case (i.e., a used fix/step) is conditional to the availability of controls (i.e., available locations where a fix was not recorded) selected based on where a fix could have occurred given the observed distributions of step lengths and turn angles. Used and available locations associated with each step form strata, and the SSF is estimated using conditional logistic regression. The SSF methodology thus constrains the availability of environmental covariates in time and space to the movement characteristics of an individual and is commonly used to study animal movement in heterogeneous landscapes (Forester et al. 2009; Thurfjell et al. 2014).

Selecting available points using the empirical (i.e., observed) distributions of step lengths and turn angles requires three sequential fixes at the defined fix rate, and frequent gaps in a dataset will reduce the frequency of these instances. We selected available points using parametric distributions of step length between two consecutive fixes and bearing relative to true north (Forester et al. 2009). We estimated the rate of exponential decay (λ) of the observed step lengths of each individual and sampled step lengths from an exponential distribution with the estimated λ. We sampled bearings from a uniform distribution from 0 to 2π. Sampling in this fashion naturally oversamples around the used point due to increasing area of a circular sector with increasing distance from the used point (i.e., hyperdispersion of points increases with distance from the centroid). We transformed sampled step length l as the square root of the ratio between the observed sampled step length and the maximum sampled step length for an individual times the squared maximum sampled step length, $l = \sqrt{(l_{observed}/l_{\max}) \times l_{\max}^2}$, to correct for oversampling. We paired 10 available points to each used fix (i.e., 11 points per stratum). We modeled the probability of selecting each point within a stratum as a

function of proportional coverage of each of 5 land cover types (deciduous, coniferous, mixedwood, water, and treed wetlands) within a circular 50 m radius buffer. Other land cover types (e.g., grassland, developed) typically comprised 12 % of buffers but were not explicitly included in the regression (i.e., they serve as a reference category for the other cover types). We also included the step length (i.e., distance between consecutive fixes) to accommodate any bias introduced by using parametric distributions of step length (Forester et al. 2009). We included interactions between these main effects and (1) temperature (°C), centered on previously reported summer thresholds for heat stress in moose (i.e., 14 °C; Renecker and Hudson 1986) such that positive values represented temperatures likely exceeding moose thermal neutral zones, and (2) the time of day a fix was recorded, transformed using four circular time harmonics, $\sin(2\pi t/24)$, $\sin(4\pi t/24)$, $\cos(2\pi t/24)$, and $\cos(4\pi t/24)$, to assess changes in habitat selection across the diurnal cycle (Forester et al. 2009). Four time harmonics were included to accommodate individual variation in activity patterns—that is, an individual may be more active during peak light/dark periods than crepuscular periods, or may exhibit more than one or two peak periods of activity. Because both temperature and time of day were constant within strata, they were considered only as interaction terms. In total, we estimated six main effects and five interactions per main effect (i.e., 36 coefficients). This model structure permits evaluation of whatever temperature effect on habitat selection remains after accommodating the time of day effect on selection patterns.

We estimated these models separately for each individual animal in the Minnesota and Ontario datasets. Averaging the individual regression coefficients within a given dataset produced the population-level coefficients and confidence intervals reported in Table A2 in supplementary materials. Such averaging accommodates within-animal variation in habitat selection and approximates a mixed effects modeling approach (Fieberg et al. 2010) but effectively reduces sample size for any estimated model. If sample sizes are small or model predictors are highly correlated, the variance of coefficients estimated by standard statistical models is often quite large. Modern telemetry data are typically not sample size limited, but correlated variables compounded by the dynamic nature of animal relocation typically produce low explanatory

power of fitted models and unreliable out-of-sample prediction (Beyer et al. 2010). We thus fitted our SSFs using conditional logistic regression with lasso (least absolute shrinkage and selection operator; Reid and Tibshirani 2014). The lasso maximizes the likelihood of the data subject to a constraint, determined by an additional tuning parameter (s), that limits the summed absolute value of model coefficients (Tibshirani 1996). When s is very large (i.e., approaching infinity), the lasso produces coefficients identical to ordinary regression; at values of s approaching 0, the lasso reduces the coefficients of uninformative predictors. This framework offers an appealing alternative to model averaging when the number of predictors is large relative to effective sample size (Hooten and Hobbs 2015). We selected our model coefficients as the estimates minimizing the cross validation statistic (Reid and Tibshirani 2014).

We binned used and available locations by the hour in which a fix was recorded and the ambient temperature as reported by the nearest weather station. We calculated the average proportional cover by land cover types in used and available locations across bins to visualize how used and available cover change across both diurnal and temperature gradients in both study sites and fit lowess regressions to both used and available bins to generate smoothed proportional coverage curves (Figs. 2, 3). We also calculated model-based estimates of selection strength (i.e., log relative risk) for each land cover class across time of day and temperature, holding either temperature constant at the upper thermoneutral limit of moose (i.e., $\Delta T = 0$ °C; Renecker and Hudson 1986) for time of day plots, or time of day constant at noon (1200 h) for temperature plots (Figs. 4, 5). We ranked the predicted selection strength at a given time or temperature to evaluate changes in relative selection strength across the diurnal cycle and temperature gradient, including selection for land cover types not included in the models (i.e., predicted selection = 0).

Lastly, we conducted a separate cross validation procedure for our step selection models based on a comparison of observed use of land cover covariates versus expected values predicted by the models. Specifically, we:

1. Fit step selection models to data from either Ontario or Minnesota. The data used to fit the model correspond to "training data". The data

Minnesota
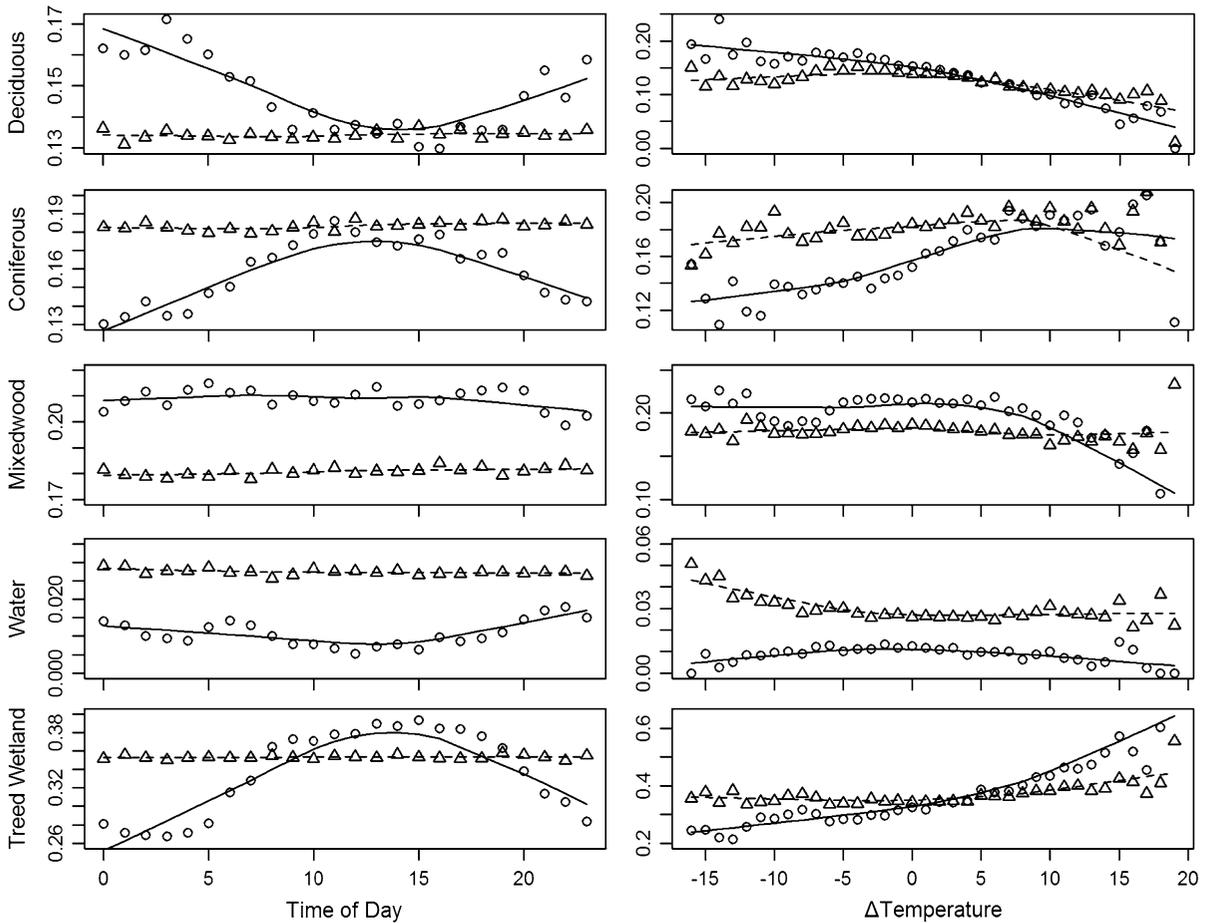
Fig. 2 Average used (*solid lines* and *circles*) and available (*dashed lines* and *triangles*) proportional representation within 50 m buffers of land cover classifications included in the analysis during summer (June 1–September 30) in Minnesota. Patterns of use and availability change across both time of day (*left column*) and temperature (°C) scaled to moose (*A. alces*) upper thermal optima (*right column*)

that were not used in this step were treated as "test data".

2. Using the fitted model from step [1], we estimated the probability of choosing each location (both used and available) in the test data:

$$\hat{p}_{i,k} = \frac{\exp(x_{i,k}\beta)}{\sum_{j=1}^{11} \exp(x_{j,k}\beta)},$$
$$(i = 1, 2, \ldots, 11, \quad k = 1, 2, \ldots, n_{strata}),$$

where i indexes a location (used or available) within stratum k, $x_{j,k}$ is a vector of covariate data for the j-th observation in stratum k, β is a vector of model coefficients, and n_{strata} gives the number

of strata (equivalent to the number of used locations).

Given the estimated probabilities $\hat{p}_{i,k}$, we calculated the expected proportional cover of the p-th land cover class in stratum k, $E[Z_k^p]$, as:

$$E[Z_K^p] = \sum_{i=1}^{11} \hat{p}_{i,k} Z_{i,k}^p,$$

where $Z_{i,k}^p$ is a scalar, representing the proportional cover of the p-th land-cover class associated with the i-th observation within stratum k.

We then plotted the average observed and expected values for each land-cover class across both

temperature and time of day to validate model fit across study sites (Figs. A1, A2, Supplemental Materials). Models and aggregated land cover were considered informative if observed patterns of use coincided with expectation.

All work was conducted using the base packages of Program R (R Core Team 2015) and the clogitL1 package (Reid and Tibshirani 2014).

Results

Cross validation of SSFs demonstrated high predictive accuracy of our models across sites (Figs. A1, A2 IN supplementary materials), indicating that the aggre-gated land cover classification was informative and that our models capture variation in habitat selection across sites. We detected changes in proportional cover of land cover types associated with used locations in Minnesota across both time of day and temperature. On average, proportional cover of decid-uous habitat decreased, and coniferous and treed wetland increased, in used locations at mid-day (Fig. 2). At all times of day deciduous cover was higher and coniferous cover lower in used locations compared to available locations. By contrast, treed wetland cover was greater at used relative to available locations only at mid-day, consistent with a switch toward positive selection for treed wetlands from approximately 0900–1800 h. Proportional coverage of
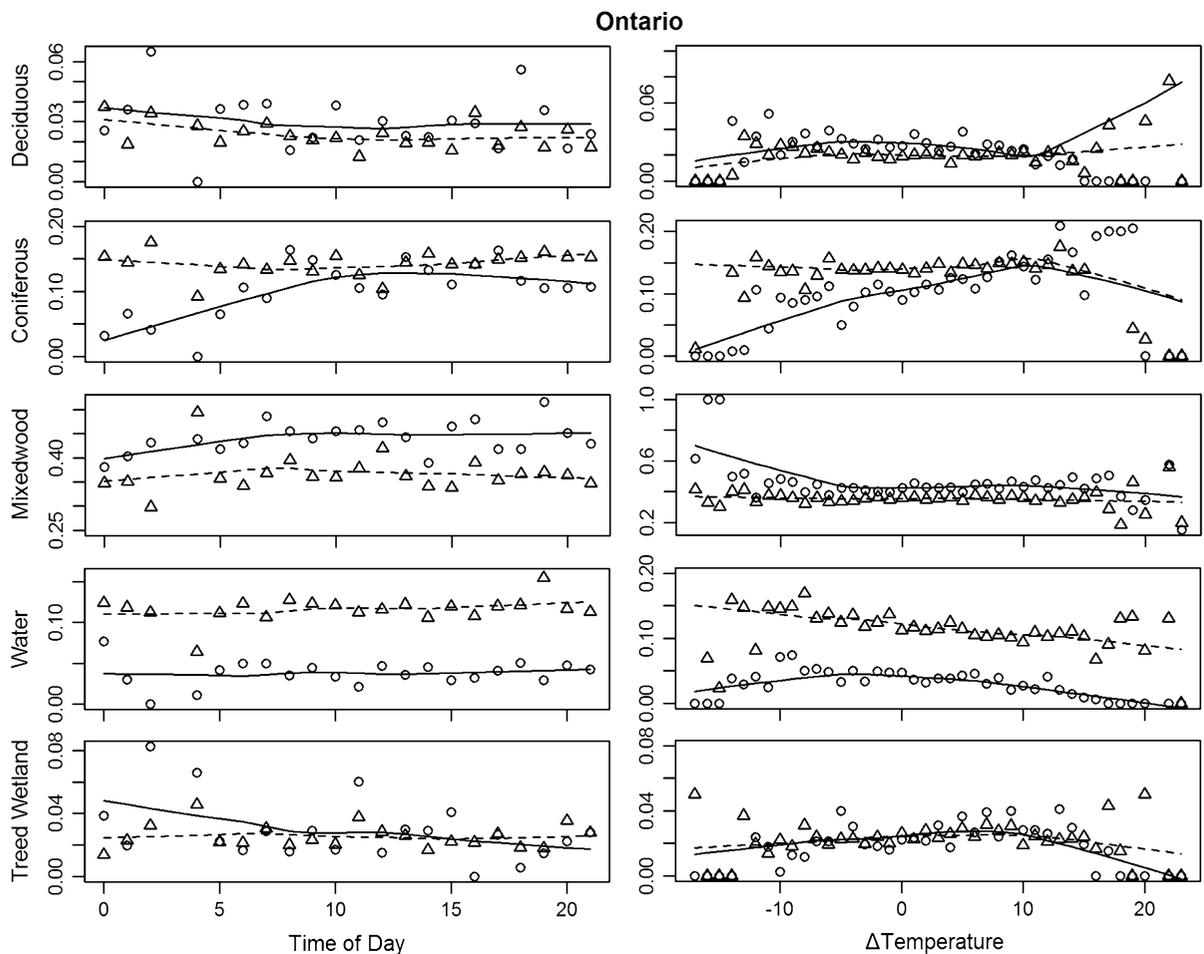
Fig. 3 Average used (*solid lines* and *circles*) and available (*dashed lines* and *triangles*) proportional representation within 50 m buffers of land cover classifications included in the analysis during summer (June 1–September 30) in Ontario.

Patterns of use and availability change across both time of day (*left column*) and temperature (°C) scaled to moose (*A. alces*) upper thermal optima (*right column*)
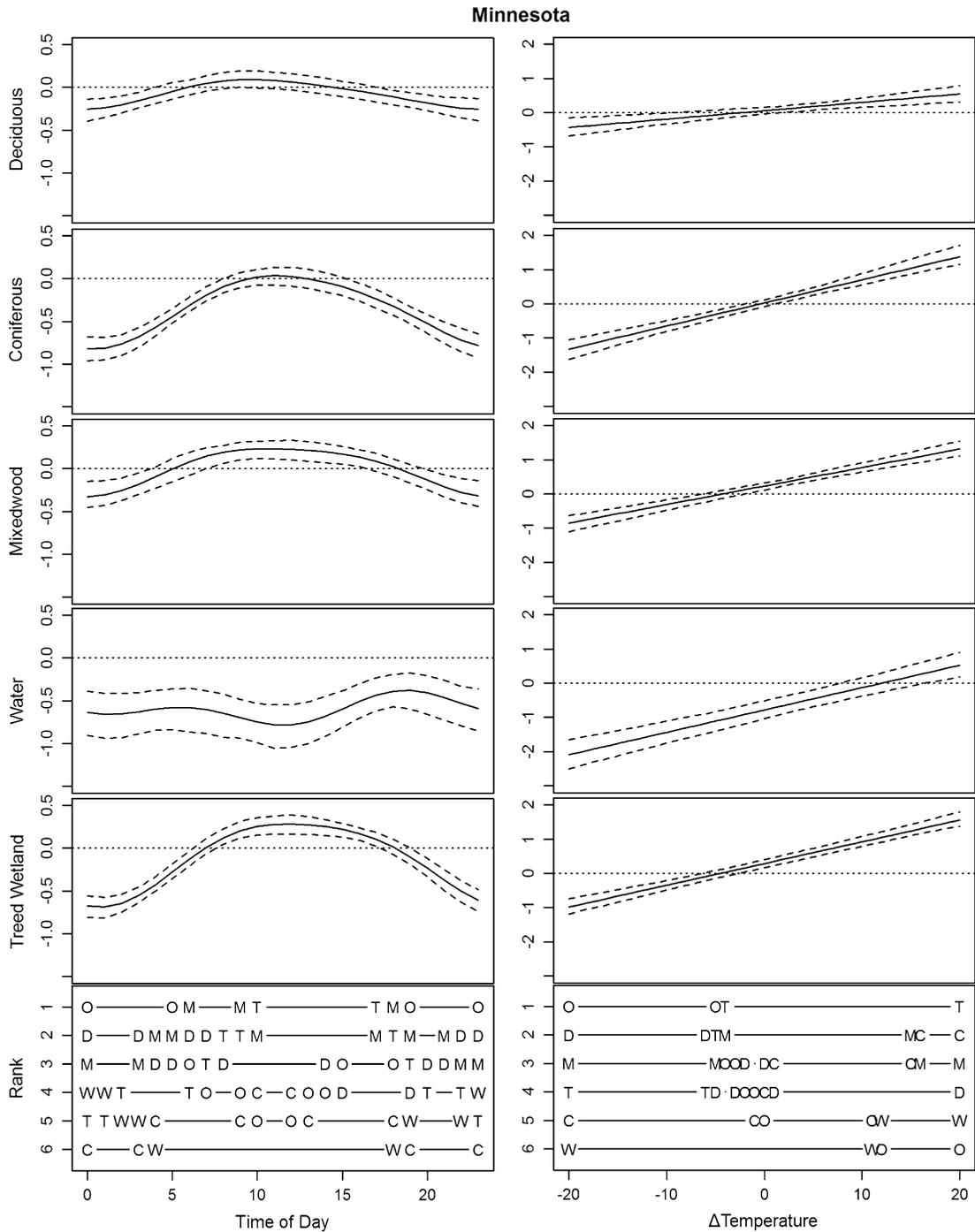
Minnesota

Fig. 4 Predicted selection strength (log relative risk, *solid lines*) by moose (*A. alces*) with 95 % Confidence Intervals (*dashed lines*) for 100 % cover by land cover classifications during summer (June 1–September 30) in Minnesota across both time of day (*left column*) and temperature (°C) scaled to moose upper thermal optima (*right column*). Temperature is held constant at the moose upper thermal optimum (i.e., ΔTemperature = 0 °C) in time of day plots, and time is held constant at noon in ΔTemperature plots. *Bottom panels* indicate relative rank of selection strength for each land cover class (*D* deciduous; *C* coniferous; *M* mixedwood; *W* water; *T* treed wetland; *O* other) across the diurnal cycle and temperature gradient

deciduous and mixedwood associated with used locations declined with increasing temperature, and coniferous and treed wetlands increased with temperature. All four coverage types experienced a switch in directionality of use:availability ratios at temperatures exceeding approximately 10 °C above moose thermal optima (i.e., ~24 °C; Fig. 2).

Conversely, proportional cover associated with used and available locations in Ontario was less dynamic. We detected a marginal decline in treed wetland use and an increase in coniferous cover across time of day, but proportional cover at both used and available locations was otherwise consistent across the diurnal cycle (Fig. 3). Use of conifer increased, and use of mixedwood decreased, at warmer temperatures, but use of other land cover types exhibited little to no change in use across temperature. Thus between study sites we observed similar patterns of use of conifer with time of day, and conifer and mixedwood with temperature, but different patterns of use of deciduous and treed wetland habitats.

Predicted selection strength (i.e., log relative risk of selection) for the five land cover classifications was also inconsistent between sites. In Minnesota selection for deciduous, coniferous, mixedwood, and treed wetland stands notably increased at mid-day (Fig. 4). Despite increased selection strength for deciduous at mid-day, ranked relative selection strength was highest for mixedwood and treed wetland at mid-day (Fig. 4, bottom left), with ranked selection for deciduous declining at mid-day, consistent with our empirical findings (Fig. 2). Predicted selection strength for all cover types, relative to the "other" category (what was left out of the model, i.e., selection strength = 0), consistently increased across the temperature gradient (Fig. 4). Yet, ranked selection among all land cover types indicated declining selection for deciduous at high temperatures, and increased selection for treed wetlands, conifer, and mixedwood (Fig. 4, bottom right). Selection for water was consistently low across the temperature gradient.

In Ontario, predicted selection strength for water, deciduous, mixedwood, and treed wetland habitat was relatively invariant across time of day (Fig. 5). Selection for conifer increased at mid-day, consistent with predicted selection in Minnesota. Ranked selection strength indicated selection primarily favored mixedwood across the diurnal cycle, and selection for deciduous habitat peaked at night and early morning

(Fig. 5, bottom left). Ranked selection for conifer peaked at mid-day, but treed wetland, conifer, and water were generally avoided. Selection strength, relative to "other", increased only for conifer and mixedwood habitat as temperature increased (Fig. 5). This pattern was also observed in ranked selection, with selection for conifer and mixedwood increasing across the temperature gradient (Fig. 5, bottom right).

Discussion

We found that habitat use by moose varied between two study sites differing primarily in latitude and landscape composition. In Ontario, proportional coverage of foraging stands (i.e., deciduous, mixedwood) was higher at used than available locations; nonforaging stand coverage was used less than its availability. In contrast, moose in Minnesota exhibited marked changes in patterns of habitat use across both time of day and temperature, most notably a decline in the use of deciduous and an increase in coniferous and treed wetland at mid-day. Use of these habitats may result in reduced foraging efficiency if quantity/quality of forage is lower than in deciduous stands (Peek et al. 1976; Belovsky 1981) and points to the importance of abiotic environmental conditions driving habitat selection patterns of moose in Minnesota. However, ranked selection was consistent between the two sites, with selection for conifer peaking around mid-day and at the highest temperatures. These results suggest that moose primarily select habitat during the summer based on foraging considerations (i.e., energy acquisition) except at the highest temperatures, consistent with previous studies (Peek et al. 1976; Belovsky 1981; Van Beest et al. 2012; Street et al. 2015).

We detected an increase in selection strength for all land cover types, relative to an "other" category (i.e., what was not in the model), as a function of temperature in Minnesota (Fig. 4). However, ranked selection declined for deciduous habitat and increased for coniferous, mixedwood, and treed wetlands with increasing temperature. This indicates a change in preference for habitat types across the temperature gradient and should produce a detectible shift in space use and distribution (Beyer et al. 2010), particularly at high temperatures. Indeed, at high temperatures moose in Minnesota used deciduous habitat
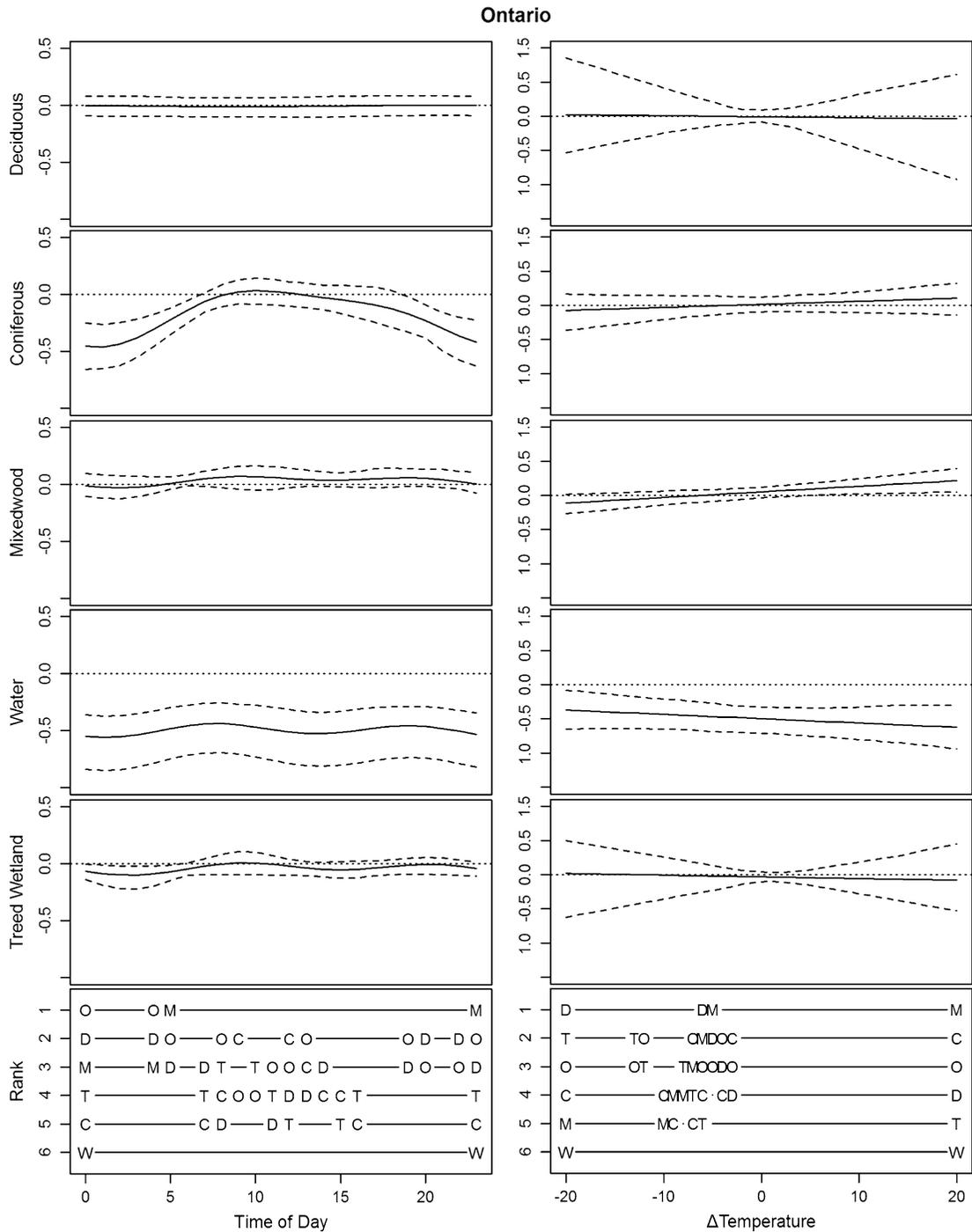
Fig. 5 Predicted selection strength (log relative risk, *solid lines*) by moose (*A. alces*) with 95 % confidence intervals (*dashed lines*) for 100 % cover by land cover classifications during summer (June 1–September 30) in Ontario across both time of day (*left column*) and temperature (°C) scaled to moose upper thermal optima (*right column*). Temperature is held constant at the moose upper thermal optimum (i.e., ΔTemperature = 0 °C) in time of day plots, and time is held constant at noon in ΔTemperature plots. *Bottom panels* indicate relative rank of selection strength for each land cover class (*D* deciduous; *C* coniferous; *M* mixedwood; *W* water; *T* treed wetland; *O* other) across the diurnal cycle and temperature gradient

substantially less than at lower temperatures, favoring instead conifer and treed wetlands (Fig. 2). Thus at temperatures exceeding moose thermal optima (Renecker and Hudson 1986), moose in Minnesota selected more strongly for those habitats providing thermal cover—that is, conifer and treed wetlands (Peek et al. 1976; Belovsky 1981; Van Beest et al. 2012; Street et al. 2015). It is worth noting that during the night and at low temperatures, the "other" category was actually most favored based on ranked selection (Figs. 4, 5), suggesting that during these periods moose may utilize habitat types not represented in our models (e.g., agricultural land, shrublands). These habitat types may provide additional foraging or bedding opportunities that we do not consider here, but universally these habitat types do not provide cover of any sort, which may be why they are favored at night when moose will be harder to detect and during cooler periods when temperatures are not limiting. Further research on selection and use of non-forested or "sub-prime" foraging habitats would further enlighten this observation, but we lack sufficient data to address this here.

If moose exposed to elevated ambient temperatures alter habitat selection toward thermal cover, why did moose in Ontario not substantially alter their habitat use (not selection) at high temperatures? Neither study site was substantially warmer on average than the other during data collection (15.8 and 14.6 °C in Ontario and Minnesota, respectively), but the two sites differ markedly in proportional coverage by land cover types. The Minnesota site contains a larger proportion of deciduous cover than Ontario, which in turn has twice as much dense mixedwood and very little deciduous cover (Figs. 2, 3). Reduced availability of deciduous habitat in Ontario may be attributable to differences in OLC and NLCD deciduous forest classification (see "Methods" section; Anonymous 2004, Jin et al. 2013), but the increased availability of dense mixedwood forest is telling. Mixedwood stands simultaneously provide foraging opportunities and thermal cover (Belovsky 1981; Van Beest et al. 2012), thus moose in high mixedwood landscapes such as Ontario are commonly in sufficient thermal cover regardless of time or location. These findings suggest that moose in Ontario are only forced to modify their habitat preferences under the most thermally stressful conditions (e.g., high temperatures at mid-day; Street et al. 2015), which is corroborated

by evidence that moose in southern Ontario typically do not exhibit the population declines expected at the southern extent of the species range (Murray et al. 2012). Conversely, the Minnesota site contains a greater abundance of deciduous vegetation, which provides ample vegetation but a less dense canopy, thus moose in this site have the opportunity to consistently select forage-rich environments that provide less thermal cover. Ironically, it is by virtue of living in a landscape of greater forage abundance that moose in Minnesota may experience foraging limitations under thermally stressful conditions, whereas moose in Ontario appear to be freed from this constraint.

The primary implication of these findings, then, is that foraging animals may experience a trade-off between acquiring resources (i.e., energy intake) and maintaining homeostatic conditions (i.e., energy expenditure) across environmental gradients (Speakman and Król 2010). Reducing net energy intake by reducing foraging opportunity has negative effects on animal fitness (Ritchie 1990; McLoughlin et al. 2006, 2007; Hodson et al. 2010), and selection for thermal cover in lieu of foraging habitat could result in reduced body mass and lifetime reproductive success (Van Beest et al. 2012; Monteith et al. 2015). However, recent research has demonstrated that reducing energetic expenditure by increasing efficiency of heat dissipation is an important component of endotherm fitness and may contribute more to net fitness in some circumstances than energy supply (Speakman and Król 2010). This seems particularly plausible if animals change their habitat preferences in response to landscape composition and abiotic conditions (i.e., habitat functional response; Mysterud and Ims 1998). Under conditions of thermal stress, animals exhibiting a functional response for habitat selection might utilize thermal cover more frequently while simultaneously increasing selection strength for high quality foraging habitat to compensate. We detected a significant increase in selection for deciduous habitat both at high temperatures and at mid-day by moose in Minnesota (Fig. 4) concurrent with declining average use of deciduous habitat (Fig. 2), suggesting that the habitat functional response occurs as moose attempt to mitigate the potentially adverse effect of reduced foraging opportunity caused by increased use of thermal cover.

How successful this strategy may be is likely variable across landscapes. For example, Lenarz et al.

(2010) found that moose in Minnesota exhibit net negative population growth and suggested that this decline is attributable to increasing temperatures during winter. Monteith et al. (2015) found similar results for moose in the U.S. Rocky Mountains due to both increasing summer temperature and changes in flowering phenology. In contrast, moose populations in southern Ontario are on average stable or increasing (Murray et al. 2012), despite experiencing temperatures comparable to or greater than those described here or in other studies (Lenarz et al. 2010; Monteith et al. 2015). These studies state that changes in moose demographic rates and survivorship may be explained by changes in forage availability or increasing heat stress, but they agree that the precise mechanism driving population level responses to climate change requires investigation. We suggest that landscape configuration may be the mechanism explaining these discrepancies across regions. The functional response may permit reduction or negation of the fitness costs associated with reduced foraging habitat availability, allowing animals to modify behavior to both maximize energy intake and minimize energy expenditure given a certain environmental context. Although we focus on one example of how this functional response may arise—that is, through temperature-mediated changes in habitat selection—the habitat functional response could mitigate fitness loss due to any changes in space use. Our understanding of endotherm fitness would benefit from an explicit assessment of the contribution of discrete habitat types to fitness across changes in both landscape composition and abiotic conditions. Research synthesizing fitness and space use would permit investigation of explicit hypotheses of drivers of population decline across bioclimatic and latitudinal gradients and would be invaluable to the ecology and management of this and other species of concern.

Although the SSF methodology is now widely used in habitat selection and movement studies (Thurfjell et al. 2014), our use of the lasso is relatively uncommon in the ecological literature (Dahlgren 2010, but see Hooten and Hobbs 2015). The lasso places a cap on the sum of the absolute value of the regression coefficients and is a form of regression shrinkage (Tibshirani 1996; Dahlgren 2010; Reid and Tibshirani 2014). Shrinkage reduces the magnitude of regression coefficients associated with statistically unimportant variables and improves prediction

accuracy, a common shortcoming of habitat selection models (Fielding and Bell 1997; Beyer et al. 2010). Further, the lasso can be used for variable selection in cases where the number of parameters is large relative to effective sample size since uninformative predictors can be (and often are) reduced to 0 (Tibshirani 1996; Dahlgren 2010; Giudice et al. 2012). Currently, model selection in ecology is most often achieved using information theoretic criteria (Burnham and Anderson 2002; Stephens et al. 2005; Giudice et al. 2012). Although extremely flexible and useful when properly employed, some authors (e.g., Stephens et al. 2005, Giudice et al. 2012) have noted that over-reliance on information theoretic methods may lead to underconsideration of alternative hypotheses and ecological phenomena, instead depending on a suite of competing models to suggest ecological significance. Shrinkage estimators provide an alternative to information theoretic methods while requiring deeper consideration of the hypotheses and ecology under investigation. Given their utility and the availability of packages in most statistical software, these methods are a valuable tool for ecologists and managers and should be considered alongside other alternatives such as information theoretic methods (Babyak 2004; Giudice et al. 2012; Fieberg and Johnson 2015; Hooten and Hobbs 2015).

Investigating animal space use across spatially distinct regions allows researchers to investigate how environmental and geographic gradients influence habitat selection, space use, and movement patterns (Matthiopoulos et al. 2011). Here we demonstrate a strong effect of temperature, diurnal cycles, and landscape composition on patterns of habitat selection and space use, and identify a functional response in selection for foraging habitat driven largely by increased use of thermal cover. We suggest that the habitat functional response may serve as a mechanism mitigating fitness loss due to changes in space use which reinforces the importance of accommodating broad scale bioclimatic variation in studies of habitat selection. Habitat selection is context dependent, and similar models of habitat selection may produce markedly different realized patterns of space use driven by differences in landscape composition. Further studies examining how environmental factors (e.g., predator pressure, disturbance, weather) influence variation in fitness due to individual space use will provide insight into the ecological processes

driving population dynamics and distributions across spatiotemporal scales.

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